ICLARM Technical Reports 49

Cymatium muricinum and Other Ranellid Gastropods: Major Predators of Cultured Tridacnid Clams

Hugh Govan

ICLARM
International Center for Living
Aquatic Resources Management

Cymatium muricinum and Other Ranellid Gastropods: Major Predators of Cultured Tridacnid Clams

Hugh Govan

1995

INTERNATIONAL CENTER FOR LIVING AQUATIC RESOURCES MANAGEMENT
MANILA, PHILIPPINES

Cymatium muricinum and Other Ranellid Gastropods: Major Predators of Cultured Tridacnid Clams

H. GOVAN

1995

Printed in Manila, Philippines

Published by the International Center for Living Aquatic Resources Management,
MCPO Box 2631, 0718 Makati, Metro Manila, Philippines.

Govan, H. 1995. *Cymatium muricinum* and other ranellid gastropods:
major predators of cultured tridacnid clams. ICLARM Tech. Rep. 49, 136 p.

Cover: Cymatium muricinum in adult and larval *(inset)* stages.
Cover design by Christopher M. Bunao

ISSN 0115-5547
ISBN 971-8709-70-3

ICLARM Contribution No. 1115

Dedicated to my parents
and to the people of Solomon Islands

An adult giant clam, Tridacna gigas. *This specimen is kept as broodstock at the Coastal Aquaculture Centre in Guadalcanal, Solomon Islands.*

Contents

List of Tables

List of Figures

List of Plates

Foreword

Behind the bland title of this publication lies a story of considerable endeavor. Hugh Govan's association with ICLARM began in 1986 when, as an employee of Voluntary Services Overseas, he was assigned to work alongside Graham Usher, who was on assignment from the United Kingdom Overseas Development Agency, in the development of ICLARM's new Coastal Aquaculture Centre, on Guadalcanal in the Solomon Islands. I had the privilege of leading this small group.

As an Affiliate Scientific Assistant, one of Hugh Govan's initial tasks was to roam the Solomon Islands in search of giant clam broodstock, and to ship large numbers of these vast creatures, alive, back to Guadalcanal. In doing this, he became something of an expert on the coral reef and lagoon systems of the Solomon Islands and on village culture. This led in turn to his becoming responsible for developing our village-based giant clam farming trials, which led in turn to his interest in predation on giant clams and in ways for foiling the wide variety of very smart predators which imperilled our stocks. In turn again, this led to the Australian Centre for International Agricultural Research funding a two-year study of this topic with Hugh Govan as Project Leader. This book is the cumulative outcome of these endeavors which have served, in no small way, in making village-based giant clam cultivation an economic reality in the Solomon Islands and elsewhere.

Dr. J.L. Munro
Director
Coastal and Coral Reef Resource
Systems Program, ICLARM

Abstract

The recent development of technology for the ocean culture of juvenile giant clams (family Tridacnidae) in the South Pacific has brought attention to the predatory activities of a hitherto little studied mesogastropod genus, *Cymatium* (family Ranellidae). The results of research into relevant aspects of the biology of four species of *Cymatium* are presented together with estimates of their impact on ocean-nursery culture of *Tridacna gigas* and methods of predator control.

Cymatium muricinum, and to a lesser extent *C. aquatile, C. nicobaricum* and *C. pileare*, have been found preying on cultivated tridacnids at most ocean-nursery sites in the South Pacific. It is estimated that ranellid predation can represent a major cause of mortality during the ocean culture of *T. gigas*, based on field and laboratory data from Solomon Islands. In certain cases the activities of ranellid predators may negate the economic viability of tridacnid culture if left uncontrolled.

C. muricinum, C. aquatile and *C. pileare* were only observed to attack bivalves while *C. nicobaricum*, although attacking bivalves on occasion, actively selected gastropods. Ranellids attacked bivalves using their extensible probosci to inject prey with toxic or immobilizing salivary secretions. The snails could also feed on the tissues of live prey if these were too large to be immobilized.

The growth of these species of *Cymatium* was found to be episodic and in the presence of an abundant food supply was exceptionally fast in the period directly following settlement. During this period, juvenile *Cymatium* spp. exhibited very high relative consumption rates which decreased with increasing snail size to levels, in adult snails, similar to those reported for other predatory gastropods.

Reproduction of the four species of ranellid was studied and brooding of the cup-shaped egg masses by the female was observed. The planktotrophic veligers were thought to remain in the plankton for several months after which they may settle directly into tridacnid culture cages.

Wide fluctuations in recruitment were observed, most probably caused by factors affecting the larvae during their planktonic dispersal. Evidence is presented that hydrographic processes, sometimes forced by environmental factors such as wind direction and strength, may account for part of the observed variation in recruitment.

A range of predator control options is available but frequent visual inspections of culture cages and manual removal of predatory ranellids remain vital. Other options include the exclusion of adult snails using off-bottom culture techniques or reduced mesh sizes and avoiding the placement of cages in areas, or during seasons, of expected high ranellid larval settlement. Potential exists for the development of biological control using specialist predators of gastropods such as *Conus textile* or *Pleuroploca filamentosa*.

CHAPTER 1

Introduction: Giant Clam Mariculture and Ranellid Gastropods

1.1 Giant Clams (Bivalvia: Tridacnidae)

Giant clams of the family Tridacnidae are some of the most striking inhabitants of coral reefs, not only because of the large size attained by some species but also because of the beauty of their frequently richly colored mantles. It is hardly surprising that these bivalves have attracted a constant trickle of research for more than a century (c.f., bibliography by Munro and Nash 1985). However, research has intensified in the last decade owing to interest in establishing a mariculture industry using tridacnids.

The distribution of living species of tridacnid clams is confined to the Indo-Pacific region and is largely contiguous with that of reef-building corals (Munro 1989). These clams are normally found in close association with coral reefs in shallow waters rarely exceeding 30-m depth. Since the comprehensive revision of tridacnid taxonomy and distribution by Rosewater (1965), the geographic range of the larger species of Tridacnidae has been considerably reduced, either by exploitation, deterioration of coral reef environments or other ecological factors (Lucas 1988a; Munro 1989).

Nine species of living tridacnid clams have been described in two genera: *Tridacna* and *Hippopus* (Rosewater 1965, 1982; Lucas et al. 1990; Sirenko and Scarlato 1991). *T. gigas** is the largest species, reaching 137 cm in shell length (SL) and a weight of around 500 kg (Crawford et al. 1987). *T. gigas*, together with the other large species, *T. derasa* and *H. hippopus*, have received most attention from prospective mariculturists (Plate I). All but one of the other species have also been cultured including *T. squamosa, T. maxima, T. crocea* and the recently described species *T. tevoroa* (Lucas et al. 1990) and *H. porcellanus* (c.f., Fitt 1993a). Sirenko and Scarlato (1991) described *T. rosewateri* from shells recovered in the Saya de Malha Bank in the Indian Ocean. This species has not been cultured and its status as a new species has yet to be widely accepted (c.f., Braley 1992).

Anatomy and Biology of the Tridacnidae

Tridacnid clams are members of the superfamily Cardiacea and are thus related to the burrowing cockles of the family Cardiidae (Yonge 1980). However, the Tridacnidae possess a

* Taxonomic authorities for all species mentioned in the text are provided in Appendix I.

Plate I. Commonly cultivated species of tridacnid clam. From left to right these are *Hippopus hippopus, Tridacna gigas* and *T. derasa.* (Photo by H. Govan).

number of anatomical and biological features which clearly distinguish them from other members of the superfamily and indeed other bivalves in general. Principal among these features is their symbiotic association with dinoflagellate algae (*Symbiodinium microadriaticum*) known as zooxanthellae which provide the clams with nutrients (Yonge 1975).

The zooxanthellae are located in a system of tubes originating in the stomach but which proliferate in the outer levels of the siphonal mantle (Norton et al. 1993). The morphology of giant clams is modified such that when the umbo and byssal orifice of the shell are resting on the substrate the highly developed siphonal mantle extends along the entire upper surface of the gaping valves (Yonge 1975, 1980) and is thus exposed to sunlight. Sugars and amino acids are transferred from the algae to the host and are sufficient to meet the daily energy and growth requirements of all but the smallest clams (Fitt 1993b).

The life cycle of tridacnids is not dissimilar to that of other bivalves. Giant clams are protandrous hermaphrodites and for most of their adult lives are capable of producing eggs and sperm (Wada 1954). Spawning may extend throughout the year in equatorial regions but is restricted to the summer months at higher latitudes (Crawford et al. 1986). Tridacnids are very fecund; an adult *T. gigas* may produce 500 million eggs in one spawning (Crawford et al. 1987), and the eggs have an associated chemical which triggers spawning in other individuals (Munro et al. 1982). This process results in chain spawning reactions but, as pointed out by Munro and Heslinga (1983), renders the species liable to nonfertilization of eggs in depleted populations.

Fertilized eggs hatch into trochophores which develop into veligers and then pediveligers before settling on the substrate and metamorphosing into juvenile clams, the entire process occurring over 6-10 days (Heslinga et al. 1984; Crawford et al. 1986). The growth rate of giant clam juveniles is slow in the initial months but thereafter growth is relatively rapid, particularly in the larger species in which rates of up to 8 mm· month^{-1} SL may be attained (Munro and Heslinga 1983; Calumpong 1992).

1.2 Mariculture of Giant Clams

The History of Giant Clam Mariculture

Given the high prices commanded by tridacnid products in Southeast Asia, particularly for the adductor muscle (up to US$30/kg, Dawson 1986), and the rapid decline in the stocks of the larger species, it is hardly surprising that the mariculture of tridacnids became a serious consideration. Munro and Heslinga (1983) concluded that the large-scale mariculture of tridacnids was feasible and could make a major contribution to the economies of the island states. Giant clams were heralded as "the only phototrophic potential farm animals known to mankind".

Early work on the induction of spawning (Wada 1954) and larval biology (La Barbera 1975; Jameson 1976) of tridacnids set the stage for the first concerted attempts to raise larvae of these species in Palau (Beckvar 1981; Fitt and Trench 1981) and Papua New Guinea (Gwyther and Munro 1981). By the early 1980s, mass culture of *T. derasa* was a reality at the Micronesian Mariculture Demonstration Centre (MMDC) in Palau (Heslinga et al. 1984). In 1984, funding was received at James Cook University, Queensland, to attempt mass culture of *T. gigas* at the Orpheus Island Research Station (OIRS) and to coordinate a multinational Giant Clam Mariculture Project (GCMP) in collaboration with the International Center for Living Aquatic Resources Management (ICLARM).

The major component of ICLARM's contribution to the GCMP was the development of a Coastal Aquaculture Centre (CAC) on Guadalcanal, in collaboration with the Solomon Islands government. Construction of the CAC commenced in late 1986, focusing initially on a pilot-scale giant clam hatchery. The present author joined the project in early 1987.

Solomon Islands presents a number of features which make it ideal as a site for the CAC. Independent since 1978, Solomon Islands comprises some 800 islands extending over 1,400 km in the western equatorial Pacific Ocean (see Figs. 1.1 and 1.2) between latitudes 5° and 13°S and longitudes 155° and 168°E. Solomon Islands is one of the few countries in the region with relatively good stocks of tridacnid clams. There is a great diversity of coastal marine habitats (UNEP/IUCN 1988) and a wide range of sociocultural contexts in which clam farming systems could be tested (Govan et al. 1988; Govan 1993; Hviding 1993). Furthermore, the establishment of the CAC was in line with the priorities of the Solomon Island National Development Plan with regard to aquaculture (Govan et al. 1988).

Giant Clam Culture Technology

Research at the institutions collaborating on the giant clam mariculture project has resulted in the technology to successfully culture all tridacnid species. Slight variations exist at different institutions; the techniques used at MMDC are described by Heslinga et al. (1990), those used at OIRS by Braley et al. (1988) and Lucas et al. (1988) and those used at the CAC by Usher and Munro (1988), Usher (1990) and Munro et al. (1993). Comprehensive overviews of current giant clam mariculture technology are provided by Braley (1992, 1993), and Calumpong (1992).

Four phases may be distinguished in the mariculture of tridacnid clams using the terminology of Crawford et al. (1988): hatchery phase, nursery phase, ocean-nursery phase and grow-out. These phases as pertaining to the CAC are briefly described below.

Hatchery phase. In this phase broodstock clams are induced to spawn and the fertilized eggs are held in indoor tanks. The larval tridacnids are fed with algal or micro-encapsulated

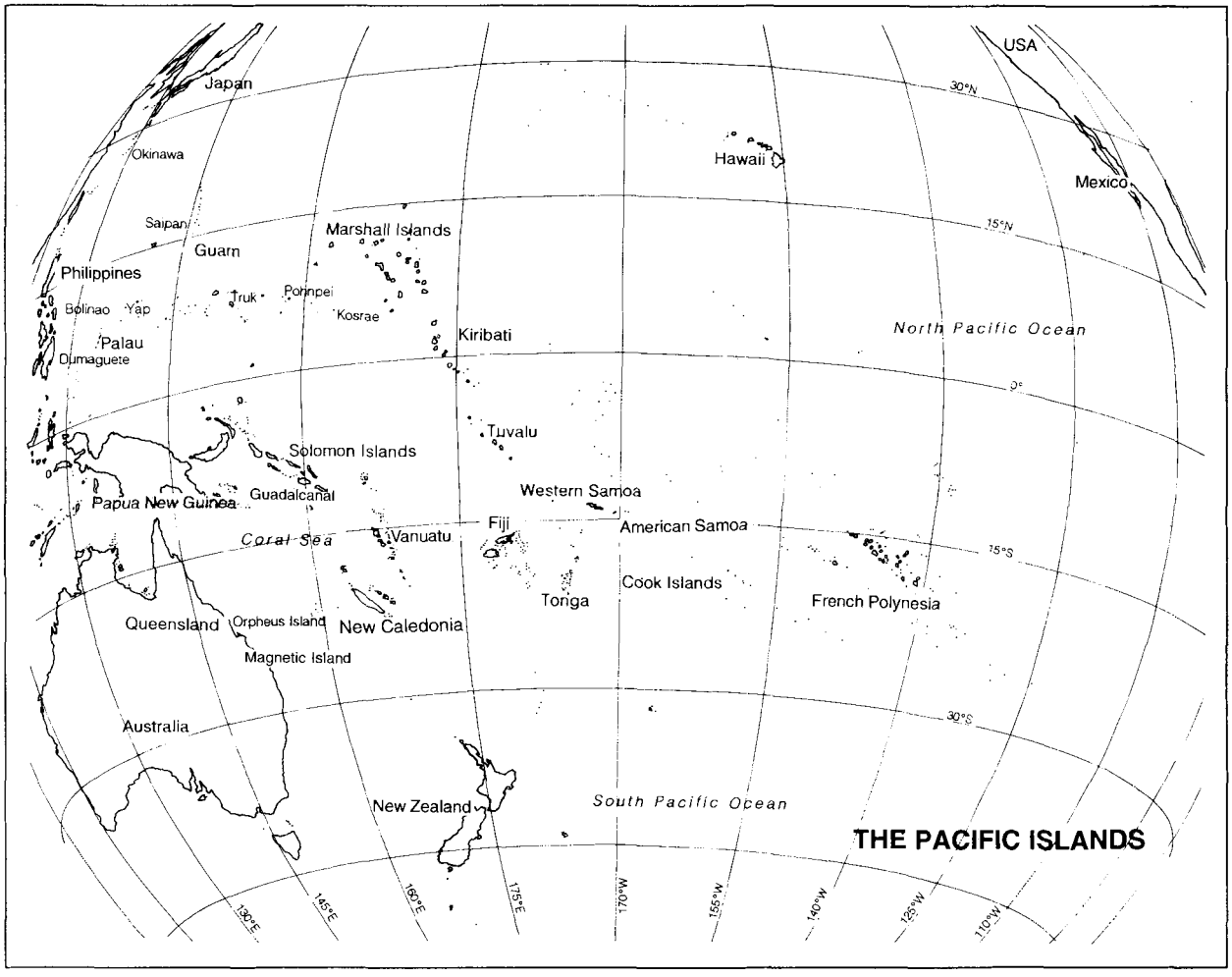

Fig. 1.1. Map of the Pacific Ocean showing the location of Solomon Islands and other places mentioned in the main text. (Courtesy of Mario David).

diets and inoculated with zooxanthellae from adult clams. After about 2 weeks, most of the surviving larvae have metamorphosed and settled and are ready to be transferred to the first nursery phase.

Land-based nursery phase. Recently settled juvenile tridacnids are placed in large, flat-bottomed, outdoor tanks and once byssally attached are provided with aeration and flowing seawater. Blooms of fouling algae have to be controlled, either manually or by using herbivores. Growth of clams (and fouling algae) may be enhanced by the addition of inorganic fertilizers. Clams may be transferred to floating ocean-nurseries at a size of 2-3 mm or maintained in the land-based nursery to a shell length (SL) of 20-25 mm.

Ocean-nursery phase. Clams are placed in the sea, protected from predators by mesh cages until large enough to be virtually free from predation, about 150-200 mm SL depending on species and local conditions. This phase is further described below.

Grow-out phase. Large juvenile clams are reared in relatively unprotected conditions on the seabed until ready for harvest. Harvest size depends on the market targetted and species cultivated but may range from less than 4 cm SL in the case of *T. crocea* intended for the aquarium trade to 40-50 cm SL in the case of *T. gigas* intended for the adductor muscle market.

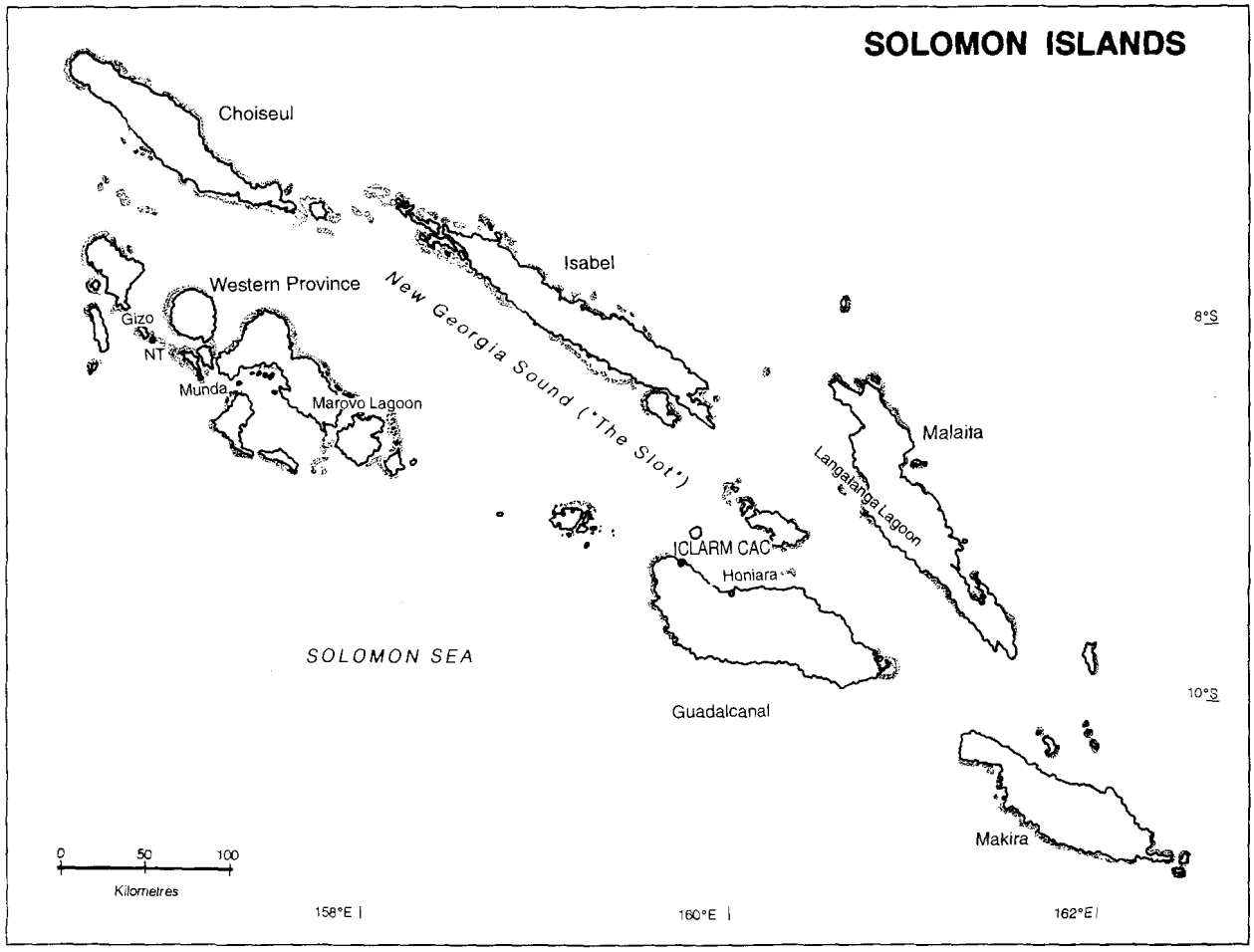

Fig. 1.2. Map of the Main Group Archipelago of Solomon Islands showing places mentioned in the text. Areas where coral reef predominates are shown by stippling. Research facilities run by the International Center for Living Aquatic Resources Management in collaboration with the Solomon Island Government are the Coastal Aquaculture Centre (ICLARM CAC) and the Nusatupe field station (NT). (Courtesy of M. David).

Currently a number of tridacnid culture facilities are in operation around the Pacific and some or all of the above culture phases have been carried out in: American Samoa, Australia, Cook Islands, Federated States of Micronesia (Kosrae, Pohnpei, Truk and Yap), Fiji, Indonesia, Marshall Islands, New Caledonia, Northern Mariana Islands (Saipan), Palau, Papua New Guinea, Philippines, Solomon Islands, Tonga, Tuvalu, Western Samoa, and even the Netherland Antilles in the Caribbean (Fitt 1993a and Govan, unpubl. data). In Australia, Palau and the Marshall Islands commercial or semi-commercial giant clam farms are in operation (Tisdell et al. 1993).

Ocean-Nursery Culture of Tridacnid Clams

Ocean-nursery culture carried out by ICLARM in Solomon Islands takes place at a field station run by ICLARM at Nusatupe near the town of Gizo in Western Province (see Fig. 1.2). Ocean-nurseries also operate at the CAC and at more than 20 village sites around the country (Govan 1993). Three forms of ocean-nursery culture are employed: benthic culture, trestle culture and floating culture.

Benthic culture. Cages are placed directly on the sea floor in shallow subtidal areas. Cages are usually square or rectangular and made of galvanized wire mesh with a cement base (Plate II). The area of such cages is typically between 0.5 and 1.1 m^2 and construction details are given by Govan (1992b) and Tafea (1993). They are used at Nusatupe and the village ocean-nurseries.

Trestle culture. Cages are raised about 0.5 m above the seabed on frames made of steel reinforcing rod (Tafea 1993). The cages are similar to those used in benthic culture (Plate II). They are also used at Nusatupe and village ocean-nurseries.

Floating ocean-nurseries. Cages are suspended near the sea surface from floats. A number of designs exist (Lasi 1993; Munro et al. 1993) but during the course of this work the most common design consisted of two sealed plastic pipes forming a catamaran from which a cement-based cage of 0.50-0.75 m^2 was suspended (Plate II). The use of floating cages enables spat to be transferred to the ocean-nursery at a smaller size, usually about 4 mm SL but as little as 2-3 mm compared to 25-30 mm for benthic cages (Munro et al. 1993). Floating cages are used at Nusatupe and the CAC.

Plate II. Methods used for raising cages off the seabed used in the ocean-nursery culture of tridacnid clams in Solomon Islands. Upper: Trestles. Note the square cages which may also be placed directly on the seabed. Lower: Floating ocean-nursery system. (Photos by H. Govan).

Ocean-nursery culture practices vary at the different institutions around the Pacific. Benthic culture is the method most widely used (Copland and Lucas 1988), but trestles are used in the Philippines and Western Samoa (Gomez and Belda 1988; Govan et al. 1993) and the use of floating cages is reported from the Marshall Islands (Munro et al. 1993). Benthic cages are used at OIRS on the Great Barrier Reef in Queensland, but these are placed in the lower intertidal zone and cages and clams are partially exposed during low tides (Lucas et al. 1988).

Predation in Tridacnid Mariculture

Serious predator-related mortality in ocean-nurseries was first reported at the MMDC in Palau caused by a ranellid gastropod, *Cymatium muricinum*. By 1988, *C. muricinum* had been reported to be

a serious problem in the Cook Islands (Sims and Howard 1988) and Yap in the Federated States of Micronesia (Price and Fagolimul 1988) and had been recorded in Papua New Guinea (Bell and Pernetta 1988) and Solomon Islands (Govan, unpubl. report).

An international workshop attended by collaborators in the GCMP identified predation as an important area for future research (Copland and Lucas 1988). By 1990, funding had been secured through ICLARM from the Australian International Development Assistance Bureau (AIDAB) for the International Collaborative Study of Predators of Cultured Tridacnid Clams (ICSPCT).

The present author was appointed coordinator of the ICSPCT in 1990 which enabled studies of ranellid predators of tridacnids already in progress to be continued (Govan, unpubl. report). One of the first steps was to determine the extent to which ranellids were a problem in tridacnid ocean-nurseries throughout the Pacific. This was achieved by interviews with researchers and operators, correspondence with institutions and direct observations. The results (Table 1.1) showed that ranellid predators occurred at most of the locations where the ocean-nursery

Table 1.1. Ranellid gastropods reported or observed to prey on cultured tridacnid clams in ocean-nurseries in the Pacific. Species and approximate numbers of clams held in ocean-nurseries are shown along with an indication (*) where these predators are perceived as a major pest. See map in Fig. 1.1 for geographic locations of places mentioned in this table.

Location	Species cultivated	Number of clams	Ranellid species
American Samoa	Td	3,000	Cm*
Australia, Queensland			
Orpheus Island	Tg, Hh	30,000	none
Reeffarm	Tc, Tg?	?	?
Magnetic Island	Tg	<100	Cm, Cp
Cook Islands	Td	185	Cm*
Federated States of Micronesia			
Kosrae	Tg, Td, Hh	5,600	Cm*, Cn
Pohnpei	Td, Hh	6,000	Cm*
Truk	Td	2,000	Cy*
Yap	Td	6,000	Cm*
Fiji	Td, Tg, Ts	50,000	Cm*, Cp, Ca
Marshall Islands			
Neil Skinner	Td	14,000	Cm*
Pacific Industries	Td	6,000	Cy
Rob Reimers	Tg, Tm, Hh	>10,000	Cy
Northern Mariana Is.			
Saipan	Td	5	Cy?
Palau	Tg,Td,Ts,Tm Tc,Hh,Hp	>100,000	Cm*
Papua New Guinea	Tg,Ts,Tc,Hh	?	Cm
Philippines			
Bolinao, Luzon	Tg,Td,Tm Hh,Hp	2,500	Cm, Cp, Ca, Cn
Dumaguete, Negros	Tm,Ts,Hh,Hp	700	Cm, Ca
Solomon Islands	Tg, Hh	50,000	Cm*,Ca*,Cp*,Cn
Tonga	Td	8,000	Cm
Tuvalu	Td	150	Cm, Ca
Western Samoa	Tg,Td,Hh	400	Cm*, Cp, Cn

Abbreviations:

Ca: *Cymatium aquatile*
Cn: *C. nicobaricum*
Cy: *Cymatium* sp.
Hp: *H. porcellanus*
Td: *T. derasa*
Tm: *T. maxima*
* : Major pest
Cm: *C. muricinum*
Cp: *C. pileare*
Hh: *Hippopus hippopus*
Tc: *Tridacna crocea*
Tg: *T. gigas*
Ts: *T. squamosa*

culture of tridacnids takes place and are considered the major pest at all the larger ocean-nurseries except OIRS. The species most often reported is *C. muricinum* but *C. aquatile, C. pileare* and *C. nicobaricum* also occur. No ranellids have ever been found in the benthic and off-bottom ocean-nurseries at OIRS on the Great Barrier Reef (J. Lucas, pers. comm.).

1.3 Ranellidae

Gastropods of the family Ranellidae (tritons) belong to the same superfamily, the Tonnacea, as the Tonnidae (tun shells), Cassidae (helmet shells), Ficidae (fig shells), Personidae and Bursidae (frog shells) (Beu 1980, 1988).

Ranellids usually possess a roughly sculptured shell with a moderate to long siphonal canal. Shells are characterized by the absence of any anal canal, prominently variced outer lip and a frequently conspicuous and even thick and bristly periostracum (Beu 1980; Kilburn and Rippey 1982). The ranellids, which are carnivorous mesogastropods, resemble the muricacean neogastropods in most of these features except that ranellids never possess more than two varices per whorl and these are never spiny as in Muricidae (Beu 1980; Kilburn and Rippey 1982).

The family Ranellidae has been universally known as the Cymatiidae since 1913 but questions of priority and synonymy forced a change and the family should now only be referred to as Ranellidae Gray 1854 (Beu and Cernohorsky 1986).

Three subfamilies of Ranellidae are recognized (Beu 1980; Beu and Cernohorsky 1986; Beu 1988; Waren and Bouchet 1990): Cymatiinae (=Neptunellinae), Ranellinae and Pisanianurinae. The subfamily Cymatiinae contains the genus *Cymatium* and other genera of interest in the present work such as *Cabestana, Charonia, Sassia* and *Linatella.* Members of this subfamily are predominantly tropical with long planktonic larval lives and may be distinguished from the other subfamilies by their varices which occur at intervals of 2/3 of a whorl (Beu 1980; Waren and Bouchet 1990).

The four species of *Cymatium* of interest as predators of juvenile tridacnids belong to 2 subgenera: *Gutturnium* and *Monoplex* (Beu 1985). The four species are described below and shown in Plates III and IV.

Cymatium (Gutturnium) muricinum (Plate III). Shell dirty-grey in color and relatively unornamented. Adults easily distinguished by their large thick parietal wall and columellar shield. Size up to 75 mm. Personal observations indicate that the body color is white to light tan with larger dark brown spots and smaller, round, light brown spots fringed with white. Also the shell color of juveniles appears to vary from white to orange to dark purple with white stripes (Plate III).

Habitat and abundance. Reported from sandy lagoon floors, lagoon shelves, fringing reefs and rocks from the low tide line to depths of 50 m (Demond 1957; Houbrick and Fretter 1969; Taylor 1976, 1984). Reportedly common (Hinton 1975), Kay (1971) found this species to be one of the most conspicuous epifaunal gastropods at Fanning Island, Kiribati, but only on subtidal patch reefs on the lagoon floor. Taylor (1976) found densities of 0.82 *C. muricinum* m^{-2} near seagrass habitat at Aldabra Atoll in the Indian Ocean and of around 0.2 m^{-2} in algal turf on a Guam fringing reef (Taylor 1984).

Distribution. *C. muricinum* is cosmopolitan in all tropical seas and has also been recorded in the Mediterranean (Beu 1985; Emerson 1991).

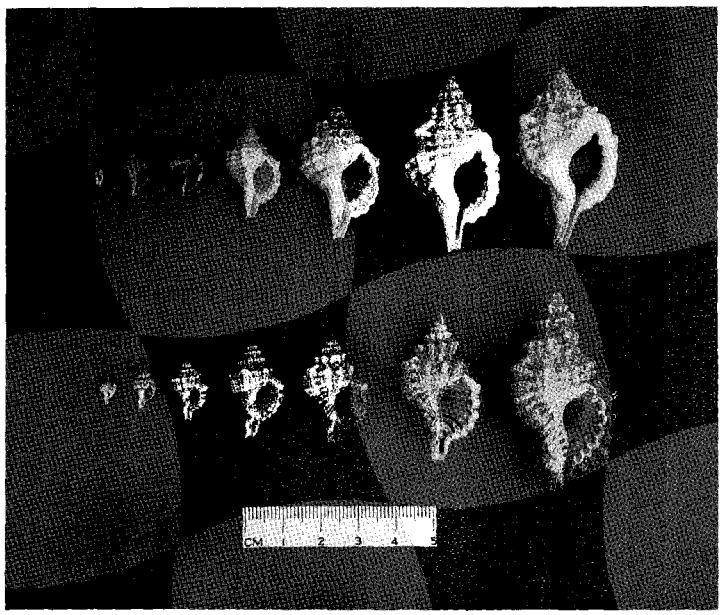

Plate III. Growth series of *Cymatium muricinum* (top row) and *C. nicobaricum* (bottom row). (Photo by H. Govan).

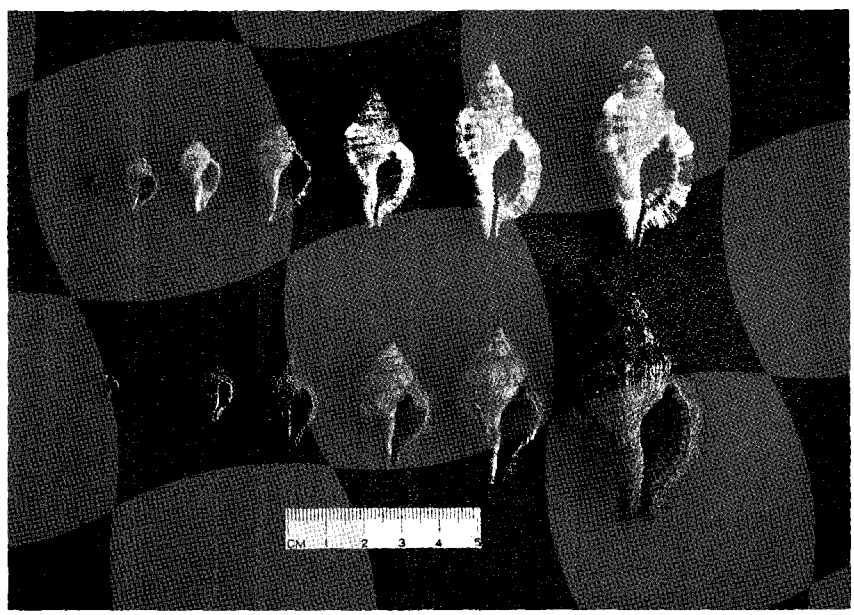

Plate IV. Growth series of *Cymatium aquatile* (top row) and *C. pileare* (bottom row). Note the prominent periostracum of *C. pileare* with its characteristic hairy appearance. (Photo by H. Govan).

C. (Monoplex) aquatile (Plate IV). Moderately solid shell, light tan with white and rusty brown blotches. Two varices at every whorl, 4-6 knobs between varices. Aperture light-pink to orange with 18-20 fine white columellar pleats and edge of aperture with 7 short white pleats that give rise to 7 pairs of denticles near the lip. Thick hairy periostracum. Similar to *C. pileare* but distinguished by the coarser spiral structure, more flaring aperture, shorter plications inside outer lip, columellar plications are regular and do not merge posteriorly, and lighter coloration inside aperture. Whereas *C. pileare* usually has paired small denticles on the outer lip that continue as ridges deep into the aperture, *C. aquatile* has two parallel rows of paired marginal denticles (Kilburn and Rippey 1982; Beu 1988). See Chapter 4 for differences in protoconch morphology and Beu (1988) for descriptions of other species in the *C. pileare* complex. Size up to 60 mm. The body color of specimens observed at the CAC was light pink-orange with rusty brown fringed pink-red spots.

Habitat and abundance. Reported to be uncommon (Hinton 1975). Few reports of habitat preferences or abundance, probably subtidally to intertidally on coral reefs, rubble and in crevices (c.f., Beu 1988).

Distribution. Pantropical, found in the Indo-Pacific and Atlantic (Beu 1988).

C. (M.) nicobaricum (Plate III). Shell solid and heavy, creamy white to light tan in color, flecked with rusty brown. Two varices at every whorl and 3-5 knobs between varices. Aperture usually orange to red, outer edge of lip white with 7-14 white denticles, columella with 11-19 plicae. Personal observations suggest that juveniles may be distinguished from juveniles of *C. muricinum* and *C. aquatile* by their sharply pointed nodes and varices. Size up to 70 mm. Body color in specimens examined: underside of foot white-light grey with grey and fawn irregular spots. Body white-light grey, large darker spots with smaller light spots.

Habitat and abundance. A common shallow water reef species found on rocks, coral rubble, outer edges of windward reef flats and occasionally on sand (Demond 1957; Cernohorsky 1967; Houbrick and Fretter 1969; Kay 1971; Taylor 1986). Taylor (1978) found densities of 0.1-0.2 *C. nicobaricum* m^{-2} on hard reef flats and seagrass beds at Addu Atoll in the Maldives and of 0.1 *C. nicobaricum* m^{-2} on intertidal platforms at Rottnest Island, Western Australia (Taylor 1993).

Distribution. Found in tropical seas, Indo-West Pacific, East and West Atlantic (Beu 1985).

C. (M.) pileare (Plate IV). Similar to *C. aquatile* (see above) but distinguished by its narrower form, darker color, deep red aperture with longer plications and finer axial and spiral sculpture (Hinton 1975; Beu 1988). Up to 100 mm. The pattern of body coloration is similar to that of *C. aquatile* but the colors are slightly darker with a brown-violet tinge. Juvenile *C. pileare* are conspicuous because of their exceptionally thick, hairy periostracum.

Habitat and abundance. Common on shallow coral reefs, patch reefs and seagrass beds (Cernohorsky 1967; Kay 1971; Hinton 1975; Taylor 1978). Taylor (1978) found densities of 0.1 and 0.3 *C. pileare* m^{-2} on a reef flat and a seagrass bed, respectively, at Addu Atoll, Maldives.

Distribution. *C. pileare* is limited to the Indo-West Pacific (Beu 1985). The wide distribution of these species of *Cymatium* is noteworthy as it amply encompasses the areas where tridacnid culture takes place or may be developed. This wide distribution is at least partially explained by the long larval stage of members of the subfamily Cymatiinae, extending to up to 1 year in some cases (Scheltema 1977; Beu 1980).

Habitat Preferences of Ranellid Predators of Tridacnids

The broad range of habitats occupied by *C. muricinum* and the other species of *Cymatium* covers most of the habitats considered for tridacnid mariculture (Calumpong 1992). The scant published information on abundance of ranellids does suggest that these are relatively uncommon compared to other species of predatory gastropod.

As part of the present study, the relationship between habitat type and ranellid occurrence was examined at the tridacnid ocean-nurseries in Australia, Fiji, Philippines, Western Samoa (c.f., Table 1.1) and at 20 village-based ocean-nurseries in Solomon Islands. Information on habitat features such as substrate type, turbidity, salinity, temperature, water circulation and exposure to wave action was collected. Less exhaustive information was obtained in correspondence with the operators of the remaining ocean-nurseries in Table 1.1.

Data were obtained for 34 ocean-nurseries in the Pacific (Table 1.1). *C. muricinum* was collected at 31 of these ocean-nurseries covering a wide range of habitats, from sand and

seagrass to coral rubble and rocks, and from intertidal to subtidal. The three sites where no *C. muricinum* were recovered are described below.

At OIRS near Townsville, Queensland, *Cymatium* spp. were never recovered in intertidal, subtidal or floating ocean-nurseries (J. Lucas, pers. comm.). Most clams (*T. gigas*) were kept on an intertidal reef flat. The tidal range is wide (a couple of meters) and consequently the area is well flushed. Although there are large rivers on the mainland, the salinity is consistently high (S. Lindsay, pers. comm.) and the relatively high turbidity does not appear to affect coral growth in the subtidal reef areas. Alan Beu (pers. comm.) reports that ranellids are rare at OIRS but he did recover one dead adult shell each of *C. muricinum* and *C. pileare*. Thora Whitehead (pers. comm.) reports that *C. muricinum, C. aquatile, C. nicobaricum* and to a lesser extent *C. pileare* are uncommon in Queensland. However, ranellids are found at the oyster farm on Magnetic Island, a few hundred kilometers from OIRS (Table 1.2).

Table 1.2. Records of ranellid gastropods as predators of cultured bivalves throughout the world.

Ranellid species	Prey species	Location	References
Cymatium aquatile	*H. hippopus, T. maxima*	Philippines	Abdon-Naguit and Alcazar (1988)
	T. gigas, T. squamosa, T. maxima	Solomon Islands	This work
C. corrugatum amictum	*Anadara tuberculosa*	Costa Rica	Villalobos and Baez (1983)
C. martinianum	*Crassostrea rhizophorae*	Jamaica	Littlewood (1991)
C. muricinum	*C. rhizophorae*	Jamaica	Littlewood (1988)
	T. derasa, T. gigas	Palau, Yap	Perron et al. (1985)
	T. gigas, T. squamosa, T. maxima	Solomon Islands	This work
	Saccostrea echinata	Queensland, Aust.	Personal observation
C. nicobaricum	*Pinctada maxima, P. margaritifera*	Okinawa	M. Muramatsu (pers.comm.)
	T. gigas	Solomon Islands	This work
C. parthenopeum (keenae?)	*C. rhizophorae*	Venezuela	Velez (1975)
	Perna perna	Venezuela	Urosa (1972)
C. parthenopeum parthenopeum	"Oysters"	Australia	Coleman (1975)
	"Bivalves"	Australasia?	Laxton (1971)
C. pileare	*Crassostrea gigas*	Israel	Hughes-Games (1977)
	P. maxima, P. margaritifera	Okinawa	M. Muramatsu (pers.comm.)
	T. gigas, T. squamosa, T. maxima	Solomon Islands	This work
	S. echinata	Queensland, Aust.	Personal observation
C. vespaceum	*H. hippopus*	Philippines	Perio and Belda (1988)
Linatella caudata	*Crassostrea madrasensis*	India	Thangavelu and Muthiah (1983)
	Pinctada fucata	India	Dharmaraj et al. (1987)

A few *C. nicobaricum* and no *C. muricinum* were recovered at a village trial in Ghulavu, W. Guadalcanal. This trial closed in 1990 due to a storm. The site had seasonal freshwater influence and was generally slightly turbid. Coral appeared to grow well subtidally; live *Porites* were observed on the reef flat. *C. muricinum* was never recovered from the shallow subtidal cages situated on the coral rubble reef flat.

No ranellids were recovered at a trial ocean-nursery in the Langalanga lagoon, Malaita, situated near a river and sheltered from the ocean by a barrier reef. This site was turbid and the trial was of relatively short duration because the clams died due to siltation and possibly excessive freshwater influence.

The main environmental features common to the three sites where ranellids were rare or absent are unusually high turbidity and close proximity to a river. None of the sites where *C. muricinum* were recovered shared these characteristics.

Tridacnid clams are generally grown in high salinity and relatively clear waters. A. Beu (pers. comm.) states that *Cymatium* spp. do not tend to occur where there is silt or freshwater

influence. Littlewood (1989) reports that *C. pileare* is predominantly marine and therefore not a problem in brackishwater culture of mangrove oysters.

The morphology of larval *Cymatium* spp. is discussed in detail in Chapter 4 but it is probable that prior to settlement these tritons possess four large velar lobes as described by Lebour (1945). Heavy silt loadings would probably represent a severe hazard to larvae with such velar lobes, causing death or early settlement.

The contention that factors affecting the larval stages of these ranellids determines their absence at certain sites is supported by the finding that although *Cymatium* spp. are rarely found in land-based nurseries throughout the Pacific, recently settled *C. muricinum* and *C. nicobaricum* are often collected from tanks and pipework at the clam hatchery in Kosrae. Most tridacnid hatcheries in the region operate centrifugal or "mono" high-pressure pumps for seawater intake but the Kosrae hatchery is unique in using submersible axial flow pumps. The operating mechanism of such pumps appears to be less likely to damage organisms in the intake water (Fraenkel 1986) and may allow higher percentages of ranellid larvae to enter the hatchery seawater system at Kosrae than at other hatcheries.

Ranellid Predators of Other Cultured Bivalves

Gastropods of the families Muricidae, Fasciolariidae, Melongenidae and Naticidae are well known predators of cultured bivalves worldwide (Galtsoff 1964; Hancock 1974; Kilburn and Rippey 1982; Gibbons and Blogoslawski 1989). However, only a few reports exist of Ranellidae preying on cultured bivalves other than tridacnids (Table 1.2).

The reports of ranellid predation on cultured bivalves shown in Table 1.2 are reviewed in detail in the following chapters. Interestingly, all the reports are from tropical or subtropical areas where bivalves were being cultured above the substrate in full salinity seawater. The ranellid species involved were almost all of the genus *Cymatium* with the exception of *Linatella caudata*. In most cases, these predatory tritons are reported to settle on their prey as larvae or only become apparent in their prey as young juveniles.

Given the widespread occurrence of ranellid predators at tridacnid culture facilities throughout the Pacific it is somewhat surprising that there have been so few reports of ranellids in other bivalve culture operations within the distribution range of these ranellid species. One reason is that the countries within this range are relatively poor and in many cases still developing their aquaculture industries which are consequently poorly documented.

However, the main reason for the few reports of ranellid predators of cultivated tropical bivalves may well be that much of such cultivation in Latin America and Asia takes place in brackishwater and/or silty sediment laden waters (c.f., Broom 1985; Angell 1986; McCoy and Chongpeepien 1988; Vakily 1989; Hernandez 1990). These water conditions may well be intolerable to larval ranellids of the subfamily Cymatiinae, as suggested above. Thus, these predators would not be expected to occur at the sites of most coastal bivalve culture operations in the tropics, located as they are on the shores of large land masses with heavy rainfall and large rivers.

Aims and Scope of the Present Work

Ranellid predators appear to pose a threat to the development of viable cultivation systems for tropical bivalves in certain situations. Indeed in the case of pearl oyster cultivation in Okinawa, Japan, depredations of ranellids already cause serious economic losses (M. Muramatsu, pers. comm.).

The taxonomy of ranellid gastropods is relatively well understood thanks largely to the work of Dr. A. Beu (e.g., 1980, 1985, 1988), but the biology of this group has received very little attention (Beu and Kay 1988; Morton 1990b).

In view of the potential threat that gastropods of the family Ranellidae represent to tropical bivalve culture and the lack of knowledge regarding the biology of this group, the aim of the present work was: to study aspects of the biology of *C. muricinum, C. aquatile, C. pileare* and *C. nicobaricum* relevant to controlling the impact of these animals on the cultivation of tridacnid clams in particular and tropical bivalves in general.

The results of research into the feeding biology of the studied species are presented in Chapter 2. The rates of feeding and growth of the four species of *Cymatium* are examined in Chapter 3 based on laboratory studies. Chapter 4 contains observations on reproduction and recruitment of the studied species and a review of current knowledge. Factors that may influence variability in recruitment of ranellids in tridacnid ocean-nurseries in Solomon Islands are examined in Chapter 5 based on field data and results presented in the previous chapters. Chapter 6 presents estimates of the impact of ranellid predators on different types of tridacnid cultivation used in Solomon Islands and examines factors that may increase this impact. Finally, Chapter 7 discusses potential methods of controlling ranellid predation based on the research presented in the preceding chapters.

CHAPTER 2

Feeding Behavior of *Cymatium* spp.

2.1 Introduction

The Ranellidae are carnivorous mesogastropods known to feed on polychaetes, bivalves, ascidians, gastropods, echinoderms and crustaceans (Houbrick and Fretter 1969; Hughes 1986; Morton 1990b). In common with most of the evolutionarily more advanced neogastropods, these predators differ from grazers in the development of a siphonal canal in the anterior lip of the shell. This canal receives a fold of the pallial mantle margin that directs the inhalant water current on to the highly developed osphradium used in the chemoreception of prey scents. Other differences include modifications of the proboscis and associated glands for attacking prey (Hughes 1986).

There are relatively few studies of the anatomy and biology of ranellids (Beu and Kay 1988; Morton 1990b). Most accounts of feeding in Ranellidae describe the use of a long pleurembolic proboscis inserted into the prey, frequently associated with the discharge of anesthetic, toxic or acidic saliva (Houbrick and Fretter 1969; Laxton 1971; Thangavelu and Muthiah 1983; Muthiah et al. 1985; Morton 1990b; Littlewood 1991). What is known of ranellid anatomy is consistent with these modes of feeding. Houbrick and Fretter (1969) report bulky salivary glands in *Cymatium muricinum*, *C. nicobaricum* and *C. pileare* which excrete acid at pH 2.0 through the long proboscis. Morton (1990b) reports that the salivary glands of another member of the subfamily Cymatiinae, *Linatella caudata*, produce strong sulfuric acid. The secretions of the foregut glands of *C. intermedium* and three other species of *Cymatium* are currently being investigated and appear to contain substances of low pH and also various types of biologically potent molecules (J.D. Taylor, pers. comm.).

Houbrick and Fretter (1969) and Morton (1990b) have studied the feeding behavior and preferences of ranellids and Perron et al. (1985), Govan et al. (1993) and Govan (1994) examined aspects of feeding preferences in relation to tridacnid culture. Houbrick and Fretter (1969) studied the diets of four ranellid species in captivity. *Cymatium nicobaricum* (the most voracious) and *C. gemmatum* consumed only gastropods while *C. muricinum* and *C. pileare* consumed bivalves. These four species appeared to feed more regularly at night. *C. nicobaricum* was observed attacking gastropods by inserting the proboscis into the mantle cavity of the prey. Areas near the heart and visceral ganglia of prey examined soon after an attack were observed to be in a semi-digested or fluid state.

Morton (1990b) observed *L. caudata* cutting through the testes of ascidians with the radula after which the proboscis was inserted. Bivalves were attacked by inserting the proboscis between the parted shell valves (Morton 1990b). The preferred prey of this triton were bivalves, but ascidians, gastropods and barnacles were also eaten.

Perron et al. (1985) studied the predation of *C. muricinum* on cultured tridacnid clams in Palau. Larvae of *C. muricinum* were reported to settle directly on clams in benthic ocean-nurseries. The newly metamorphosed tritons were often found between the mantle and shell sometimes causing characteristic blisters on the inside of the latter. These tritons often killed the infested clam and emerged to prey on surrounding bivalves. Larger tritons were generally observed to attack juvenile giant clams (*T. derasa* and *T. gigas*, 80-110 mm shell length [SL]) through the byssal orifice using their thin extensible probosci. Because a gravel substrate was used for clams to adhere to, this method of attack made the tritons difficult to detect but no decrease in susceptibility to attack was noticed when a solid cement substrate was used (Perron et al. 1985).

The potential destructiveness of the tritons was observed by Perron et al. (1985) to increase rapidly with size. Tritons of 10 mm SL took 10-15 days to kill *T. gigas* of around 100 mm SL, whereas the same size of clams were killed in less than 5 days by 30 mm tritons. Tritons over 30 mm in size were capable of killing juvenile *T. derasa* up to 150 mm SL and juvenile *T. gigas* over 170 mm SL. Perron et al. (1985) suggest that the reason for the resistance of larger clams to *C. muricinum* attack is that they have their byssal orifices more tightly pressed against the substratum and are capable of dislodging tritons that attempt to crawl over the mantle.

Perron et al. (1985) also showed that juvenile tridacnids of another genus, *Hippopus hippopus*, are much less vulnerable to *C. muricinum* predation than *T. gigas* or *T. derasa* for 80-95 mm SL clams. The reason suggested for this is the zipper-like byssal orifice of this species which grows closed, effectively excluding predators, unlike the byssal orifice of species of *Tridacna* which remains partially open.

Govan (1994) found that *C. muricinum* (c.f., Perron et al. 1985) and three other species of ranellid (*C. aquatile, C. pileare* and *C. nicobaricum*) were the most important predators of cultured tridacnids in Solomon Islands. These gastropods consumed all the species of tridacnid offered, namely: *T. gigas, T. squamosa, T. maxima* and *H. hippopus*. Govan et al. (1993) found *H. hippopus* to be less susceptible to the attack of *C. muricinum* and *C. pileare* than other species of tridacnid. However, all attacks were observed to take place between the valve gape of clams rather than through the byssal orifice (c.f., Perron et al. 1985).

The methods used by *Cymatium* spp. to prey on cultured tridacnids appear poorly understood, and have not been reported at all for *C. aquatile, C. pileare* and *C. nicobaricum*. Study of the impact of these ranellids on the cultivation of tridacnids required a better understanding of their feeding methods.

In the present work, feeding method observations were made to elucidate the mechanisms involved in ranellid attacks on juvenile tridacnids and to ascertain whether the study species of *Cymatium* preferred attacking by day or night. Based on these observations the size of the ranellid proboscis appeared to be critical in the success of attacks so an experiment was designed to measure the length of probosci of living tritons.

Ocean-nurseries for tridacnids frequently contain a number of wild molluscs such as fouling oysters and herbivorous gastropods. Prey preference (or vulnerability) experiments were performed to examine whether *T. gigas* was actually the preferred prey of the study species of *Cymatium*. Similar experiments examined whether *T. gigas* was a preferred or more vulnerable prey than *H. hippopus*, as reported by Perron et al. (1985). The preference of both small and

adult *C. muricinum* for different sizes of *T. gigas* was also examined in this series of experiments.

A critical factor for clam farmers is the identification of an "escape size" for the cultivated clams at which the bivalves are resistant to most predators and therefore need minimum protection. In addition to the size preference experiment, the likely escape sizes of *T. gigas* with regard to *C. muricinum* predation were examined in two experiments which measured the time taken by juvenile and adult *C. muricinum* to kill juvenile clams.

2.2 Materials and Methods

The following conditions applied to all experiments and any variations are stated in the appropriate subsection below. Test organisms were obtained from the ocean-nursery at the ICLARM CAC. The numbers of available wild animals fluctuated seasonally and the availability of cultured clams of appropriate size was often constrained. Due to these constraints the number of test animals used for each experiment was reduced. Thus a major assumption in the interpretation of the results is that the average behavior of a small number of test organisms is indicative of the behavior of a larger population.

Experiments and observations were carried out between June 1989 and October 1992, although the bulk of experiments were performed in the last two years of this period. Experiments were performed in one of the following three types of aquaria: 2.5-l static aquaria with aeration and three weekly water changes, water temperature ranged from 26 to 29°C. Two types of aquaria receiving a constant flow-through of seawater between 28 and 31°C were used; a series of eight 24-l glass aquaria and one 40-l aquarium divided into 20 compartments is more fully described in Section 3.2.

Results that required analysis of goodness-of-fit with a null hypothesis, such as in the attack location and prey preference experiments, were tested using the maximum likelihood statistic G with Williams' correction, as described by Sokal and Rohlf (1981). When sample sizes were 25 or less the probability of encountering a particular ratio was calculated on the basis of the binomial expansion. Whenever the two-tailed probability was 5% or less the deviation was considered significant.

Feeding Methods

More than 40 observations were made on starved specimens of the four study species of *Cymatium* presented with *T. gigas* of 15-70 mm SL in 2.5-l and 80-l aquaria. Tritons of all four species were routinely confined in the 20 flow-through compartments and fed *ad libitum* on byssally detached *T. gigas* of 30-mm mean shell length. These tritons were observed 5 days per week and records kept of whether attacks took place through the valve gape or the byssal orifice of clams. For 4 days every week records were kept of whether tritons attacked on the previous night or during the day.

In order to measure the lengths of their probosci, starved tritons of varying sizes were confined in wire mesh cages inside 2.5-l aquaria. A portion of dead clam tissue was placed near the wire cage. As a triton extended its proboscis in an attempt to feed, the tissue was moved progressively further away. Maximum length of the triton proboscis was estimated against a graduated background.

Preference Experiments

All test organisms were acclimated for 1 week before experiments started, under identical conditions to those of the experiment. Predators were starved for this period. Prey organisms for replenishment of these experiments were maintained in similar aquaria throughout the course of the experiment and often for much longer periods. As no mortality was observed amongst these animals the use of controls was not deemed necessary. All species-preference experiments were performed in 24-l flow-through aquaria.

The first preference experiment tested the preference of three species of *Cymatium* (*C. muricinum, C. aquatile* and *C. pileare*) for two size classes of *T. gigas* (25-40 mm SL and 15-20 mm SL), two size classes of fouling pearl oyster *Pinctada maculata* (40 mm SL and 20 mm SL) and adult herbivorous gastropods *Cerithium tesselatus*. Two late juvenile specimens of each triton species were tested in separate aquaria over 10 weeks. Because these tritons were still growing they were measured at the beginning and end of the experiment. Equal numbers of bivalves from each species and size class were available to the predators, usually one or two. Two *Ce. tesselatus* were kept in all tanks. Consumed prey were removed, measured and replaced with live prey.

C. nicobaricum was reported to consume gastropod prey exclusively (Houbrick and Fretter 1969) so a second preference experiment was performed separately for this species. Sixteen *C. nicobaricum* were divided into four groups of four according to size and placed in separate aquaria. Four specimens of the gastropod *Ce. tesselatus* (20 mm SL), the pearl oyster *P. maculata* (30 mm SL) and *T. gigas* (30 m SL) were placed in the aquaria and replaced when consumed. The experiment ran for 18 days.

A third experiment tested the preference of *C. muricinum* for two tridacnid species. *T. gigas* and *H. hippopus* (40-50 mm SL) were offered to the predator in aquaria. Five byssally attached specimens of each clam species were placed in aquaria with individual predators. Dead clams were counted, removed and replaced with live clams daily. Experiments lasted 3 weeks. Four adult specimens of *C. muricinum* (mean size 43.8 mm) and eight juveniles (mean size 20.6 mm) were tested. This experiment was partially reported in Govan et al. (1993).

The fourth preference experiment was intended to test the existence of size preference by *C. muricinum* for juvenile *T. gigas*. Two sizes of *C. muricinum* were tested: adult (mean shell length of 35.4 mm, range 32.4-37.3) and juvenile or immature tritons (initial mean shell length of 17.3 mm, range 15.7-18.5). Four tritons from each of the two size classes were placed individually in static 2.5-l aquaria with two specimens of *T. gigas* from each of 3 size classes: 10 mm (mean SL 9.7 mm, 7.7-12.1), 30 mm (mean SL 30.9 mm, 21.3-39.8) and 50 mm (mean SL 49.8 mm, 41.2-57.1). The duration of the experiment was 3 weeks, during which time consumed clams were replaced with clams from the same size class and the tritons were re-measured after 10 and 21 days.

Time Required by C. muricinum *to Kill* T. gigas

The first experiment examined the time taken by recently settled juvenile *C. muricinum* to kill juvenile *T. gigas*. Twelve *C. muricinum* of 4-5 mm SL were placed individually in flow-through compartments with juvenile *T. gigas* of 12-113 mm SL. Time until death of the clams was measured. The biomass of the test clams was estimated, based on the allometric relationship

calculated in Appendix 2. In the second experiment five adult *C. muricinum* of known size (43-44 mm SL) and proboscis length were confined individually in 24-l flow-through aquaria with a juvenile clam of 110-170 mm SL. Time taken to kill the prey and method used were recorded.

2.3 Results

Feeding Methods

The same methods and behavior were observed for each of the four study species of *Cymatium* when attacking juvenile *T. gigas*. However, most feeding observations were made on the most abundant ranellid—*C. muricinum*.

Ranellids placed in aquaria promptly extend and elevate the inhalant pallial siphon, which appears to be used in receiving chemical stimuli judging by the movements of the siphon and, subsequently, those of the triton. If the triton is hungry and tridacnid prey are present, the latter are rapidly detected and the triton approaches, siphon foremost.

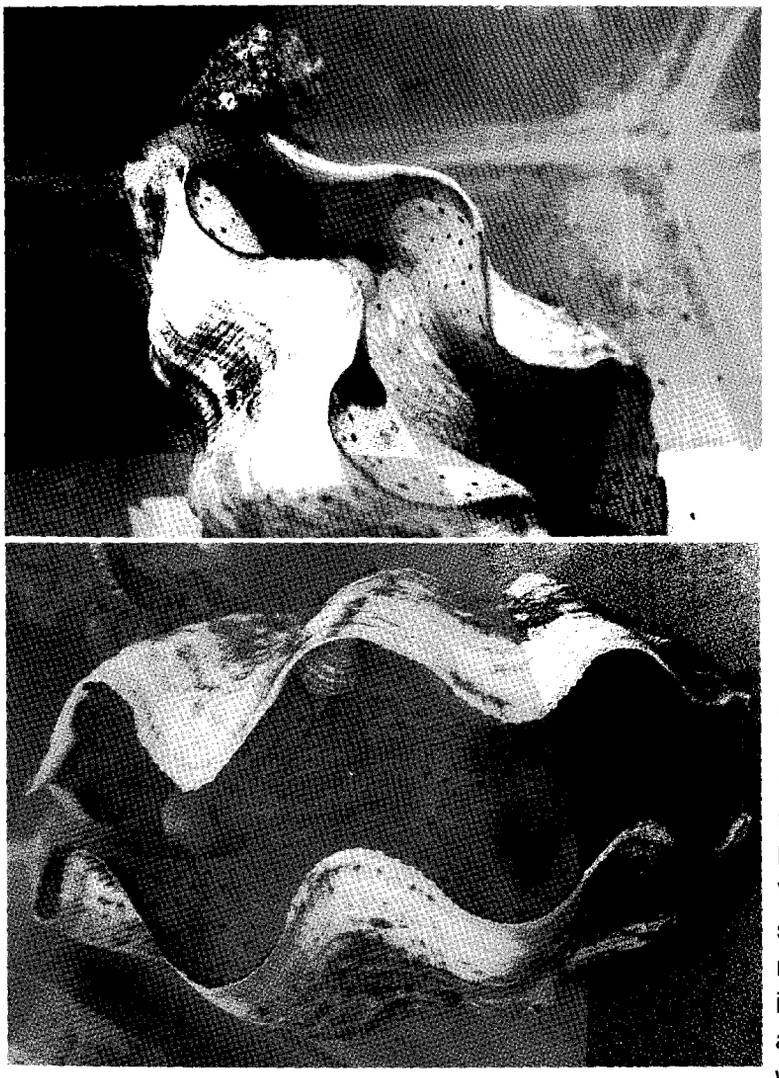

Plate V. Feeding methods of *Cymatium muricinum*.Upper: An adult *C. muricinum* attempting to penetrate the mantle of a juvenile giant clam, *T. gigas*, with its extended proboscis in order to paralyze or kill the clam with salivary secretions. Lower. A juvenile *C. muricinum* feeding at the mantle edge of a live juvenile *T. gigas*. (Photos by H. Govan).

On reaching the tridacnid prey, the triton usually climbs up the outside of the clam's valves and palps the mantle edge and surface with its cephalic tentacles. This process elicits a minimal response from the prey and may last from 1 to 10 minutes at the end of which the gastropod's head is level with the edge of the clam's valve. The predator generally extends from its shell at this stage.

Suddenly, the triton everts its long extensible proboscis and stabs the bivalve through the mantle between the gaping valves (Plate V). Sometimes two or three quick stabs are required to penetrate the mantle. The clam reacts by closing its valves, sometimes repeatedly, and often trapping the proboscis, which rarely appears to trouble the predator. Pumping movements of the proboscis may sometimes be observed.

Within minutes the clam begins to relax and die and the triton proceeds to devour the prey using its proboscis (Plate V). The internal organs are generally consumed before the mantle. The time taken to paralyze and eat the clam depends on the relative sizes of the predator and prey. In cases where even a small triton was removed from its prey immediately after the first successful stab, the clam subsequently died. In the unsuccessful attacks observed the gastropod often waited for the clam to re-open its valves and then proceeded to attack again in the same fashion.

Attacks were observed to take place from any location around the edge of the clam's valves and sometimes through the byssal orifice but almost invariably the proboscis was angled towards the center of the clam's mantle cavity. It appears that the tritons use some form of toxic salivary secretions to kill or paralyze their prey. *C. muricinum* harassed using a vice or small hammer were induced to evert their probosci defensively and produced both acidic (pH 2-3) and basic (pH 8) emissions detected using pH paper. Seawater measured pH 6 on this scale.

Judging by the angle of penetration of the proboscis and the rapid immobilization of the clam prey the target is probably the heart, pericardium or kidney. These organs appear to be approximately centrally situated in lateral views of tridacnids according to work carried out on the anatomy of *T. gigas* by Yonge (1980) and Norton and Jones (1992).

The method described above is frequently successful when employed by large juvenile or adult *Cymatium* spp. attacking small *T. gigas* up to about 100-150 mm SL. However, sometimes tritons are observed feeding on the clam, either through the valve gape or byssal orifice without succeeding in killing the clam outright. The triton may crawl into the clam and feed under the mantle edges (Plate V) or even inside the body cavity. This is the method favored by recently settled juvenile tritons but all sizes of *Cymatium* spp. have been observed attacking large clams in this fashion.

The logical consequence of the above observations appeared to be that no clam is immune to ranellid attack but smaller clams were more likely to die as a result. To test this, three adult *C. muricinum* (37-48 mm) were placed in a tank containing adult *T. gigas*. The tritons rapidly located a clam (410 mm SL) and having scaled the sides of the clam's valves they promptly inserted their probosci under the mantle edge of the clam to feed on the softer tissue there. This elicited violent reactions from the clam such as prolonged partial mantle retraction but did not appear likely to cause death. Adult *C. muricinum* have been observed using this method on broodstock *T. derasa* and *Hippopus hippopus* in an ocean-nursery in the Philippines (pers. obs.).

From the above, it appears that the probability of a triton killing *T. gigas* prey in an initial attack may bear relation to factors such as clam mantle toughness and the distance from valve edge to the centrally located vital organs. The relationship between length (SL) and shell height (SH) of *T. gigas* was calculated based on data available at the ICLARM CAC (see Appendix 2):

$$SH = 0.66 \times SL \quad (r^2 = 0.99) \qquad \textbf{...2.1)}$$

From equation (2.1) the vital organs of *T. gigas* may be at a minimum distance from the upper valve edge roughly equivalent to one-third of the clam's shell length, assuming these are centrally located.

The proportion of attacks by the four study species of *Cymatium* observed to take place between the valve gape of clams as opposed to through the byssal orifice are shown in Table 2.1. The null hypothesis (H_o) tested was that an equal proportion of attacks could be expected

at each location (1:1). This hypothesis was strongly rejected in the case of *C. muricinum* in which 85% of attacks took place through the valve gape. Similar proportions were observed for the other species but, due to the small sample size, no significant difference in attack site was found for these data using binomial expansion.

Rough measurements were made of the linear dimensions of the perimeter of the valves of *T. gigas* of the size range tested. The byssal orifice was found to represent 12-16% of the length of the valves around the valve gape. This proportion is similar to the proportion of attacks observed through the byssal orifice for *C. muricinum* (15%).

The proportion of attacks taking place at night for each triton species are shown in Table 2.2. Observations were recorded between 0700 and 1600 hours 4 days a week, data from Mondays and the weekend were not used. H_0 was that tritons had equal chances of feeding at any time of day or night. As the observations corresponding to "day" attacks were made during 9 hours of the day and remaining attacks were lumped as "night" attacks; the ratio tested supposing equal chances of day/night attacks was 9/15. The results were strongly biased and between 89 and 96% of attacks took place between 1600 and 0700 hours, the period of actual darkness extended for approximately 12 hours from 1830 hours.

The observations on feeding methods and the results of size preference experiments reported below prompted an experiment to measure the maximum extent to which *Cymatium* spp. can extend their probosci *in vivo*. The measurement of the probosci of dead tritons was difficult and deemed not to be relevant to the true amount of proboscis extension the live animal is capable of.

The results of the proboscis length experiment are shown in Fig. 2.1. The proboscis of *C. muricinum* measured on average 123% of the triton's shell length and up to 165% in adult and larger tritons. For this species the relationship between triton length (SL) and proboscis length (PL) could be described by the equation

Table 2.1. Location of attack of four species of *Cymatium* fed *ad libitum* on juvenile *T. gigas* (mean size 30 mm). Percentages are shown in brackets. See text for full details of methods used to calculate probability. G = maximum likelihood statistic, *** $p<0.001$, ns not significant. Where $n\leq25$ probability was calculated by binomial expansion (B).

	Location of attack		
	Byssal orifice	Valve gape	G
C. muricinum	12	67 (85%)	41.94***
C. aquatile	2	4 (67%)	B^{ns}
C. pileare	1	5 (83%)	B^{ns}
C. nicobaricum	2	10 (83%)	B^{ns}

Table 2.2. Number of attacks by four species of *Cymatium* fed *ad libitum* on juvenile *T. gigas* (30 mm mean shell length) recorded at night. "Night" represents a period from 1600 to 0700 hours. G = maximum likelihood statistic, *** $p<0.001$.

	Time of attack		
	n	"night"(%)	G
C. muricinum	322	304 (94)	181.98***
C. aquatile	102	98 (96)	65.89***
C. pileare	82	73 (89)	29.35***
C. nicobaricum	192	175 (91)	82.76***

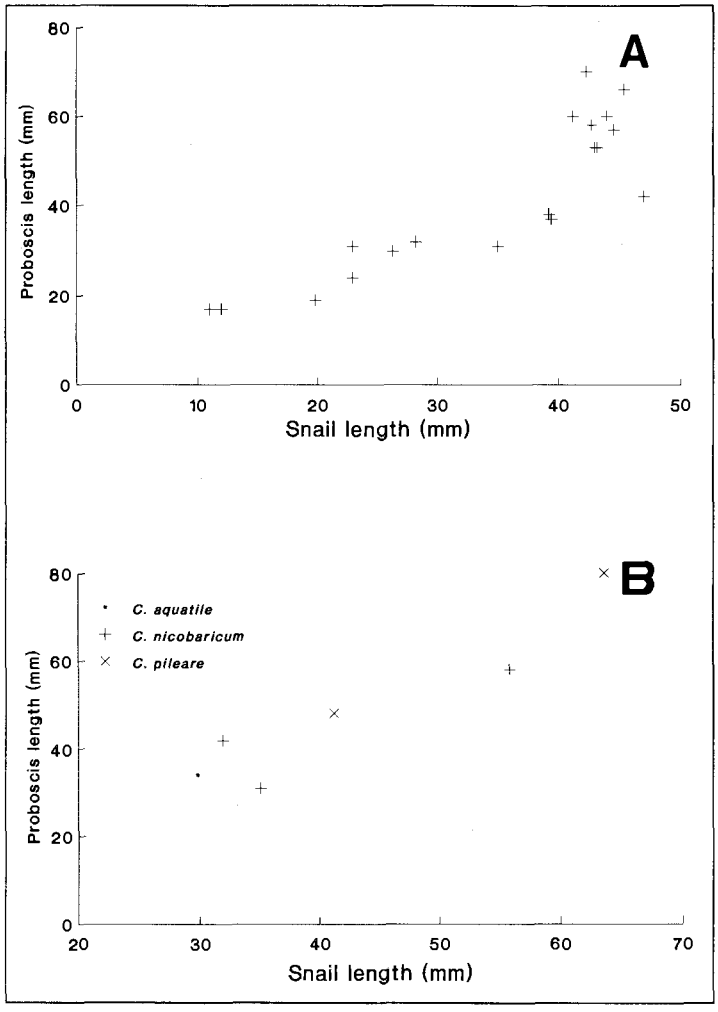

Fig. 2.1. Relationship between size of live ranellid and maximum extension of its proboscis under experimental conditions. A: *Cymatium muricinum*. B: *C. aquatile, C. nicobaricum* and *C. pileare*.

$$PL = 1.23 \times SL \quad (r^2 = 0.76) \qquad \textbf{...2.2)}$$

Fewer observations were made on the less common species of *Cymatium* but proboscis length also appeared to be in the region of 120% of shell length for the individuals tested (Fig. 2.1B).

It may not be strictly correct to describe the relationship between triton and proboscis length in linear form as the latter may be a function of triton tissue weight and therefore relate to shell length as a power function. There is slight evidence of this in Fig. 2.1A and if true, equation (2.2) would tend to overestimate the proboscis length of small tritons and underestimate that of large tritons.

Preference Experiments

The term "preference" is used here in a loose sense as meaning a bias in the diet of the predator to certain prey types (Murdoch 1969). None of the attacks by *Cymatium* spp. observed during the preference experiments were of the "parasitic" or slow type described above.

The results of the first preference experiment are shown in Table 2.3. The null hypothesis that consumed prey were evenly distributed between species is clearly rejected when the lumped data for each predator species is tested. The reason for the uneven distribution appears to be a bias towards the consumption of *T. gigas*, the larger size class in particular. *C. aquatile, C. muricinum* and *C. pileare* only consumed bivalves and the gastropod *Cerithium tesselatus* was not killed at all.

In the second preference experiment (Table 2.4) *C. nicobaricum* was observed to consume *Ce. tesselatus*. The data are too sparse for the calculation of the maximum likelihood statistic G but probability tests based on binomial expansion of the gastropod prey consumed versus the total bivalve prey show a strong preference of the two largest size classes of *C. nicobaricum* for gastropods ($p = 0.008$ and $p < 0.001$, respectively). No significant preference by the two smaller size classes of triton was found.

The results of the third experiment testing the preference of *C. muricinum* for *T. gigas* and *H. hippopus* are shown in Table 2.5. Offered prey were all byssally attached and all attacks were observed to take place between the valve gape. Overall, both small and large *C. muricinum* showed strong preference for *T. gigas* although there was some variation between individual tritons.

Table 2.3. Prey species preferences of two individuals each of *Cymatium aquatile*, *C. muricinum* and *C. pileare*. Prey consisted of juvenile *Tridacna gigas*, *Pinctada maculata* and *Cerithium tesselatus* (*Ct*) over a 10-week period. G = maximum likelihood statistic, *** p<0.001.

Species	Mean size	Prey species: *T. gigas* (25-40 mm)	*T. gigas* (15-20 mm)	*P. maculata* (40 mm)	*P. maculata* (20 mm)	Ct	G
C. aquatile	32.9	10	4	2	1	0	26.8***
C. aquatile	31.7	4	5	1	0	0	
C. muricinum	29.5	8	4	1	1	0	31.4***
C. muricinum	30.2	8	4	1	0	0	
C. pileare	45.3	8	5	3	2	0	23.5***
C. pileare	35.3	7	7	1	1	0	

Table 2.4. Numbers of three available prey species consumed by *Cymatium nicobaricum* over 18 days. *C. nicobaricum* were divided into four groups of four similarly sized snails.

Group	1	2	3	4
Cerithium tesselatus (20 mm)	12	14	7	1
Pinctada maculata (30 mm SL)	4	1	1	3
Tridacna gigas (30 mm SL)	2	3	6	0
Mean size of *C. nicobaricum*	35.4	32.0	29.0	14.4

Table 2.5. Quantities of prey consumed by two size classes of *Cymatium muricinum* presented with a choice of *Tridacna gigas* or *Hippopus hippopus* (40-50 mm shell length). G = maximum likelihood statistic, * 0.05>p>0.01, ** 0.01 > p > 0.001, *** p<0.001, ns not significant. Where n≤25 probability was calculated by binomial expansion (B).

Mean snail size	*T. gigas*	*H. hippopus*	G
42 mm	5	4	Bns
43 mm	8	1	B*
44 mm	9	0	B**
45 mm	7	1	Bns
Total (adult snails)	29	6	16.21***
17 mm	5	0	Bns
18 mm	2	3	Bns
20 mm	4	0	Bns
21 mm	9	1	B*
21 mm	4	1	Bns
22 mm	5	0	Bns
22 mm	8	0	B**
23 mm	9	0	B**
Total (juvenile snails)	46	5	37.61***

The results of the size preference experiment where three size classes of *T. gigas* were offered to *C. muricinum* are shown in Table 2.6. As the calculated expected frequencies are greater than 10 for the total consumption figures of both size classes of triton the maximum likelihood statistic G was calculated (Conahan 1970 in Sokal and Rohlf 1981). For both small and adult tritons the prey eaten were not evenly distributed between size groups, small clams were consumed less than the other two size classes ($p = 0.014$ and $p < 0.001$, respectively,

Table 2.6. Size preference of juvenile and adult *Cymatium muricinum* for three size ranges of juvenile *Tridacna gigas* over a 3-week period. G = maximum likelihood statistic of pooled results for each size range of snail, * 0.05>p>0.01, ** 0.01>p>0.001.

Mean snail size	Size class of *T. gigas* 10 mm	30 mm	50 mm	G
19.2	2	4	4	
19.9[a]	0	4	2	
20.3	2	3	2	
20.8	1	6	4	
Total (small snails)	5	17	12	6.84*
32.6	2	5	5	
35.1	1	6	8	
35.9	2	6	9	
37.1	2	3	6	
Total (big snails)	7	20	28	13.55**

[a]Snail died after 10 days.

based on binomial expansion). Small tritons appeared to consume most clams in the medium size class (30 mm SL), a trend which is clear in all the replicates. Most of the clams consumed by large tritons belonged to the large size class (50 mm SL), a trend visible in three of four replicates.

Time Required by C. muricinum *to Kill* T. gigas

Fig. 2.2 shows the relationship between clam size (measured as both shell length and estimated biomass) and time taken for recently settled *C. muricinum* to kill their prey. Small clams (<20 mm SL) are killed within 3 or 4 days while clams of around 80 mm SL may take more than a month to die. The data are sparse and no attempt at linear regression was made as the relationship can be expected to be a complex one. Major factors are probably the growth rate and size specific consumption rate of the tritons and the amount of tissue clams may lose or regenerate before death ensues.

The time required for adult *C. muricinum* to kill large juvenile *T. gigas* is shown in Fig. 2.3. The few clams available

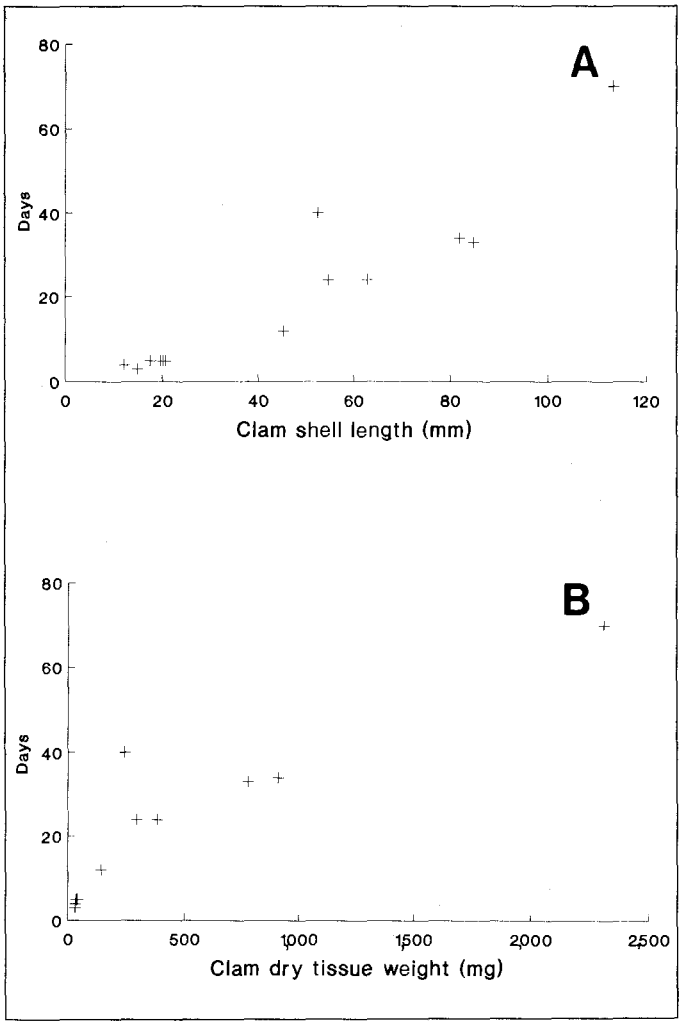

Fig. 2.2. The relationship between size of juvenile *Tridacna gigas* and time required to be killed by juvenile *Cymatium muricinum* (4-5 mm initial shell length) in aquaria. A: Size of *T. gigas* in terms of shell length. B: Size of *T. gigas* in terms of estimated dry weight biomass.

for this experiment were relatively old for their size and were deemed to have thick, heavy mantles. Tritons attacking the clams failed to penetrate the mantle with their probosci and fed on the soft tissues between valve and mantle. The results show an increase in survival time with increased size of clam. The 170 mm SL clam survived the 11-day duration of the experiment.

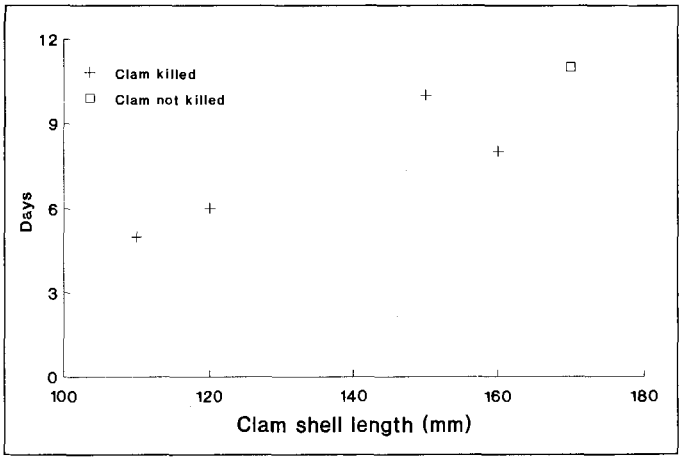

Fig. 2.3. Relationship between size of *Tridacna gigas* in terms of shell length and time required to be killed by adult *Cymatium muricinum* in aquaria.

2.4 Discussion

Feeding Methods

The observed feeding method of *Cymatium aquatile, C. muricinum, C. nicobaricum* and *C. pileare* in which the proboscis is inserted between the valves of the bivalve prey is broadly similar to that described for other ranellids such as *C. parthenopeum* (Laxton 1971), *Linatella caudata* (Muthiah et al. 1985; Morton 1990b), *C. muricinum* and *C. pileare* (Houbrick and Fretter 1969). Indeed these methods are very similar to those used by certain snails of the, evolutionary more advanced, Neogastropoda such as *Hemifusus ternatanus* (Morton 1986) and *Buccinum undatum* (Nielsen 1975). These two species use the inhalant siphon and cephalic tentacles in prey detection, as observed in this study for *Cymatium* spp. Nielsen (1975) also reported that *B. undatum* was able to feed with its proboscis partially trapped between the valves of its prey.

The species of *Cymatium* studied fed predominantly at night, in line with the findings of Houbrick and Fretter (1969) with the exception that starved individuals fed at any time of day on available prey, including carrion. Most attacks on *T. gigas* occurred between the valve gape rather than through the byssal orifice but this is probably due to the larger area of the former rather than any active preference exercised by the triton.

The feeding methods of *C. muricinum* are highly versatile and opportunistic. These methods range from the almost instant killing of prey, often larger than the triton itself, to parasitism of juvenile or adult giant clams. The rapid eversion of the triton's proboscis through the tissue barriers of mantle and internal organs and the emission of toxic saliva represents a formidable weapon that easily circumvents defences evolved by bivalves against boring and crushing predators (Vermeij 1978). It is possible that the acidic salivary secretions not only serve to immobilize the prey but also aid in digestion (Houbrick and Fretter 1969; Morton 1990b) or facilitate the penetration of the proboscis through tissue.

The predatory *Cymatium* do not appear to choose a feeding method. If the initial rapid attack fails, the triton still uses its proboscis to feed on the clam. Recently settled ranellids feed on tridacnids almost parasitically and may often be observed inside the mantle cavity or between shell and mantle of infested clams.

Three factors may determine whether these species of *Cymatium* may kill a tridacnid clam in an initial attack:

i. The relationship between triton size and clam size. The length of the triton's proboscis is related to the size of the triton and the distance from the byssal orifice or valve edge of the clams to the internal organs targeted during attacks is related to clam

size. Thus, in the absence of other factors, the ratio of triton proboscis length to distance of the clam's internal organs from the valve's periphery could determine the maximum size of clam killed. Using equations (2.1) and (2.2) derived for these parameters it can be estimated that an adult *C. muricinum* (35-45 mm SL) could theoretically kill up to 130-167 mm SL *T. gigas*. Occasionally, larger *Cymatium* are found in ocean-nurseries such as a 64 mm specimen of *C. pileare* found in this study. Other factors aside, this triton could possibly kill *T. gigas* up to 240 mm SL.

ii. The toughness or thickness of the clam mantle. Tritons were observed to fail to penetrate the mantle of certain clams. These clams were generally relatively old and appeared to have heavier, thicker mantles. Fast growing clams were relatively large but appeared to have thinner mantles than slow growing or adult clams. Thus increased mantle thickness would seem to increase the resistance of clams to the more destructive methods of *Cymatium* predation.

iii. The ability of clams to close their valves tightly and the sharpness of these. The tight closure of clam valves could prevent tritons penetrating the mantle with the proboscis. Tightly trapping the proboscis of an attacking triton could prevent feeding and even damage of the triton. These effects would be more pronounced if the valve edges were particularly sharp and close-fitting. This factor appears a likely explanation for the preference shown for *T. gigas* over *H. hippopus* by *C. muricinum* discussed below.

Prey Preference

The degree of differential feeding of predators on prey of different sizes or species is commonly characterized by passive and active components (Pennings 1990). The physical features of prey, predator and environment govern the passive components which are chiefly encounter rates and capture success probability. The role of active choice by the predator (i.e., the probability of an attack given an encounter) is a major question in the field of foraging ecology (Pennings 1990), but accumulating evidence suggests that many gastropods do make behavioral diet selections (Hughes 1986).

The results of the present prey preference experiments can be explained largely in terms of encounter rates and "capture" success. However *C. muricinum, C. aquatile* and *C. pileare* do appear to actively select bivalves and were never observed to attack gastropods (Table 2.3). *C. nicobaricum*, on the other hand, actively selected the gastropod *Cerithium tesselatus* over bivalve prey but was also observed to attack bivalves. These findings are in broad agreement with those of Houbrick and Fretter (1969) although these authors do not report *C. nicobaricum* feeding on any bivalves.

The prey encounter rates of *Cymatium* spp. in the preference experiments (and possibly in the field) may be determined by the ease with which different prey are detected by chemical or visual stimuli or by random encounters during foraging. In any case it seems reasonable to suppose that the biomass or size of prey plays a major role in the encounter of prey. The factors determining the success of attacks have been discussed in the previous subsection.

The order in which bivalves were preferred by *C. aquatile, C. muricinum* and *C. pileare* was: large *T. gigas* > small *T. gigas* > large *P. maculata* > small *P. maculata*. Encounter rates alone cannot explain this ratio of preferences as tritons preferred large and small *T. gigas* to *P. maculata* of either size. This discrepancy may be explained by the narrower valve gape of the

pearl oysters and the capacity of bivalves of this group to retract mantle and vital organs a considerable distance from the valve edge (Yonge 1953 in Vermeij 1978). Both these features could greatly reduce the probability of successful attacks on the oysters.

Large *C. nicobaricum* clearly prefer the gastropod *Ce. tesselatus* to either *T. gigas* or *P. maculata* (Table 2.4) while no such clear preference may be observed for the smaller *C. nicobaricum*. It is possible that prey preferences vary with size or age of gastropod predator (Broom 1983) but in this case the explanation most likely lies in the constant size of prey offered to all size groups of predator. The specimens of *Ce. tesselatus* (20 mm) used were actually larger than the *C. nicobaricum* in the smallest size group (14.4 mm) which may have seriously reduced the chances of capture success.

The strong preference shown by *C. muricinum* for *T. gigas* over *H. hippopus* is consistent with the results of Perron et al. (1985). However, more variation between individual tritons was observed in the current experiment (Table 2.5) which was of longer duration and employed smaller clams than those used by Perron et al. (1985). The greater resistance of *H. hippopus* to attack when compared with *T. gigas*, was attributed to the tightly closing byssal gape of the former species (Perron et al. 1985). This does not explain the results obtained here as no attacks took place through the byssal gape on either species.

Another distinguishing feature of the shell morphology of *H. hippopus* is the precise fit of the interdigitating valve margins which are sharp and angled to face each other (Yonge 1980). The internal anatomy of *H. hippopus* has also been shown to differ from that of *Tridacna* spp. having a lower visceral mass and anteriorly displaced pericardium (Yonge 1980; Shelley and Reid 1988). Both these differences could be expected to reduce the probability of successful *Cymatium* attacks on *H. hippopus* as the proboscis of the predator could be damaged by the sharp valves of the clam and the internal organs of *H. hippopus* may be more inaccessible than those of similarly sized species of *Tridacna*.

The results of the size preference experiments can also be explained in terms of passive components of prey selection rather than active selection. Encounter rates by tritons should increase with increased clam size thus larger clams would be more often attacked. The success of the attack would depend on the relative sizes of clam and triton. Large tritons (mean size 35 mm) in the size preference experiments consumed clams preferentially in inverse order of size: large > medium > small. This size of triton should have no difficulty in handling 50 mm SL *T. gigas* according to equations (2.1) and (2.2). This is not the case with the smaller tritons, which consumed less large clams than medium sized ones. Applying the same criteria, these tritons (some of which started the experiment at a size of less than 16 mm) could be expected to have difficulty killing clams of 41 to 57 mm SL although the calculated proboscis lengths would be just sufficient to reach the center of the clams.

Care has to be taken in the interpretation of results from these preference experiments. Firstly, most experiments were performed with a restricted number of test organisms and all in laboratory conditions. Secondly, although all predators were starved before the experiments, the effects of "ingestive conditioning" (Murdoch 1969; Hughes 1986) of the animals in the wild may introduce an unwanted variable in the experimental results. Predators were collected from ocean-nurseries containing *T. gigas*, seasonally variable numbers of fouling oysters, gastropods and a small number of *H. hippopus*. It is possible that the predators in these experiments were more likely to respond to stimuli from a prey species previously consumed in abundance. Furthermore, a "functional response" of gastropods exposed to an abundance of a certain prey type

may be to "learn" to handle it efficiently (Jory et al. 1984). Provided the results are used in the context of tridacnid ocean-nurseries this second factor may not be critical.

Time Required by C. muricinum *to Kill* T. gigas

The factors determining whether a ranellid can kill *T. gigas* prey rapidly are discussed above. If the bivalve prey is not killed instantly the triton usually feeds on the clam's tissues regardless. There is apparently no size limit to the tridacnids which may be fed on in this way but the relative sizes of triton and prey and the duration of feeding appear to determine whether a clam may survive the attack. Recently settled *C. muricinum* may feed on juvenile clams for more than 2 months before causing death.

Perron et al. (1985) suggested that *C. muricinum* was capable of killing *T. gigas* exceeding 170 mm SL and that adult tritons could kill 100 mm SL *T. gigas* in 4 to 5 days. These results are consistent with the current work. The effects of attacks through the byssal orifice were not examined in this study but are probably similar to attacks through the valve gape under laboratory conditions.

Implications for the Ocean-Nursery Culture of Tridacnid Clams

Encounter rates and physical features of predator and prey seem to be the major factors determining the impact on tridacnid clams of predation by *C. aquatile, C. muricinum, C. pileare* and, in the absence of other gastropods, *C. nicobaricum. T. gigas* appears particularly vulnerable to the predation methods used by these ranellids whereas *H. hippopus* is relatively resistant. This result is reflected in the lower predator-related mortalities of this species in ocean-nurseries (Heslinga et al. 1990; Govan et al. 1993).

Owing to the use of chemical stimuli by *Cymatium* spp. in the detection of prey it would appear advisable to remove extraneous potential prey items such as fouling pearl oysters from ocean-nurseries in order to avoid increased production of attractant chemical stimuli.

The maximum size of clam that a ranellid can kill is proportional to the size of triton. As reported by Perron et al. (1985), *T. gigas* over 170 mm SL are not necessarily immune to attack by ranellids. The minimum size at which a clam farmer may deem his clams to be resistant to predation by *Cymatium* spp. will depend on the species of clam, but also on features such as the mantle thickness (possibly related to age) and the substrate upon which the clams are placed.

Juvenile tritons feeding on larger clams may do so continuously and from inside the clam. The only indication of this type of attack may be a loss in clam condition prior to death. Large tritons feeding on large clams are likely to do so nocturnally as during daylight these tritons would provide tempting targets for other molluscivores such as fish. This would explain the lack of reports of *Cymatium* spp. attacking adult clams as most dives on ocean-nurseries are carried out in daytime.

The type of substrate on which the clams are placed may play a crucial role in providing a refuge from which tritons may attack clams through the byssal orifice (c.f., Perron et al. 1985) and escape detection by the clam farmers or other predators. The use of gravel or rubble substrates would appear to be undesirable in this respect. Cement substrates are used at the ICLARM CAC to avoid this problem (Govan 1992a).

The capacity of these tritons to immobilize or weaken clams much larger than themselves may benefit other scavenging organisms in ocean-nurseries and grow-out areas which consume clam tissue but are not capable of killing larger tridacnids.

Stocks of clams must be checked frequently by clam farmers and tritons removed. Attempts to prevent access of larger and more destructive tritons to clams such as the use of trestle legs on cages would seem appropriate (Govan et al. 1993).

This work, that of Perron et al. (1985) and particularly that of Govan et al. (1993) suggests that *Hippopus hippopus* and perhaps other tridacnid species that are also relatively fast growing initially may have better chances of reaching escape size from ranellid predation than *T. gigas*. This would explain the higher survival of *T. derasa* and *H. hippopus* than for *T. gigas* generally observed in ocean-nurseries around the region (Batibasaga, Hambrey, Heslinga, pers. comms.).

Evolutionary Adaptations of Bivalves to Ranellid Predation

It is interesting to speculate what adaptations, if any, coral reef bivalves have evolved to defend themselves against these highly persistent and voracious predators. Vermeij (1978) indicated a number of adaptations of tropical bivalves that confer greater resistance to drilling and crushing predators, in particular the development of sturdy valves.

Adaptations that may relate to the type of predation used by ranellids and described here were not mentioned by Vermeij (1978) in his comprehensive review. The zipper-like hinge of *Hippopus hippopus* may be such an adaptation as suggested by Perron et al. (1985). The directional jet of water ejected through the exhalent siphon by clams reported by Stasek (1965) to deter grazing fish has occasionally been observed to dislodge predatory ranellids during the course of this work. The scutes of certain adult and all juvenile tridacnids, the lamellae and extended lips of the Pteriidae and Pinnidae and the shell projections of bivalves such as the Spondylidae may serve to keep ranellids further away from the bivalve's vital organs. The capacity of some tropical pteriomorph bivalves to retract the mantle a considerable distance from the valve edge (Yonge (1953), in Vermeij (1978)) would also seem to be a good defence against ranellid predation. Investment in the formation of such shell structures at an early stage in the life of the bivalve would make sense in these terms. Perhaps the evolution of these structures in turn explains the prodigious development of the ranellid proboscis.

CHAPTER 3

Growth Rates and Consumption of Prey by *Cymatium* spp.

3.1 Introduction

Ranellid gastropods are often abundant predators in tridacnid ocean-nurseries (Govan 1994). In some cases most of the predatory ranellids are recently settled juveniles while in other cases the bulk of tritons are mature or adult (Heslinga et al. 1990; Govan et al. 1993).

Perron et al. (1985) reported that potential destructiveness increases rapidly with size in the case of *Cymatium muricinum* attacking *Tridacna gigas*, measured in terms of time taken for various sizes of triton to kill 100 mm SL clams. No quantitative data have been published regarding the consumption rates of ranellids with the exception of limited work on adult *Linatella caudata* by Morton (1990b) and Thangavelu and Muthiah (1983).

The relative impact of different sizes of *Cymatium* spp. in terms of clams killed or consumed is of great interest to clam farmers as potential methods of predator control vary according to the size of ranellid targeted (Govan et al. 1993).

This chapter details work carried out to estimate growth rates and consumption of *C. muricinum, C. aquatile, C. pileare* and to a lesser extent *C. nicobaricum*. In subsequent chapters, the calculated rates will be applied to field data obtained from Solomon Island ocean-nurseries in order to obtain estimates of the impact of these species on clam farming and insights into factors affecting their recruitment in ocean-nurseries.

Gastropod Growth

Energy used for somatic growth is that remaining after expenditure on metabolism, secretion, excretion and reproduction. Metabolism accounts for most of the energy absorbed in gastropods and thus the amount of energy available for growth and reproduction is largely determined by rates of ingestion and respiration which in turn are functions of body size, food supply and temperature (Hughes 1986).

Growth in gastropods is most easy to measure as a linear increment of the shell, converted to somatic growth by using the relationship between tissue weight and shell size. This approach assumes that snails keep the same shape throughout life and that body weight is directly proportional to internal volume of the shell and hence the cube of any of its linear dimensions (isometric growth). This assumption is rarely met (Hughes 1986) and regressions of body weight

on shell size giving an allometric relationship have to be calculated for the species in question in the form of:

$$W = aL^b$$

where W and L are weight and length, respectively, "a" and "b" are constants (for given units of L and W), "b" assuming the value "3" in the case of isometric growth.

Even then, shell size may not be an accurate index of biomass or even shell weight (Palmer 1981) and care must be taken when trying to interpret shell growth in terms of tissue growth over short time intervals (Hughes 1986).

In this context Laxton (1970a, 1970b) found that the growth of three species of New Zealand Ranellidae (*Cabestana spengleri, Cymatium parthenopeum* and *Ranella australasia*) was discontinuous consisting of periods of rapid growth of up to half a whorl after which a flared lip is produced. Growth may proceed after the formation of this lip (or varix) or it may cease for an undefined dormant period followed by another period of growth. This episodic pattern of shell growth is characteristic of certain members of Ranellidae, Bursidae, Cassidae and Muricidae (Laxton 1970a, 1970b; Linsley and Javidpour 1980). In the case of ranellids studied by Laxton (1970a), shell growth was found to be independent of tissue growth which may proceed at a more steady rate sometimes greatly exceeded by shell growth.

Shell growth in terms of length of *Cymatium* spp. was of prime interest in the present study as field data could only be obtained in this format. Moreover, weighing test organisms in the growth studies was deemed too complicated and disruptive to the animals (see Section 3.2 and Wilbur and Owen 1964). In an effort to supplement the linear measurements obtained, allometric curves were constructed for each of the study species.

Shell deposition involves the production of a largely proteinaceous, organic matrix upon which calcium carbonate crystals are deposited (Wilbur 1964; Barnes 1980; Hughes 1986). The tissue responsible for forming the shell is the mantle, thus the rate of increase of shell area is a function of mantle area whereas the rate of increase in thickness and weight is a function of the secretion rates of the organic matrix and calcium carbonate (Wilbur 1964). Secretion of the organic matrix constitutes the major organic cost of shell secretion and is a significant portion of the energy budget (Hughes 1986).

The first shell or protoconch is laid down by the larva and consists of the first whorls at the apex of the shell, the remaining whorls or teleoconch are laid down by the mantle edges of the growing snail (Barnes 1980). The gastropod shell consists of a number of layers of calcium carbonate in various crystal arrangements and in some snails, such as the Ranellidae, an outer periostracum composed of a quinone-tanned horny protein material called conchiolin (Wilbur 1964; Laxton 1970a; Barnes 1980).

Growth in most animals decelerates as they extend beyond a certain size, usually reached as early juveniles. Growth can be described for most of an animal's life as an asymptotic curve such as that described by the von Bertalanffy Growth Function (von Bertalanffy 1957; Hughes 1986). This implies that the proportion of absorbed energy used for tissue production (production efficiency) changes with body size. Production efficiency is equivalent to growth efficiency (proportion of ingested energy used for somatic growth) up until the onset of sexual maturity after which an increasing fraction of production is channeled to reproduction (Hughes 1986). Production efficiencies of gastropods are widely reported to be highest during the larval or younger stages (Edwards and Huebner 1977; Bayne and Scullard 1978; Hughes 1986; Morton 1986, 1990a).

The von Bertalanffy Growth Function (VBGF) is the most widely used model to describe growth patterns in fisheries ecology (Wootton 1990) and has been found to be generally applicable to bivalve growth as well (Vakily 1992). The VBGF has been used to describe growth in gastropods (Broom 1982; Hughes 1986) and for *C. muricinum* in particular (Perron et al. 1985). These last authors did not check, however, that the basic assumptions of the VBGF applied to gastropods.

By assuming that the rate of energy absorption obeys a "surface law" and that metabolic rate obeys a "volume law" (i.e., proportional to the square and cube of a linear dimension of the body, respectively) von Bertalanffy (1957) derived an equation describing an asymptotic curve (Hughes 1986). The integrated form of this equation for length is commonly given as presented by Beverton and Holt (1957):

$$L_t = L_\infty\left(1 - e^{-K(t-t_0)}\right) \qquad \text{...3.2)}$$

where

- L_∞ is the asymptotic length, i.e., the mean length the animals would reach if they grew indefinitely;
- K is a growth coefficient with dimension time^{-1};
- t_0 is a location parameter indicating where the growth curve crosses the time axis; and
- L_t is the predicted length at age t.

In fisheries ecology it has been found that the assumptions implicit in equation (3.2) of growth being limited by an isometrically growing surface and weight being proportional to the cube of length are not realistic (Gaschütz et al. 1980; Pauly 1981 in Soriano et al. 1990). In the case of gastropods Hughes (1986) reports considerable departures from the surface law for ingestion rates, and metabolic rates falling between the expectations of the volume and surface laws. Therefore it seems more appropriate to use the "generalized" form of the VBGF in which the above assumptions are relaxed (Gaschütz et al. 1980). This physiologically more correct model (equation 3.3) introduces the gill surface factor "D" (Pauly 1979 in Vakily 1992) which allows departures from the surface and volume laws mentioned above to be accounted for. In this case D = b - a where "a" is the exponent of the relationship between length and the surface and "b" is the exponent of the the same relationship with weight or volume (Wootton 1990).

$$L_t = L_\infty\left(1 - e^{-KD(t-t_0)}\right)^{\frac{1}{D}} \qquad \text{...3.3)}$$

Other useful modifications of the VBGF include models that account for seasonal growth oscillations (Gaschütz et al. 1980) and animals that present two distinct growth phases (Soriano et al. 1990).

Gastropod Consumption Rates

Consumption rates of prey by predatory gastropods can be expected to depend on the successful encounter and attack of the prey (see Section 2.4) and the ingestion rate. If appropriate prey are super-abundant (as is the case with *C. muricinum* and *T. gigas* in ocean-nursery cages), then ingestion rate may be relatively more important along with environmental factors affecting metabolic rate such as temperature (Hughes 1986). Ingestion rate is largely

determined by mechanical properties of the feeding apparatus (Hughes 1986), particularly by the area of the absorptive surfaces. Therefore, if growth were isometric, ingestion rate would be expected to be proportional to (body weight)$^{2/3}$ (or (length)^2). In many gastropods there are considerable variations from this relationship (Hughes 1986).

Laboratory feeding estimates usually lead to estimates of gross food conversion efficiency (K1) which are obtained for small intervals from (Pauly 1986):

$$K_1 = \text{growth increment / food ingested} \qquad \text{...3.4)}$$

Usually K_1 declines with body size and a standard procedure is to plot empirical values of K_1 against the mean weights corresponding to each growth increment (Pauly 1986; Silvert and Pauly 1987):

$$K_1 = cW^{\alpha} \qquad \text{...3.5)}$$

where W is the body weight and "c" and "α" are empirical constants. Pauly (1986) points out that these empirical constants have no biological meaning and that this model implies that K_1 is always > 0 even though it is known that fish cannot grow beyond certain sizes. Pauly (1986) proposed a new model that is compatible with the VBGF (Silvert and Pauly 1987) and has the form:

$$K_1 = 1 - \left(W/W_{\infty}\right)^{\beta} \qquad \text{...3.6)}$$

where W_{∞} is the weight at which $K_1 = 0$ and β is an empirical constant.

The recently proposed model (3.6) has been applied to fish (c.f., Pauly and Palomares 1987) but does not appear to have been applied to other animals. Published studies of gastropod consumption frequently express this in terms of ration, i.e., food ingested as a percentage of body weight per day (Edwards and Huebner 1977; Bayne and Scullard 1978; Ansell 1982; Hughes 1986; Morton 1986, 1990a, 1990b). Broom (1982) used the power function of equation (3.5) to relate consumption to body weight and Thangavelu and Muthiah (1983) expressed consumption of *Linatella caudata* in terms of numbers of oysters per day.

3.2 Methods

Allometric curves for the length-weight relationships of *C. aquatile, C. muricinum, C. pileare* and *C. nicobaricum* were constructed based on tritons available in the ocean-nursery at ICLARM CAC. For each triton the following parameters were recorded: shell length, growth stage, number of varices, state of periostracum, total blotted weight (Morton 1990a) and dry tissue weight.

Dry weights were obtained using a microwave oven set at low power. Samples were dried until a constant weight was attained, usually around 4 hours. This drying technique was observed to provide similar results to those obtained using conventional drying ovens (pers. obs. and P. Munro, pers. comm.). Electric power was only available 16 hours a day which combined with the high ambient humidity precluded the use of slower, electric ovens.

During laboratory experiments involving the repeated measurement of ranellids the protoconchs of tritons were occasionally damaged by the Vernier calipers, causing reductions in measured length, as reported by Morton (1986) in the case of similar studies on *Hemifusus*

tuba. The destruction of protoconchs in the present work was accounted for by correcting length measurements where necessary by adding the known size of emergent protoconch for the appropriate species. Protoconchs were removed from dead juvenile tritons of all four species and measured.

Specimens of tritons for growth and consumption studies were collected from ocean-nurseries at the smallest possible sizes (4-20 mm) and individually placed inside one of 20 different flow-through compartments in a 40-l aquarium as soon as possible. The compartments had perforated bases and were designed to maximize through water flow and minimize any mixing of water between compartments. Compartments measured 5.5 x 9.5 x 17 cm deep and the aquarium measured 29 x 70 x 20 cm deep. The water flow through the aquarium was maintained as high as possible (10-12.5 $l \cdot min^{-1}$).

The tritons were provided with their preferred prey species and size (c.f., Chapter 2), i.e., juvenile *T. gigas*. Unlike *Polinices duplicatus* (Edwards and Huebner 1977), ranellids were observed to consume prey entirely but care was still taken that clams were of a size that tritons could consume before significant amounts of tissue were lost due to putrefaction. This was generally 30 mm shell length (SL) but very small tritons received smaller clams.

The dimensions of all clams consumed were measured 5 days per week along with the location and time of day of the attack if observed. This allowed the determination of wet and dry tissue weights based on relationships between length, volume and tissue weight described in Appendix 2. Water temperature was also measured and varied between 28 and 31°C, equivalent to the water temperature in the ocean-nursery.

It was found that *C. muricinum* which were handled and measured three or more times per week in aquaria exhibited reduced growth and shell thickening so experimental tritons were handled as little as possible. Consequently weight could not be ascertained. Tritons were measured weekly at the same time of day and the stage of varical formation was also recorded, i.e., between varices, varix forming or varix formed.

Statistical Analysis and Model Fitting

All data acquired were entered into computer databases using the program DataEase running on MS-DOS based computers. Data were sorted as required and exported to a spreadsheet program (Supercalc5) for graphing, manipulation and basic statistical analysis. Data were exported from the spreadsheet in ASCII format for analysis by other programs.

Parameters of the allometric relation (equation 3.1) are commonly derived by linearizing the variables through logarithmic transformation and using linear regression (Ricker 1973, 1979; Sparre et al. 1989; Prein 1990; Hopkins 1992). This was the approach used here and the linearized equation takes the form:

$$\ln W = \ln a + b \ln L \qquad \textbf{...3.7)}$$

where the parameters are those from equation (3.1) and natural logarithms were used (ln). This same procedure was used when estimating the parameters of gross conversion efficiency (equation 3.5) and other power functions. The log transformation introduces a systematic bias into the calculations when using the relationship for conversions. This bias can be eliminated by multiplying the predicted values by a correction factor (F) obtained from:

$$F = \exp^{(SEE/2)} \qquad \textbf{...3.8)}$$

where "SEE" is the standard error of the estimate (Sprugel 1983).

The appropriate type of linear regression to be used in the case of equation (3.7), and indeed many regression analyses in biology have been the subject of some debate (Ricker 1973, 1979; Laws and Archie 1981; Sokal and Rohlf 1981; Prein 1990). It is worth summarizing here the assumptions of the main regression models (based on Ricker 1973, 1979 and Sokal and Rohlf 1981) to better justify the models used in this work.

Model I or predictive regression is the more commonly used and available in software packages. This is often the most suitable in controlled experimental situations (Sokal and Rohlf 1981) but is inappropriate in many biological regression situations (Ricker 1973; Laws and Archie 1981; Sokal and Rohlf 1981). The major assumptions of this model are: i) the independent variable X is measured without error or is under the control of the investigator, ii) the dependent variables Y for any given X are independently and normally distributed, iii) the samples along the regression line are homoscedastic, i.e, the variance around the regression line is constant and independent of the magnitude of X or Y.

Model II or functional regressions are appropriate where the two variables are distributed according to the bivariate normal distribution, with or without measurement error, where regression parameters are required rather than prediction or where the distribution of the variates is non-normal and open-ended (Ricker 1973; Sokal and Rohlf 1981). The most accurate estimate of the functional regression is given by a geometric mean (GM) regression provided that variability is mainly inherent in the material and in certain other cases (Ricker 1973). Ricker (1973) recommends the use of GM regression for a number of common regression situations in fisheries biology including allometric equations (length:weight and other morphometric analyses), estimation of routine metabolic rates and estimates of fish catchability.

The slope of the GM regression can be calculated by dividing the slope of the predictive regression by the correlation coefficient of the relationship (r) and the intercept can be calculated by substitution in the regression equation using the calculated slope and the mean values of X and Y (Ricker 1973; Sokal and Rohlf 1981; Sparre et al. 1989). Ordinary symmetrical confidence limits for the slope were calculated as recommended by Ricker (1973) and Sokal and Rohlf (1981) as these represent the most satisfactory approximation to the true values and will rarely lead to incorrect conclusions (Ricker 1973).

The GM regression was deemed appropriate for calculating allometric curves and consumption rates and unless otherwise stated is the model used throughout the chapter.

Growth data were fitted to the special and generalized VBGF of equations (3.2) and (3.3) and the biphasic growth models of Soriano et al.(1990) using a nonlinear fitting routine based on the Gauss-Newton method (kindly provided by D. Pauly of ICLARM). The constant "D" of equation (3.3) was estimated using equation (3.9) from Gaschütz et al. (1980) although the assumptions implicit in this equation do not necessarily apply to gastropods.

$$D = 3(1 - (0.6742 + 0.03574 \log_{10} W_{max})) \qquad \textbf{...3.9)}$$

W_{max} is the maximum weight recorded for the organisms of a given stock in grams.

The time/shell length datasets obtained for individuals of each species were submitted to analysis to obtain estimates of the growth parameters of the two models of the von Bertalanffy growth function following similar steps to those used by Vakily (1992). A total of 61 datasets were available of which 21 were excluded as they did not permit analysis with the nonlinear fitting routine largely owing to insufficient number of data points or stagnant growth in the case

of *C. nicobaricum*. Computed growth parameters were checked and omitted if standard errors (SE) of L_∞ or K were greater than 10 or 20%, respectively. This eliminated parameters which were invariably outside the range of expected values for L_∞ and most analyses with high residual sum of squares (rss). These steps reduced the original datasets to nineteen which fitted either or both VBGF models, ten of which belonged to *C. muricinum*.

The age of tritons was not known therefore the first point in each data set was assigned the value 0 (the start of the experiment) and subsequent data points in the set were assigned time values related to that start point. As the parameter t_0 does not influence the shape of the growth curve, it was not necessary for the comparison of growth parameters (Vakily 1992) and was omitted.

The growth performance index ϕ' (Pauly 1991) was calculated for each species where possible to facilitate comparison of the growth performance between species. The parameter ϕ' is derived from values of L_∞ and K of the VBGF using equation (3.10):

$$\phi' = \log_{10} K + 2\log_{10} L_\infty \qquad \text{...3.10)}$$

3.3 Results

Length/Weight Relationship

Tritons collected for the analysis of length/weight relationships were generally larger than 11 mm in length owing to a scarcity of smaller tritons during the collection period. Insufficient numbers of *C. nicobaricum* were collected for analysis. The parameters of the allometric equation (3.1) calculated for the remaining three species are shown in Table 3.1 for both total live weight and dry tissue weight.

Table 3.1. The relationship between length (mm) and weight (mg) for three ranellid gastropods of the genus *Cymatium* described by the function: Weight = a(Length)^b. Also shown is the 95% confidence interval (c.i.) for the parameter "b" and the correlation coefficient of the relationship.

Species	a	b	c.i.	n	r^2
Dry flesh weight (mg)					
C. muricinum	0.0035	3.095	±0.245	58	0.912
before 1st varix	0.0002	4.108	±0.524	22	0.925
after 1st varix	0.0069	2.900	±0.619	32	0.672
C. aquatile	0.0001	3.791	±0.708	17	0.885
C. pileare	0.0005	3.515	±0.519	28	0.866
Total wet weight (mg)					
C. muricinum	0.1032	2.937	±0.097	79	0.979
before 1st varix	0.0903	2.988	±0.170	39	0.971
after 1st varix	0.0851	3.009	±0.335	40	0.885
C. aquatile	0.0321	3.217	±0.137	21	0.992
C. pileare	0.0527	3.065	±0.105	41	0.989

The relationship between length and total wet weight in all three species follows the volume law in that the weight is approximately equal to length cubed (b = 3). As expected (c.f., Morton 1990a) in the case of dry tissue weights the correlations were slightly poorer resulting in larger confidence intervals so that although generally b > 3 this was not statistically significant. The size of the confidence interval was related to the number of tritons included in the analysis and thus *C. muricinum* has the smallest confidence interval and a value of "b" closest to 3.

The larger number of *C. muricinum* collected enabled a closer examination of the length/weight relationship before the formation of the first varix and after this stage. Comparison of the exponents for these two growth stages is possible owing to the use of functional regression and shows that the exponent of tritons in the first growth stage is significantly higher than that of tritons in the later stage of growth. The reason for this appears to be that smaller tritons have relatively little tissue for their shell size, particularly those under 17 mm (Figs. 3.1 and 3.2). The fact that this phenomenon is not manifest in the case of total wet weight may be accounted for by the higher specific gravity of shell material than tissue (Hughes 1986) thus the extra shell weight compensates for the relative lack of tissue. The calculated relationships are only strictly valid for tritons larger than 11 mm in length.

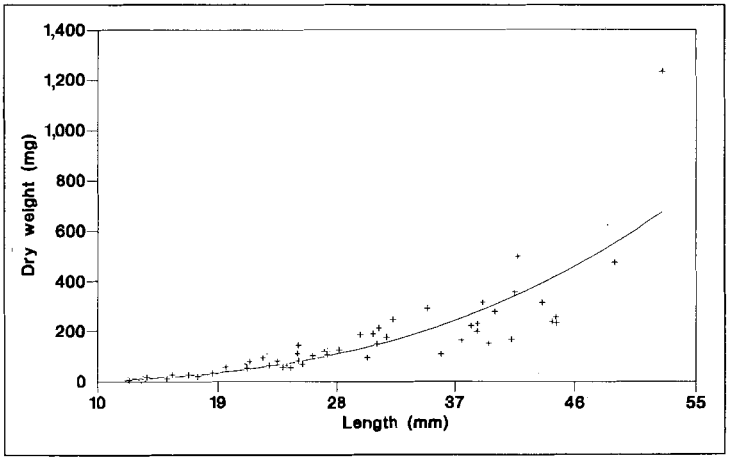

Fig. 3.1. Allometric curve of the relationship between length of specimens of *Cymatium muricinum* and their dry tissue weight.

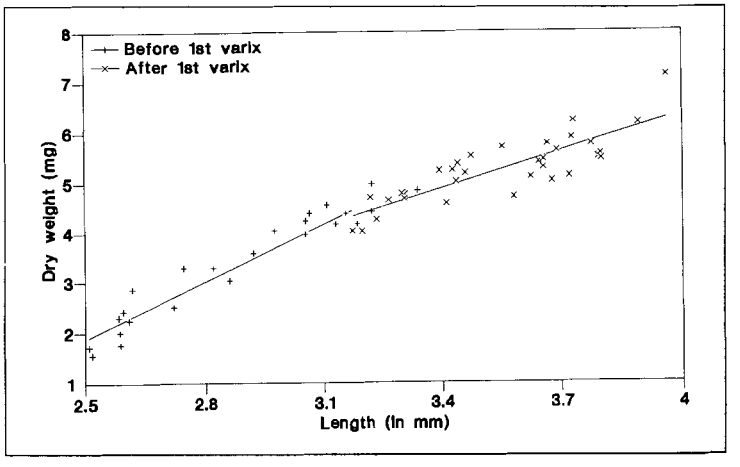

Fig. 3.2. Relationship between length of specimens of *Cymatium muricinum* and their dry tissue weight. The double log plot shows the different relationship for young tritons (without a varix) and older snails (after the formation of the first varix).

Growth of Cymatium *spp.*

C. muricinum was the only triton collected in abundance and thus more growth curves were obtained for this species (Figs. 3.3A, 3.3B, 3.3C, 3.3D). Thirteen recently settled individuals (< 5 mm) of *C. muricinum* and one of *C. pileare* were available and virtually complete growth curves were obtained for these (Figs. 3.3 and 3.5). Only larger individuals of *C. aquatile* were available (> 10 mm SL) as shown in Fig. 3.4. Tridacnids do not constitute the preferred diet of *C. nicobaricum* and thus most tritons of this species did not grow, those that did are shown in Fig. 3.6. The sex of individual specimens could not be determined and was not recorded.

Shell growth in the four species of *Cymatium* studied followed the same general pattern. At the onset of growth the periostracum, composed of a thin layer of organic material covered on the external surface by pronounced "hairs", is secreted starting from the lip

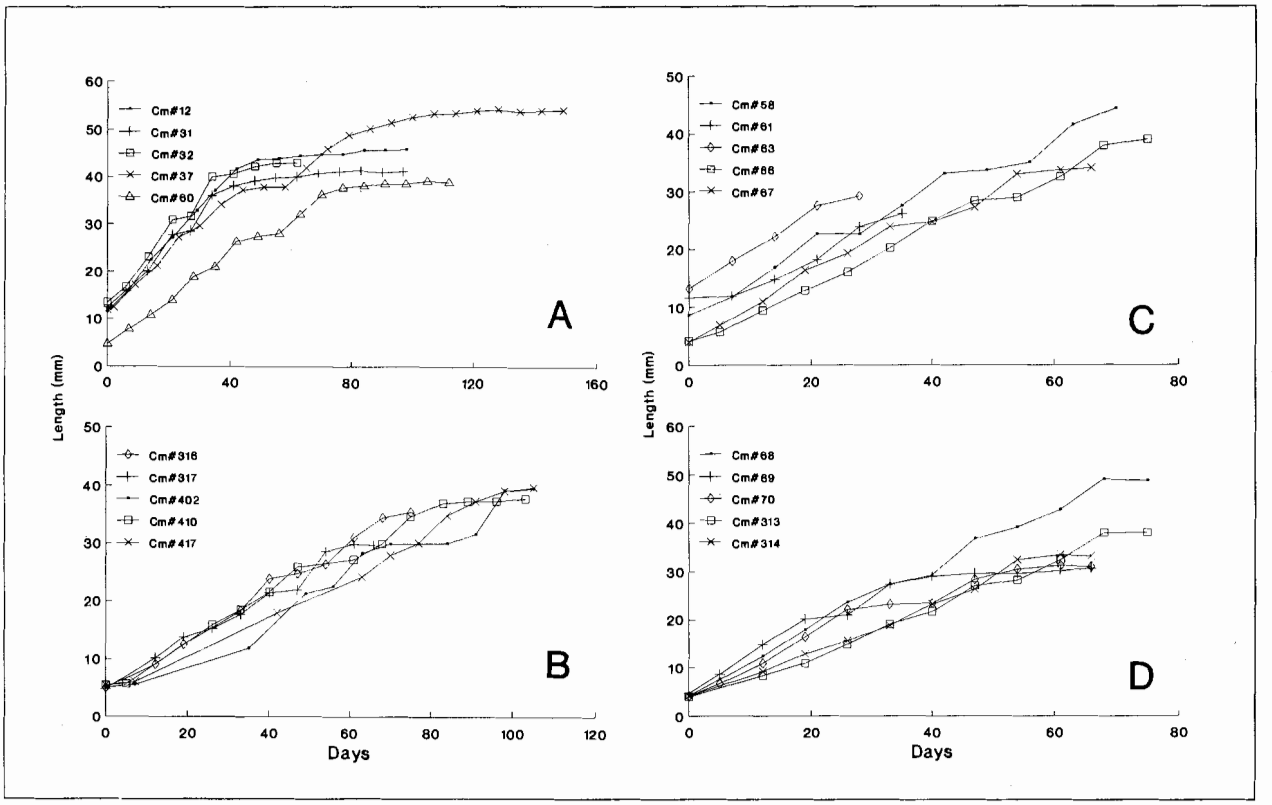

Fig. 3.3. Growth of individual specimens of *Cymatium muricinum* fed *ad libitum* on juvenile *Tridacna gigas* in aquaria. Note the rapid initial growth and pauses during varix formation.

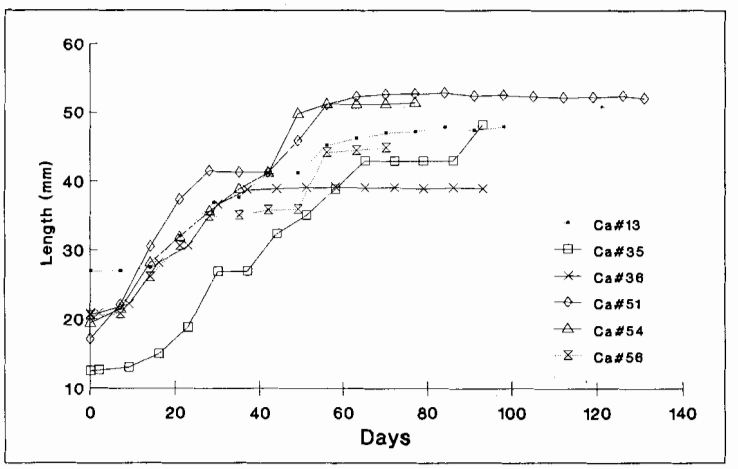

Fig. 3.4. Growth of individual specimens of *Cymatium aquatile* fed *ad libitum* on juvenile *Tridacna gigas* in aquaria. Note the rapid initial growth and pauses during varix formation.

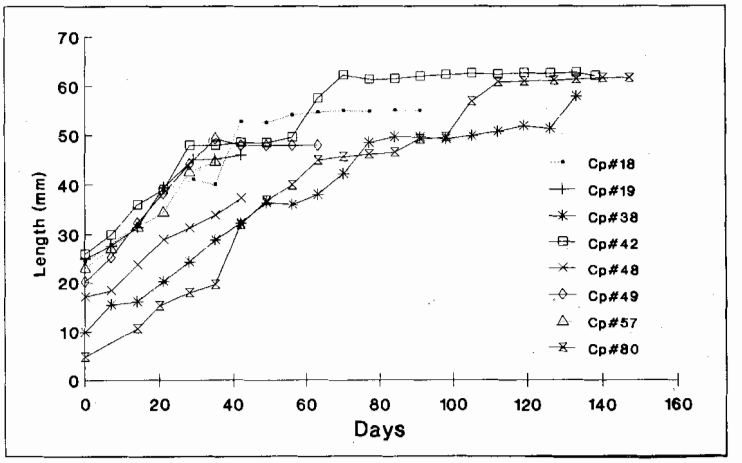

Fig. 3.5. Growth of individual specimens of *Cymatium pileare* fed *ad libitum* on juvenile *Tridacna gigas* in aquaria. Note the rapid initial growth and pauses during varix formation.

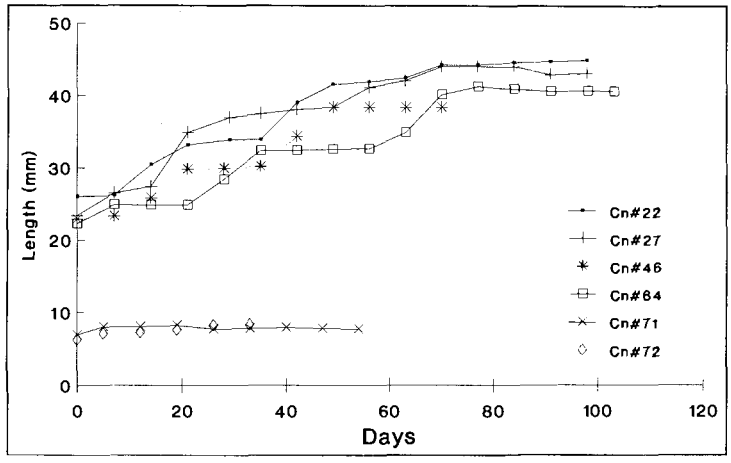

Fig. 3.6. Growth of individual specimens of *Cymatium nicobaricum* fed *ad libitum* on juvenile *Tridacna gigas* in aquaria. Note poor growth of some individuals owing to low food consumption.

of the protoconch (Plates IV and VI). The periostracum forms helical whorls which, in the case of rapid growth, remain flexible and fragile until calcified. Calcification occurs on the inner surface of the periostracum but is only noticeable at first in the case of slow growing tritons.

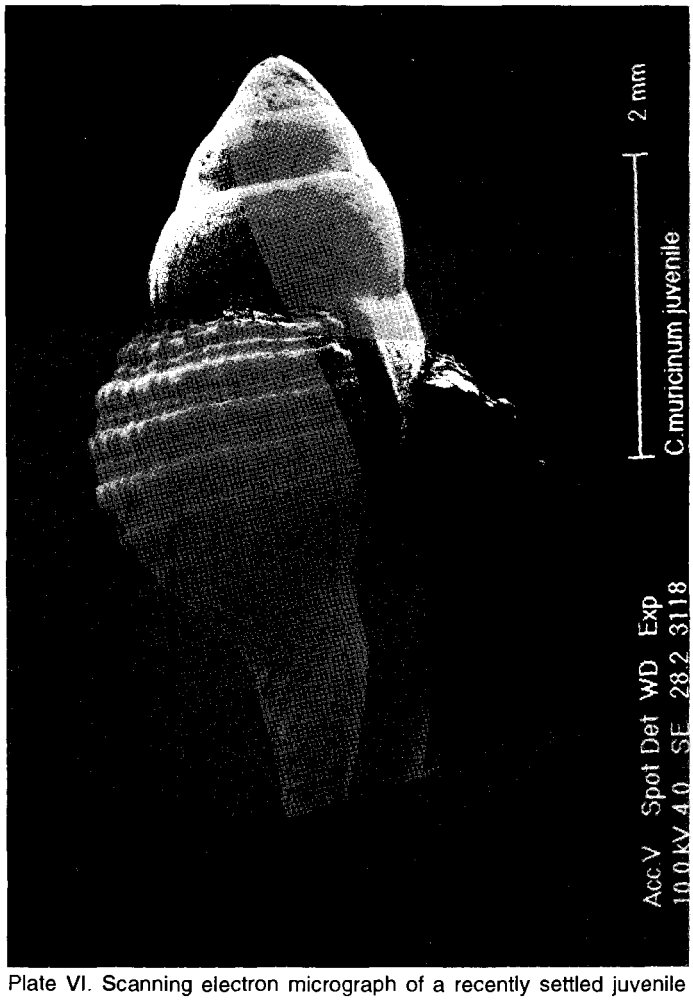

Plate VI. Scanning electron micrograph of a recently settled juvenile *Cymatium muricinum*. The first four, smooth, whorls are the protoconch II of the swimming teleplanic larva. The last, rougher, whorl is the calcified first whorl of the teleoconch. Vestiges of the periostracum may be observed at the suture between protoconch and teleoconch. (Photo by Heather Winsor).

After anything up to 5 whorls have been laid down, the growing edge of the periostracum turns outwards and then back forming a hollow ridge that constitutes the first varix or lip (Plate IV). Growth of the periostracum halts at this stage and calcification of the lip and siphonal canal take place. The rate of growth and calcification appeared to depend primarily on the consumption rate, higher consumption being accompanied by faster growth, less calcification and later formation of the first varix. Adverse conditions such as excessive handling or low temperature and oxygen levels were also thought to adversely affect growth rate. The duration of the halt and the amount of calcification of the first varix is extremely variable and may range from a few days to an indefinite period, the amount of calcification being proportional to this duration.

Growth generally resumes after the first varix, but slows towards the completion of another two-thirds of a whorl when the next varix is formed. Calcification again takes place and shell growth in length is also halted. Growth may resume again but varices subsequent to the first are always laid down after two-thirds of a whorl. After the formation of a

varix small increments in shell length were sometimes observed in *C. muricinum* due to elongation of the siphonal canal.

C. muricinum, C. aquatile and *C. pileare* were observed to form two or three varices. *C. nicobaricum* was observed to form 4 and even 5 varices, the first often very close to the protoconch although this may be due to the preferred diet of juvenile tritons of this species being unknown. The periostracum of *C. nicobaricum* was usually less hairy and was lost at an earlier stage than the other species. The protoconchs of each species were measured and the mean sizes and standard error for each species were: *C. muricinum* (3.5 mm ±0.08), *C. aquatile* (3.1 mm ±0.06), *C. nicobaricum* (3.8 mm ±0.11) and *C. pileare* (3.3 mm ±0.10).

Parameters of both the generalized and special VBGF calculated for individual tritons of all four species are shown in Table 3.2. The mean of the values obtained for the growth parameters of each model is shown. Because both models did not always fit the same data set means are

Table 3.2a. Estimated parameters of two models of the von Bertalanffy growth function for *Cymatium muricinum* and *C. aquatile* based on growth measured for snails fed *ad libitum* in aquaria. Standard errors (s.e.) of the parameters are shown and goodness of fit is measured in terms of residual sum of squares (rss).

C. muricinum

	Generalized VBGF							Special VBGF					
Tag#	D	L_∞ (mm)	s.e.	K ($year^{-1}$)	s.e.	rss	ϕ'	L_∞ (mm)	s.e.	K ($year^{-1}$)	s.e.	rss	ϕ'
cm12	0.851	47.30	0.776	18.447	1.550	4.078	4.62	48.57	1.261	12.337	1.325	35.166	4.46
cm21	0.851	43.91	1.384	11.569	2.272	3.518	4.35	43.96	1.392	9.593	1.912	13.895	4.27
cm24	0.851	48.28	0.662	24.694	2.928	3.923	4.76	49.15	1.041	15.749	2.154	32.273	4.58
cm30	0.851	-	-	-	-	-	-	34.87	0.135	44.290	4.211	1.604	4.73
cm31	0.851	42.46	0.839	19.440	2.135	5.570	4.54	43.34	1.157	13.307	1.630	35.125	4.40
cm37	0.851	56.31	0.647	9.219	0.499	13.878	4.47	56.71	0.718	7.187	0.414	70.136	4.36
cm410	0.851	52.25	5.175	5.932	1.102	4.472	4.21	-	-	-	-	-	-
cm60	0.851	46.22	2.355	8.467	1.084	7.315	4.26	49.38	3.329	5.619	0.852	36.760	4.14
cm69	0.851	32.32	1.231	21.011	3.124	3.024	4.34	33.24	1.392	14.890	2.037	12.996	4.22
cm70	0.851	36.05	2.673	13.890	2.644	3.607	4.26	-	-	-	-	-	-
Mean	0.851	45.01	1.749	14.741	1.926	5.487	4.42	44.90	1.303	15.371	1.817	29.744	4.39
s.d.		7.04		6.078		0.18		7.34		11.432			0.18
s.e.		2.35		2.026		0.06		2.59		4.042			0.06
Mean (snails fitting both models)	0.851	45.26	1.128	16.121	1.942	5.901	4.48	46.34	1.470	11.240	1.475	33.764	4.35
s.d.		6.69		5.865			0.16	6.72		3.583			0.14
s.e.		2.53		2.217			0.06	2.54		1.354			0.05

C. aquatile

	Generalized VBGF							Special VBGF					
Tag#	D	L_∞ (mm)	s.e.	K ($year^{-1}$)	s.e.	rss	ϕ'	L_∞ (mm)	s.e.	K ($year^{-1}$)	s.e.	rss	ϕ'
cn22	0.841	-	-	-	-	-	-	48.10	1.750	8.629	1.687	15.376	4.30
cn27	0.841	44.50	1.087	15.599	2.879	4.676	4.49	45.23	1.206	10.938	1.777	22.790	4.35
Mean								46.67	1.478	9.784	1.732	19.083	4.33
s.d.								1.44		1.155			0.02
s.e.								1.01		0.816			0.02

Table 3.2b. Estimated parameters of two models of the von Bertalanffy growth function for *Cymatium pileare* and *C. nicobaricum* based on growth measured for snails fed *ad libitum* in aquaria. Standard errors (s.e.) of the parameters are shown and goodness of fit is measured in terms of residual sum of squares (rss).

C. pileare

	Generalized VBGF							Special VBGF					
Tag#	D	L_∞ (mm)	s.e.	K ($year^{-1}$)	s.e.	rss	ϕ'	L_∞ (mm)	s.e.	K ($year^{-1}$)	s.e.	rss	ϕ'
cp38	0.842	63.92	3.965	6.352	0.915	15.841	4.41	66.59	4.469	4.515	0.716	76.460	4.30
cp42	0.842	67.37	1.882	10.167	1.566	21.859	4.66	68.04	1.883	7.763	1.055	111.935	4.56
cp49	0.842	51.62	1.400	26.662	4.366	3.467	4.85	-	-	-	-	-	-
cp80	0.842	70.80	3.884	7.133	0.997	30.054	4.55	72.54	4.377	5.307	0.830	133.874	4.45
Mean	0.842	63.43	2.783	12.579	1.961	17.805	4.62	69.06	3.576	5.862	0.867	107.423	4.43
s.d.		7.24		8.255			0.16	2.53		1.383			0.10
s.e.		3.62		4.128			0.08	1.46		0.798			0.06
Mean (snails fitting both models)	0.842	67.36	3.244	7.884	1.159	22.585	4.54	69.06	3.576	5.862	0.867	107.423	4.43
s.d.		2.81		1.646			0.10	2.53		1.383			0.10
s.e.		1.62		0.950			0.06	1.46		0.798			0.06

C. nicobaricum

	Generalized VBGF							Special VBGF					
Tag#	D	L_∞ (mm)	s.e.	K ($year^{-1}$)	s.e.	rss	ϕ'	L_∞ (mm)	s.e.	K ($year^{-1}$)	s.e.	rss	ϕ'
ca13	0.862	-	-	-	-	-	-	51.70	1.693	8.992	1.439	16.355	4.38
ca36	0.862	-	-	-	-	-	-	40.15	0.902	17.908	3.110	32.069	4.46
ca51	0.862	-	-	-	-	-	-	53.26	0.726	14.681	1.593	49.361	4.62
Mean								48.37	1.107	13.860	2.047	32.595	4.49
s.d.								5.85		3.686			0.10
s.e.								3.38		2.128			0.06

also shown of parameters obtained for tritons in which both models were fitted, allowing comparison. Despite the obvious two-stage growth exhibited by some tritons, attempts to fit the biphasic growth model of Soriano et al. (1990) did not produce a fit presumably because this model does not apply in this case (D. Pauly, pers. comm.).

The generalized VBGF produced better fits in terms of lower values of residual sum of squares (rss) and lower standard errors (s.e.) of L_∞, resulting in lower values of L_∞ and higher values of K (Fig. 3.7). This was expected as this model has one more parameter than the special VBGF however the values of L_∞ obtained were closer to the expected values and curves provided a better visual fit to the data. Interestingly it was found that reducing the value of D in the generalized VBGF provided increasingly better fits to the point that the best fits were obtained at unreasonable values of D such as 0.1 below which the nonlinear routine crashed.

The estimated values of L_∞ and K from both models show great variation (Fig. 3.8) but, at least in the case of L_∞, are within the range of values observed in wild specimens. From these data *C. pileare* would appear to reach the largest maximum size, followed by *C. aquatile, C. nicobaricum* and *C. muricinum* (Fig. 3.9). The possibility exists that the experimental tritons were capable of further growth and consequently the formation of more varices.

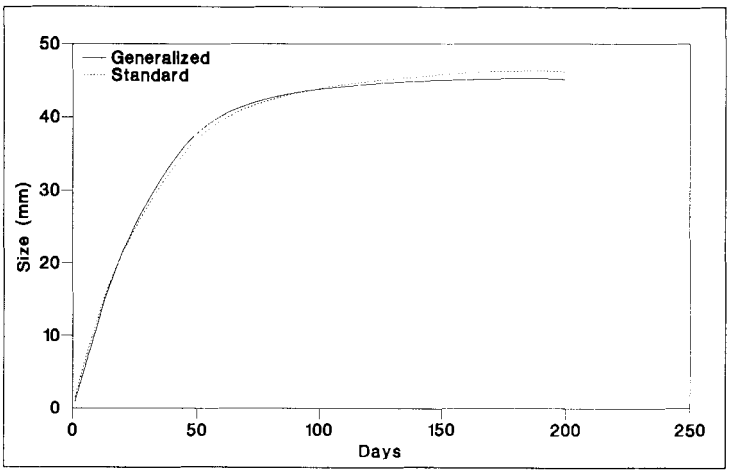

Fig. 3.7. Comparison of average growth curves estimated from data pertaining to *Cymatium muricinum* fed *ad libitum* in aquaria. Data were fitted to generalized and special models of the von Bertalanffy growth function. Note very high initial growth.

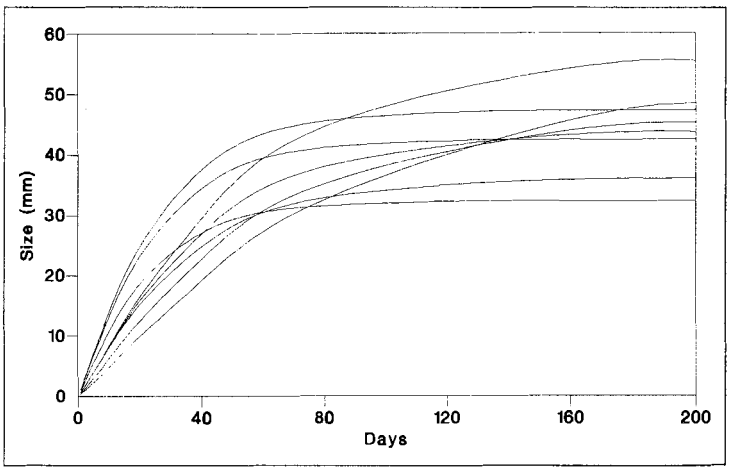

Fig. 3.8. Single growth curves estimated from data for eight individual *Cymatium muricinum* fed *ad libitum* in aquaria. Data were fitted to the generalized model of the von Bertalanffy growth function.

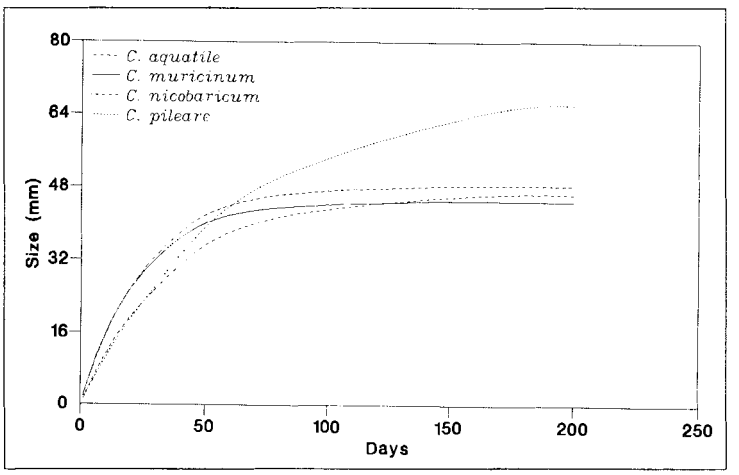

Fig. 3.9. Comparison of average growth curves estimated from data pertaining to *Cymatium muricinum*, *C. pileare*, *C. aquatile* and *C. nicobaricum* fed *ad libitum* in aquaria. Data were fitted to the generalized model of the von Bertalanffy growth function.

The growth performance index ϕ' (Pauly 1991), calculated from the growth parameters obtained for each triton, ranged from 4.3 to 4.7, these values being slightly higher if parameters from the generalized VBGF were used. Based on the few values of ϕ' available, no difference in growth performance between species could be detected using this index.

The early stages of growth in these tritons were of most interest as tritons collected from ocean-nurseries were usually small and fast growing. As this stage of growth appeared linear (Fig. 3.3) and did not fit a von Bertalanffy curve well, the early growth stage of tritons (up until

the formation of the first varix) was analyzed using predictive regression. Small *C. nicobaricum* did not grow at all in this experiment and were not included in the analysis.

The growth of 13 specimens of *C. muricinum* with a starting size under 5 mm was examined, seven of which were fed large clams which took 12 to 63 days to consume and the remaining six were fed clams under 20 mm SL which were consumed in less than 5 days (Table 3.3). These six tritons (Cm60, Cm66, Cm67, Cm68, Cm69 and Cm70), for which the most complete datasets were obtained, were considered the core for analyses of growth and also consumption (see below).

Only one specimen of the other two triton species under 5 mm in starting length was available and the early growth of *C. aquatile* and *C. pileare* was analyzed for individuals of 10 to 25 mm starting size (Table 3.4). This is reflected in the higher values of the standard error of the coefficient for these species than for *C. muricinum.*

The fit of the linear model to the early growth stage of all tritons, measured in terms of the correlation coefficient (r^2), is high supporting the impression of linearity in this stage of growth. As might be expected, the size at the first varix is correlated with the expected maximum size of the species as calculated from the VBGF and recorded in the literature (see above). The duration of the growth pause in which the first varix is formed was estimated from the graphed data, to the nearest week. Neither the size at, or duration, of the formation of the first varix appeared to correlate with the growth rate.

Table 3.3. Estimated parameters for the initial linear growth phase of *Cymatium muricinum* based on growth measured for snails fed *ad libitum* in aquaria. A linear model of the form: Length (mm) = a + b(Time) was fitted using predictive regression. Standard errors (s.e.) and 95% confidence intervals (c.i.) of the slope (b) are shown and goodness of fit is measured in terms of the correlation coefficient (r^2). "a" represents a close approximation of the snails' size at the experiments' start, "varix" refers to the size at the formation of the first varix, the duration (to the nearest 7 days) of which process is also given. Snails Cm60-Cm70 were fed small clams initially and the time taken to finish them is given as "P". Snails Cm313-Cm417 were fed larger clams and thus fed parasitically on them for the first weeks of the experiment.

#	a	b	s.e.	c.i.95%	r^2	n	Varix (mm)	Duration (days)	P (days)
Cm60	4.47	0.486	0.019	0.045	0.989	8	27.4	14	5.0
Cm66	3.29	0.523	0.014	0.033	0.995	8	28.3	7	3.0
Cm67	4.01	0.602	0.020	0.049	0.995	6	23.8	7	4.0
Cm68	4.09	0.722	0.018	0.043	0.997	6	27.4	7	5.0
Cm69	4.72	0.817	0.016	0.045	0.999	4	20.1	7	5.0
Cm70	3.42	0.695	0.036	0.092	0.990	5	22.1	14	5.0
mean	4.00	0.641	0.020		0.994		24.9	9.3	4.5
s.d.	0.52	0.115					3.1	3.3	0.8
s.e.	0.21	0.047					1.2	1.3	0.3
Cm313	2.84	0.487	0.025	0.060	0.984	7	27.0	7	24.0
Cm314	3.15	0.508	0.022	0.050	0.987	8	32.4	0	33.0
Cm316	4.21	0.458	0.036	0.092	0.976	5	23.8	7	34.0
Cm317	5.24	0.398	0.022	0.053	0.985	6	21.4	7	12.0
Cm402	3.21	0.358	0.042	0.104	0.933	6	28.2	21	40.0
Cm410	4.40	0.440	0.020	0.050	0.989	6	25.9	7	24.0
Cm417	4.52	0.325	0.011	0.027	0.994	6	30.0	-	63.0
mean	3.94	0.425	0.026		0.978		27.0	8.2	32.9
s.d.	0.82	0.062					3.4	6.3	14.9
s.e.	0.31	0.024					1.3	2.6	5.6

r
(
s
s

Table 3.4. Estimated parameters for the initial linear growth phase of *C. aquatile* and *C. pileare* based on growth measured for snails fed ad libitum in aquaria. A linear model of the form: Length (mm) = a + b(Time) was fitted using predictive regression. Standard errors (s.e.) and 95% confidence intervals (c.i.) of the slope (b) are shown and goodness of fit is measured in terms of the correlation coefficient (r^2). "a" represents a close approximation of the snails' size at the experiments' start (Min.), "varix" refers to the size at the formation of the first varix the duration (to the nearest 7 days) of which process is also given.

C. aquatile

#	Min. (mm)	a	b	s.e.	c.i.95%	r^2	n	Varix (mm)	Duration (days)
Ca35	12.6	9.38	0.491	0.123	0.317	0.788	5	26.9	7
Ca36	20.8	18.49	0.573	0.064	0.165	0.952	5	36.6	-
Ca51	17.1	16.88	0.913	0.058	0.150	0.984	5	41.4	14
Ca54	19.4	18.72	0.613	0.052	0.135	0.971	5	35.6	0
Ca56	20.5	18.82	0.553	0.071	0.182	0.937	5	34.9	21
mean	18.1	16.46	0.629	0.074		0.926		35.1	10.5
s.d.	3.0	3.61	0.147					4.7	7.8
s.e.	1.4	1.61	0.066					2.1	3.9

C. pileare

#	Min. (mm)	a	b	s.e.	c.i.95%	r^2	n	Varix (mm)	Duration (days)
Cp18	24.3	23.56	0.680	0.080	0.222	0.960	4	38.8	-
Cp19	24.9	23.35	0.725	0.075	0.193	0.959	5	45.0	-
Cp38	9.8	9.93	0.529	0.023	0.052	0.987	8	36.3	7
Cp42	25.9	25.08	0.759	0.074	0.190	0.963	5	47.9	28
Cp48	17.1	16.56	0.505	0.031	0.073	0.978	7	37.3	-
Cp49	20.1	19.76	0.871	0.021	0.053	0.998	5	44.1	-
Cp57	22.9	22.28	0.667	0.066	0.169	0.962	5	42.5	-
Cp80	4.8	1.94	0.661	0.062	0.143	0.941	8	39.9	21
mean	18.7	17.81	0.675	0.054		0.968		41.5	18.7
s.d.	7.2	7.55	0.111					3.8	8.7
s.e.	2.6	2.67	0.039					1.3	5.0

The growth rate of *C. muricinum* appeared lower in tritons that were fed large clams and consequently adopted a parasitic mode of feeding initially (Table 3.3). In order to test the significance of this, data from tritons in Table 3.3 which consumed their initial prey in 5 days or less were pooled as were data from the tritons that took longer (12-63 days). The results of the two regressions are shown in Table 3.5 and suggest that growth is significantly lower in tritons fed the larger clams.

Although growth of tritons prior to the formation of the first varix was apparently linear in terms of length, growth after this pause appeared asymptotic. Datasets in which the second growth phase appeared were edited so as to remove growth data up to and including the first varix. These modified datasets were then fitted to the special and generalized VBGF as before. The results (Table 3.6) show that this second growth stage fits both models of the VBGF very

Table 3.5. Comparison of the predictive regressions of the linear phase of growth of *C. muricinum* for lumped data of snails which fed on small clams (Cm60-Cm70) and those that fed on larger clams initially (Cm313-Cm417). See Table 3.3 for details.

	a	s.e.	b	s.e.	Confidence limits (95%)	r^2	n (data)	n (snails)
Cm60-Cm70	5.04	2.236	0.524	0.026	0.471-0.577	0.920	37	6
Cm313-Cm417	5.18	2.497	0.373	0.018	0.336-0.410	0.910	44	7

Table 3.6. Estimated parameters of two models of the von Bertalanffy growth function for *C. muricinum* in its second growth phase, i.e. after the formation of the 1st varix, based on growth measured for snails fed *ad libitum* in aquaria. Standard errors (s.e.) of the parameters are shown and goodness of fit is measured in terms of residual sum of squares (rss).

Generalized VBGF

Sp#	D	L_∞ (mm)	s.e.	K ($year^{-1}$)	s.e.	t_0	rss	ϕ'
Cm24	0.851	47.33	0.15	52.838	3.498	0.025	0.263	5.07
Cm30	0.851	-	-	-	-	-	-	-
Cm31	0.851	40.88	0.21	48.155	4.641	0.041	0.545	4.91
Cm32	0.851	42.62	0.45	75.242	14.960	0.050	0.452	5.14
Cm37	0.851	54.25	0.09	22.435	0.668	0.091	0.330	4.82
Cm60	0.851	39.14	0.28	36.971	3.689	0.110	0.331	4.75
Cm67	0.851	33.92	0.13	115.386	11.739	0.111	0.010	5.12
Cm69	0.851	30.10	0.21	71.365	8.295	0.049	0.177	4.81
Cm70	0.851	31.42	0.21	62.306	5.815	0.082	0.034	4.79
mean	0.851	39.96	0.21	60.587	6.663	0.070	0.268	4.93
s.d.		7.70		26.374		0.031		0.15
s.e		2.72		9.325		0.011		0.05

Special VBGF

Sp#	L_∞ (mm)	s.e.	K ($year^{-1}$)	s.e.	t_0	rss	ϕ'
Cm24	47.34	0.14	44.288	2.947	0.028	1.115	5.00
Cm30	34.67	0.14	44.290	4.211	-0.010	1.604	4.73
Cm31	40.89	0.21	40.068	3.856	0.044	2.169	4.83
Cm32	42.63	0.45	62.881	12.568	0.052	1.867	5.06
Cm37	54.26	0.09	18.838	0.579	0.097	1.526	4.74
Cm60	39.14	0.28	31.070	3.155	0.114	1.339	4.68
Cm67	33.92	0.13	97.362	9.963	0.112	0.041	5.05
Cm69	30.11	0.21	59.360	7.016	0.051	0.661	4.73
Cm70	31.43	0.21	52.322	5.051	0.084	0.132	4.71
mean	39.38	0.21	50.053	5.483	0.064	1.162	4.84
s.d.	7.44		21.070		0.039		0.15
s.e	2.48		7.023		0.013		0.05

Table 3.7. Summary of growth of eight *C. muricinum* described for the first phase by linear regression and for the second by the special von Bertalanffy growth function. For explanation of parameters see Tables 3.2 and 3.3.

	linear			special VBGF		
Sp#	Rate(b) ($mm \cdot day^{-1}$)	Varix (mm)	Duration (days)	L_∞ (mm)	K ($year^{-1}$)	t_0
Cm24	0.714	32.3	7	47.34	44.288	0.028
Cm31	0.724	27.8	7	40.89	40.068	0.044
Cm32	0.841	30.8	7	42.63	62.881	0.052
Cm37	0.594	37.1	14	54.26	18.838	0.097
Cm60	0.486	27.4	14	39.14	31.070	0.114
Cm67	0.602	23.8	7	33.92	97.362	0.112
Cm69	0.817	20.1	7	30.11	59.360	0.051
Cm70	0.695	22.1	7	31.43	52.322	0.084
mean	0.684	27.68	8.75	39.97	50.774	0.073
s.d.	0.111	5.29	3.03	7.70	22.243	0.031
s.e.	0.039	1.87	1.07	2.72	7.864	0.011

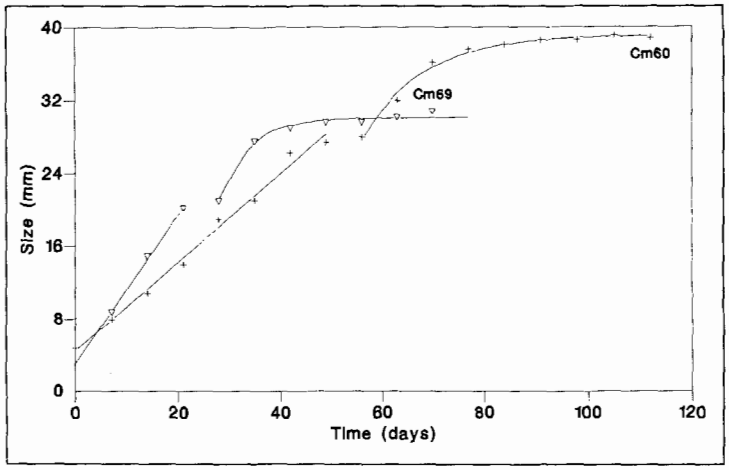

Fig. 3.10. Two-phase growth of two individuals of *Cymatium muricinum* fitted to a linear growth model for the first phase and a model of the special von Bertalanffy growth function for the second growth phase.

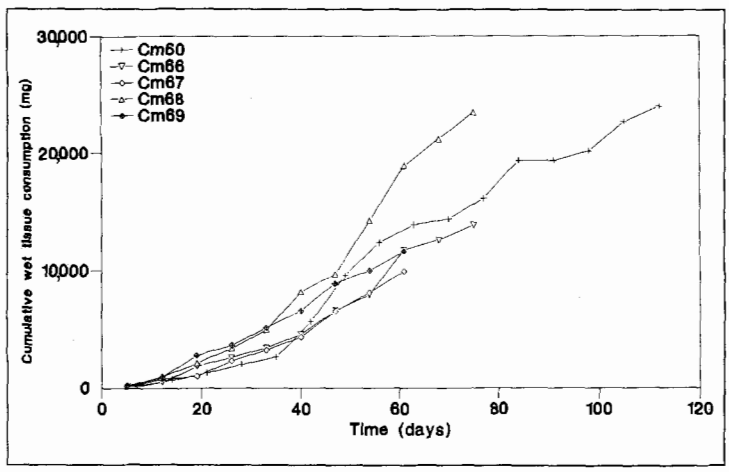

Fig. 3.11. Consumption of *Tridacna gigas* in aquaria by five recently settled *Cymatium muricinum* as a function of time.

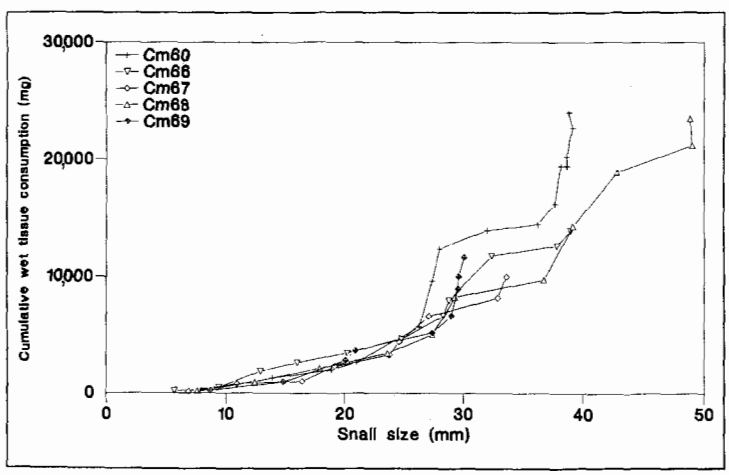

Fig. 3.12. Consumption of *Tridacna gigas* in aquaria by five recently settled *Cymatium muricinum* as a function of the size of the growing tritons.

well with low values of the residual sum of squares (rss) and standard errors (s.e.) for L_∞. The values of s.e. for K are, as in the previous analyses, higher and promote less confidence in the value of K. Table 3.7 shows a summary of growth parameters for tritons with analyses of both growth stages and Fig. 3.10 illustrates growth curves derived from these data for two particular tritons.

Consumption Rates

Examination of the growth and consumption data showed that absolute consumption tended to increase exponentially as tritons grew and leveled off after the triton had reached maximum size. The formation of the first varix did not appear to modify the consumption rates. Small tritons initially consumed remarkably large amounts of tissue with respect to their own body weights, but this rapidly declined with growth. These features can be seen in plotted values for the "core" set of *C. muricinum* (# Cm60-Cm70), i.e., consumption against time (Fig. 3.11), consumption against snail size (Fig. 3.12) and consumption per mg wet predator weight against time (Fig. 3.13).

The relationship between size and cumulative consumption was examined for both the core set of *C. muricinum* and the equally complete set of seven *C. muricinum*, which had been parasitic for the first weeks of growth (Cm313-Cm417). These data were fitted to an exponential equation (equation 3.1) using a GM regression of log transformed values (equation 3.7). This enabled a quick estimate of the relationship between consumption and size and the effects on

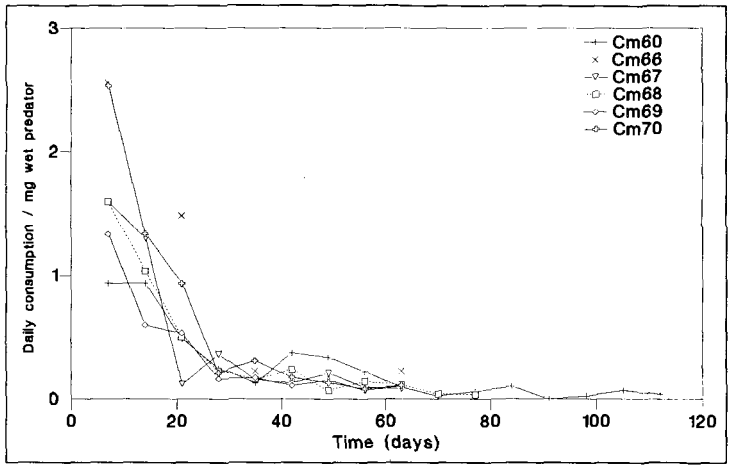

Fig. 3.13. Consumption of *Tridacna gigas* by six *Cymatium muricinum* in aquaria as a fraction of total triton weight over time.

consumption of an initial parasitic phase. A similar analysis was performed using a predictive regression for the relationship between time and consumption.

The results of these analyses are shown in Tables 3.8 and 3.9 for the complete datasets and also for the same tritons during the linear growth stage prior to the formation of the first varix. The allometric curve fitted the data well particularly in the case of the nonparasitic tritons. A source of error which may particularly affect the parasitic tritons is that the data for the consumption curves start at a mean triton size of 4.33 mm and zero consumption whereas the model forces the curve through the origin. Log-transformation requires the elimination of the initial data pairs where consumption equals zero. This results in a slight overestimate of the consumption of the smallest tritons and explains the poorer fit of the model to data from parasitic tritons which, owing to their feeding method did not provide data points in the first weeks.

Table 3.8. Estimated parameters of the exponential relationship between shell size and cumulative consumption (mg dry tissue weight) of recently settled *C. muricinum* fed juvenile *T. gigas* in aquaria. The exponent (b) and its 95% confidence limits are shown as well as the correlation coefficient (r^2). Values are shown separately for snails undergoing an initial parasitic phase and for snails during the 1st phase of rapid initial growth.

	a	b	Conf.lim.(95%)	r^2	n
All snails	0.324	2.460	(2.345-2.574)	0.939	113
All snails (1st phase)	0.357	2.469	(2.224-2.615)	0.920	51
Cm60-70	0.365	2.399	(2.285-2.514)	0.964	65
Cm60-70 (1st phase)	0.378	2.382	(2.163-2.601)	0.942	31
Cm313-410	0.253	2.510	(2.224-2.797)	0.852	48
Cm313-410 (1st phase)	0.543	2.260	(1.705-2.814)	0.754	20

Table 3.9. Estimated parameters of the exponential relationship between time and cumulative consumption (mg dry tissue weight) of recently settled *C. muricinum* fed juvenile *T. gigas* in aquaria. The exponent (b) and its 95% confidence limits are shown as well as the correlation coefficient (r^2). Values are shown separately for snails undergoing an initial parasitic phase and for snails during the 1st phase of rapid initial growth.

	a	b	Conf.lim.(95%)	r^2	n
All snails	2.888	1.529	(1.455-1.603)	0.934	120
All snails (1st phase)	3.431	1.454	(1.322-1.586)	0.904	54
Cm60-70	3.009	1.540	(1.472-1.608)	0.971	65
Cm60-70 (1st phase)	3.026	1.526	(1.401-1.651)	0.956	31
Cm313-417	0.835	1.813	(1.596-2.029)	0.842	55
Cm313-417 (1st phase)	0.766	1.829	(1.293-2.365)	0.706	23

Notably the exponent of the relationship between triton size and consumption was virtually unaffected by the tritons' initial feeding mode whereas this was not the case in the time/consumption analysis. This is not surprising as growth was significantly lower in the parasitic tritons (Table 3.5). The curves obtained for the initial growth phase and the complete datasets were very similar.

Tritons were not weighed during the experiments so weight was calculated using the length/weight relationships shown in Table 3.1 and the corresponding correction factors. As evidence had been found for deviation from isometric growth in the case of dry tissue weight of *C. muricinum* all triton weights were calculated as total wet weight. Correspondingly, weights of prey consumed were expressed in terms of wet tissue weight. Unless otherwise stated, weights discussed in the rest of this section will follow this format.

All consumption data (including partial or incomplete datasets) were pooled for each species thus data were available for 33 *C. muricinum*, 10 *C. aquatile* and 11 *C. pileare*. *C. nicobaricum* was omitted from the following analyses owing to prey preference considerations mentioned above. Consumption rates were analyzed as consumption per week calculated as a function of mean body weight, allowing comparisons with other published figures. The results of these analyses of the relationship between body weight and consumption rates are shown in Table 3.10 and plotted for *C. muricinum* in Fig. 3.14.

Table 3.10. Estimated parameters of the exponential relationship between weekly mean total wet weight (mg) of three species of *Cymatium* and weekly consumption (mg wet tissue weight) fed juvenile *T. gigas* in aquaria. The relationship is of the type: Ingestion rate = a(mean body weight)^b. The exponent (b) and its 95% confidence limits are shown as well as the correlation coefficient (r^2).

Species	a	b	c.i.95%	*n*	r^2
C. muricinum	24.45	0.549	±.066	213	0.438
C. aquatile	5.96	0.715	±.117	116	0.214
C. pileare	52.71	0.535	±.080	121	0.322

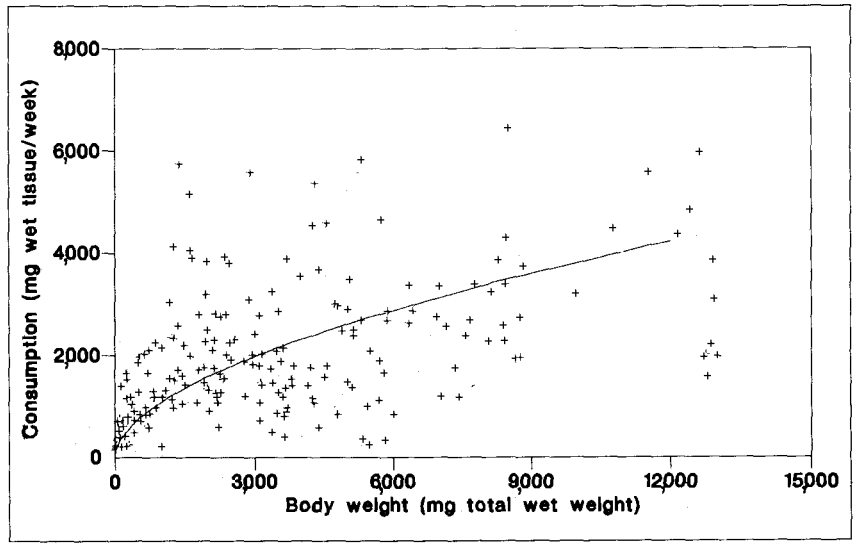

Fig. 3.14. The relationship between total weight of *Cymatium muricinum* and weekly consumption of *Tridacna gigas* in aquaria.

An attempt was made to repeat the analysis in the case of *C. muricinum* using dry weights calculated from the two different allometric relationships depending on the growth stage of the tritons. The correlation obtained was low (r^2 = 0.370, n = 212) and "b" also was lower than in the corresponding analysis for wet weights (b = 0.394, confidence limits (95%): 0.352-0.437). No further attempts were made to employ dual allometric relations as anomalies occurred at intermediate sizes.

The amount consumed by tritons at different weights as a proportion of total triton weight was plotted for *C. muricinum* (Fig. 3.15) and the ration was found to decline exponentially in relation to body weight. Some of the smallest tritons were observed to consume between 50 and 150% of their total wet weight per day with extreme values of up to 250% recorded. Using log-transformation and GM regression the relationship was found to be:

$$46.69 \text{ X (mean snail wet wt.)}^{-0.783} \qquad (r^2 = 0.792)$$

and for the other two species:

C. aquatile $177.15 \text{ X (mean snail wet wt.)}^{-0.936}$ $(r^2 = 0.524)$

C. pileare $114.98 \text{ X (mean snail wet wt.)}^{-0.840}$ $(r^2 = 0.656)$

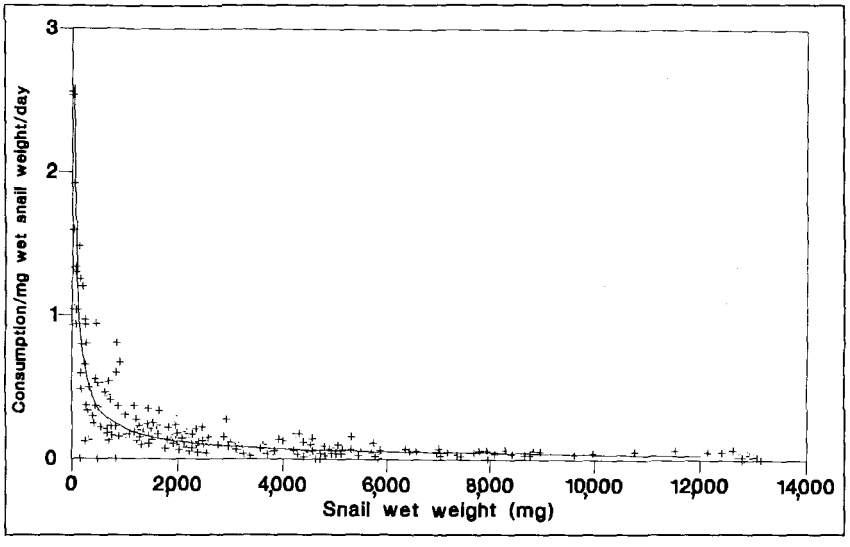

Fig. 3.15. The relationship between total weight of *Cymatium muricinum* and daily consumption of *Tridacna gigas* in aquaria, expressed as a fraction of total snail weight.

Examination of the confidence limits (95%) of the values of the exponent showed no significant difference between species.

Another measure of the consumption of these four triton species was provided by examining tritons which had reached a stable maximum size for more than 6 weeks. Consumption over a 5-week period for these tritons was averaged and is shown in Table 3.11 as total weekly consumption and weekly consumption as a proportion of estimated triton total wet weight. In addition, dry weight of one triton of each species was obtained by drying as detailed in Section 3.2.

Consumption in each of the tritons fluctuates widely from week to week but the average weekly consumption is between 16 and 47% of total triton weight or 2 to 7% calculated on a daily basis. Wet weight data for *C. nicobaricum* are not available due to the lack of a length/weight conversion relationship for this species (c.f., Table 3.1) but consumption appears to be similar to the other species. The consumption per mg dry triton tissue is slightly higher, as expected owing to the exclusion of shell weight, but still in the region of 3 to 7% per day.

The relationship between K_1 (growth/food ingested) and weight was investigated for *C. muricinum* using the core group of tritons Cm60-Cm70. A reasonable estimate of K_1 was

Table 3.11a. Mean weekly consumption of *Tridacna gigas* by adult *Cymatium muricinum* and *C. aquatile* expressed as mg wet tissue weight and mg wet tissue weight per mg total wet weight of snail estimated using previously determined length/weight relationships. Values in square brackets represent dry tissue weights determined empirically by sacrificing the snail.

C. muricinum

	Size	Weight (mg)		Weekly consumption (mg)		s.d.		Weekly ration ($mg \cdot mg^{-1}$)	
Cm12	45.1	7,600.5		2,332.8		790.4		0.307	
Cm21	41.4	5,878.2		1,219.5		881.5		0.207	
Cm24	47.5	8,803.1		2,854.0		706.0		0.324	
Cm30	35.0	3,605.8		1,362.6		919.3		0.378	
Cm31	41.1	5,769.0		1,362.0		664.0		0.236	
Cm37	54.2	13,029.3	[1,233.2]*	2064.0	[273.7]	617.8	[96.5]	0.158	[.222]
Cm60	38.6	4,813.2		1,954.5		930.4		0.406	
mean	43.3			1,878.5				0.288	
s.d.	5.8			556.2				0.084	

C. aquatile

	Size	Weight (mg)		Weekly consumption (mg)		s.d.		Weekly ration ($mg \cdot mg^{-1}$)	
Ca13	47.5	7,995.1		2,583.0		572.8		0.323	
Ca15	48.9	8,812.6		2,196.4		921.4		0.249	
Ca16	47.8	8,181.1		1,906.5		783.3		0.233	
Ca51	52.2	10,856.6	[642.4]*	2042.1	[262.6]	1,217.6	[152.8]	0.188	[.409]
Ca54	51.0	10,040.6		4,632.5		405.2		0.461	
mean	49.5			2,672.1				0.291	
s.d.	1.8			1,006.0				0.096	

* empirically derived

Table 3.11b. Mean weekly consumption of *Tridacna gigas* by adult *Cymatium nicobaricum* and *C. pileare* expressed as mg wet tissue weight and mg wet tissue weight per mg total wet weight of snail estimated using previously determined length/weight relationships. Values in square brackets represent dry tissue weights determined empirically by sacrificing the snail. Wet weight values of *C. nicobaricum* could not be estimated.

C. nicobaricum

	Size	Weight (mg)		Weekly consumption (mg)		s.d.		Weekly ration ($mg \cdot mg^{-1}$)	
Cn22	44.5	-		2,857.7		1,797.3		-	
Cn27	43.5	-		1,016.4		648.7		-	
Cn64	40.7	-	[494.8]*	1,380.2	[187.7]	915.2	[123.2]	-	[.379]
mean	42.9			1,751.4				-	
s.d.	1.6			796.2				-	

C. pileare

	Size	Weight (mg)		Weekly consumption (mg)		s.d.		Weekly ration ($mg \cdot mg^{-1}$)	
Cp17	46.5	6,860.6		3,060.2		1,354.7		0.446	
Cp18	54.9	1,1426.2		3,036.3		551.4		0.266	
Cp20	48.5	7,816.5		2,873.9		448.8		0.368	
Cp42	62.6	17,065.9	[1,195.7]*	4,815.4	[597.5]	1,513.2	[166.0]	0.282	[.500]
Cp80	61.4	16,051.7		7,542.6		3,767.4		0.470	
mean	54.8			4,265.7				0.366	
s.d.	6.5			1,785.6				0.083	

*empirically derived

obtained as suggested by D. Pauly (pers. comm.) for each ration estimate (consumption/mean triton weight) divided by the corresponding growth rate in weight for each given time period (usually 1 week). A GM regression of the plot of log(K_1) vs log weight (Fig. 3.16) allowed estimation of the parameters of equation (3.5). The raw data and calculated values are shown in Table 3.12. The parameters estimated for *C. muricinum* were:

$$K_1 = 8.618W^{-1.232} \quad (n = 60, r^2 = 0.768)$$

Similar values but a higher correlation ($n = 27$, $r^2 = .900$) were obtained if only data for tritons in the first stage of growth were used.

A plot of -log(1-K_1) vs log weight was made (Fig. 3.17) to try and estimate beta in equation (3.6) but this resulted in a poor correlation owing to the nonlinear form of the log plots.

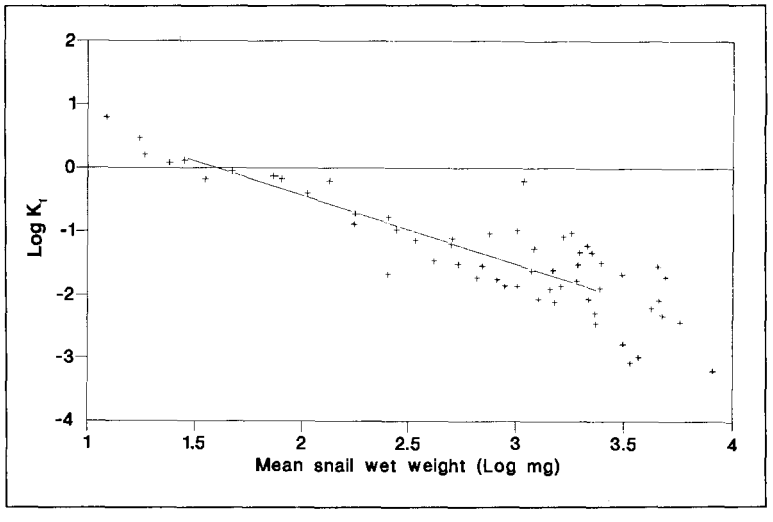

Fig. 3.16. The relationship between gross food conversion efficiency (K_1) and total snail weight for *Cymatium muricinum* fed on juvenile *Tridacna gigas* in aquaria.

Table 3.12. Weekly consumption and weight of *Cymatium muricinum* in terms of wet weight and calculations of gross conversion efficiency (K_1) for *C. muricinum* fed juvenile *Tridacna gigas* in aquaria. N/A: not available.

#	Days	Snail size	Snail weight(mg)	Weekly cons.(mg)	K_1	Log(K_1)	Log mean snail wt.	-L(1-K_1)
Cm60	0	4.8	10.52					
	7	7.9	45.45	182.82	1.309	0.12	1.45	N/A
	14	10.8	113.86	520.64	0.669	-0.17	1.90	0.4799
	21	13.9	238.92	599.49	0.190	-0.72	2.25	0.0916
	28	18.9	589.09	719.10	0.035	-1.46	2.62	0.0153
	35	21.0	802.73	615.08	0.029	-1.54	2.84	0.0128
	42	26.3	1,554.62	3,049.29	0.024	-1.62	3.07	0.0106
	49	27.4	1,753.43	3,895.79	0.083	-1.08	3.22	0.0376
	56	28.0	1,868.60	2,810.95	0.094	-1.03	3.26	0.0430
	63	32.0	2,765.92	1,529.53	0.005	-2.29	3.36	0.0022
	70	36.2	3,973.21	486.36	0.001	-3.08	3.53	0.0004
	77	37.6	4,441.61	1,760.48	0.006	-2.20	3.62	0.0027
	84	38.1	4,617.33	3,186.44	0.028	-1.55	3.66	0.0123
	91	38.6	4,797.57	0.00	0.000	N/A	3.67	0.0000
	98	38.6	4,797.57	840.20	N/A	N/A	3.68	N/A
	105	39.1	4,982.38	2,485.59	0.019	-1.72	3.69	0.0084
	112	38.8	4,870.94	1,305.79	-0.017	N/A	3.69	-0.0072

Continued

Table 3.12. Continuation.

#	Days	Snail size	Snail weight(mg)	Weekly cons.(mg)	K_1	Log(K_1)	Log mean snail wt.	-L(1-K_1)
Cm66	0	4.2	7.11		0.000	N/A	3.39	0.0000
	5	5.7	17.43	156.90	6.197	0.79	1.09	N/A
	12	9.4	75.73	340.15	0.877	-0.06	1.67	0.9090
	19	12.9	191.87	1,387.25	0.625	-0.20	2.13	0.4258
	26	16.0	361.17	717.31	0.107	-0.97	2.44	0.0493
	33	20.2	716.19	835.99	0.031	-1.51	2.73	0.0135
	40	24.8	1,308.33	1,181.49	0.014	-1.86	3.01	0.0060
	47	28.3	1,928.02	1,982.43	0.014	-1.86	3.21	0.0061
	54	28.8	2,029.78	1,345.40	0.047	-1.33	3.30	0.0208
	61	32.4	2,868.70	3,795.79	0.013	-1.89	3.39	0.0057
	68	37.8	4,511.36	890.63	0.001	-2.99	3.57	0.0004
	75	38.9	4,907.90	1,278.82	0.005	-2.32	3.67	0.0021
Cm67	0	4.0	6.16					
	5	6.9	30.54	146.28	1.634	0.21	1.26	N/A
	12	10.9	116.99	670.90	0.737	-0.13	1.87	0.5792
	19	16.4	388.34	213.34	0.022	-1.66	2.40	0.0096
	26	19.2	616.98	1,267.24	0.077	-1.11	2.70	0.0349
	33	23.8	1,159.37	961.75	0.014	-1.85	2.95	0.0061
	40	24.6	1,277.59	1,115.78	0.054	-1.27	3.09	0.0242
	47	27.1	1,697.64	2,190.58	0.025	-1.61	3.17	0.0108
	54	32.9	3,000.67	1,544.84	0.004	-2.45	3.37	0.0015
	61	33.6	3,192.07	1,797.06	0.021	-1.67	3.49	0.0093
Cm68	0	4.2	7.11					
	5	7.6	40.57	189.81	1.190	0.08	1.38	N/A
	12	12.4	170.84	764.59	0.389	-0.41	2.02	0.2137
	19	17.9	502.16	1,173.96	0.074	-1.13	2.53	0.0333
	26	23.6	1,130.98	1,284.08	0.018	-1.76	2.91	0.0077
	33	27.4	1,753.43	1,595.97	0.012	-1.91	3.16	0.0054
	40	29.3	2,135.03	3,196.11	0.030	-1.52	3.29	0.0133
	47	36.7	4,136.55	1,467.79	0.002	-2.79	3.50	0.0007
	54	39.1	4,982.38	4,586.65	0.008	-2.08	3.66	0.0036
	61	42.8	6,497.77	4,644.92	0.004	-2.43	3.76	0.0016
	68	49.0	9,667.63	2,288.36	0.001	-3.20	3.91	0.0003
	75	48.8	9,552.19	2,301.04	-0.015	N/A	3.98	-0.0063
Cm69	0	4.7	9.89					
	5	8.7	60.34	233.59	0.659	-0.18	1.55	0.4677
	12	14.8	287.26	725.11	0.129	-0.89	2.24	0.0598
	19	20.1	705.83	1,847.22	0.062	-1.21	2.70	0.0279
	26	20.9	791.56	855.34	0.093	-1.03	2.87	0.0425
	33	27.4	1,753.43	1,502.53	0.009	-2.07	3.10	0.0037
	40	29.0	2,071.46	1,456.88	0.017	-1.78	3.28	0.0073
	47	29.6	2,199.87	2,306.44	0.059	-1.23	3.33	0.0264
	54	29.6	2,199.87	1,073.81	N/A	N/A	3.34	N/A
	61	30.1	2,310.81	1,637.74	0.046	-1.34	3.35	0.0204
Cm70	0	4.1	6.62					
	5	6.7	28.02	219.43	2.961	0.47	1.24	N/A
	12	10.9	116.99	677.81	0.736	-0.13	1.86	0.5777
	19	16.4	388.34	1651.56	0.169	-0.77	2.40	0.0802
	26	22.1	932.60	974.79	0.019	-1.72	2.82	0.0083
	33	23.2	1,075.60	2,150.80	0.105	-0.98	3.00	0.0481
	40	23.3	1,089.28	1,304.28	0.617	-0.21	3.03	0.4166
	47	28.3	1,928.02	1,414.33	0.008	-2.11	3.18	0.0034
	54	30.5	2,402.16	1,252.16	0.009	-2.07	3.34	0.0037
	61	31.2	2,567.71	1,909.21	0.032	-1.49	3.40	0.0143

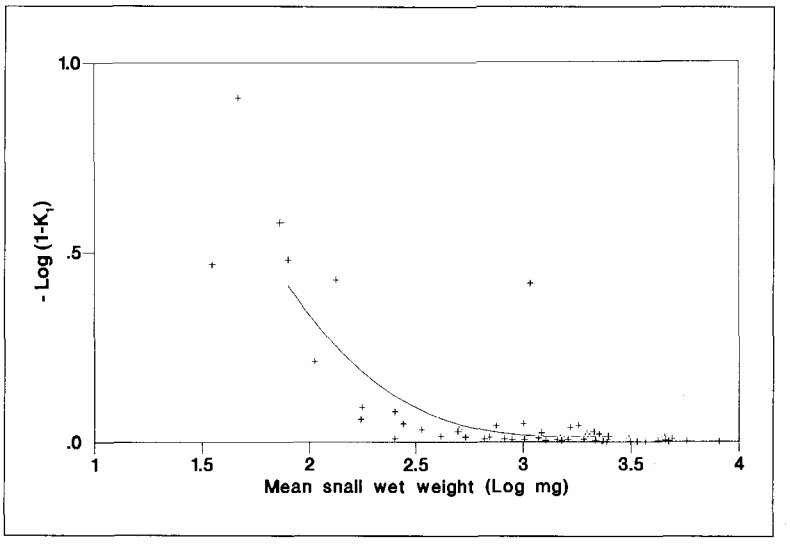

Fig. 3.17. The relationship between gross food conversion efficiency expressed as -log(1-K_1) and total snail weight for *Cymatium muricinum* fed on juvenile *Tridacna gigas* in aquaria.

3.4 Discussion

Growth of Cymatium *spp.*

Shell growth in *C. muricinum, C. aquatile, C. pileare* and *C. nicobaricum* is characterized by rapid growth followed by growth pauses in which a labial varix is formed. Such episodic growth is found in members of the Muricidae, Bursidae and Cassidae (Laxton 1970a, 1970b; Linsley and Javidpour 1980; Hughes 1986) but has only been described in Ranellidae by Laxton (1970a, 1970b) for a number of New Zealand species of the genera Ranella and Cabestana and also *Cymatium parthenopeum.*

Laxton (1970a) described periods of fast growth in which the gastropod shell is enlarged mainly by the secretion of the organic periostracum followed by growth pauses in which a varix is formed and the bulk of shell calcification takes place. In *Cabestana spengleri* the distance that the first varix is formed from the protoconch depends on the amount of food available during the initial stages of growth (Laxton 1970a). Laxton (1970a) suggests that the reason for the growth pauses may be that shell growth exceeds tissue growth requiring periodic halts to enable balance to be restored.

Morton (1986) described four phases in the growth of the Hong Kong melongenid *Hemifusus tuba.* A first 10-week phase saw much energy being invested in rapid, virtually linear, growth in shell length although tissue weight also increased. In a second 10-week phase shell growth declined and energy was put into increasing tissue bulk. A third phase consisted of an apparent endogenous growth check in which size and tissue weight barely increased but shell thickness did. After this phase, growth resumed for all parameters following standard patterns of asymptotic growth.

In the current study the initial growth phase of *C. muricinum, C. aquatile* and *C. pileare* consisted of very rapid shell growth in the form of the organic periostracum. Length:weight data for *C. muricinum* strongly suggest that this growth greatly exceeded tissue growth in the early

stages and that the balance is redressed around the time of first varix formation. Data presented by this author in Govan et al. (1993) show that shell shape in terms of length:width ratio does not vary significantly from width = 0.48 X length (r^2 = 0.99) for *C. muricinum* from 3.7 to 50.3 mm in length.

Where there is a refuge in size from predation, juvenile snails are known to favor rapid growth over shell sturdiness during their smaller, more vulnerable stage (Vermeij 1978; Palmer 1981). This phenomenon has been widely reported in temperate species particularly the abundant naticids such as *Polinices* spp. (Edwards and Huebner 1977; Ansell 1982) or muricids such as *Thais* spp. (Bayne and Scullard 1978; Palmer 1981; Burrows and Hughes 1990) or *Morula marginalba* in South Australia (Moran et al. 1984). Juvenile *Hemifusus tuba* in Hong Kong grow at rates of approximately 0.33 mm·day^{-1} at 21°C during the initial growth phase. Data presented by Laxton (1970a) for the New Zealand ranellid *Cabestana spengleri* suggested that juveniles grew at up to 0.3 mm·day^{-1}. The growth curve calculated by Perron et al. (1985) for *C. muricinum* in Palau suggested an early juvenile growth rate of 0.3-0.4 mm·day^{-1}.

Taylor (1977) found growth rates of 0.02-0.07 mm day^{-1} for recently hatched juvenile carnivorous gastropods of the families Naticidae, Muricidae, Columbellidae and Mitridae in Hawaii. By contrast she found relatively fast growth of up to 0.2 mm·day^{-1} in a juvenile wentletrap, *Epitonium ulu*, and up to 0.3 mm·day^{-1} in discontinuous growth bursts by the tonnacean, *Bursa cruentata.* Robertson (1983) also reports rapid growth in a postlarval wentletrap, *Epitonium albidum*, averaging 0.15-0.33 mm·day^{-1} and achieving up to 0.5 mm·day^{-1} over a 2-day period.

The growth rates of the *Cymatium* spp. studied here appear to be exceptionally high compared to reported values for gastropod growth, even for juveniles. *C. muricinum, C. aquatile* and *C. pileare* averaged between 0.6 and 0.7 mm·day^{-1} over 3- to 6-week periods of initial growth with some tritons of each species reaching rates of 0.8-0.9 mm·day^{-1}. Such values must rank as some of the highest obtained by gastropods although it is possible that muricids of the genus *Chicoreus* and helmets of the genus *Cassis* attain higher values during growth bursts (Inaba 1967; Linsley and Javidpour 1980).

Their high potential growth rates enable tritons with a superabundant food supply to reach the size of first varix formation in 33 days (range 20-50) in the case of *C. muricinum* and 50 and 57 days from settlement in the cases of *C. aquatile* and *C. pileare*, respectively.

At varix formation calcification of the shell is observed, and thus the vulnerability of tritons to predators is reduced by increases in size and strength. Increased shell diameter is probably one of the most effective defenses against crushing predators such as fish and crustaceans (Vermeij 1978). Varices further increase the diameter of the snail and distribute the stress of attempted crushing over a wider area while a thickened shell lip is effective in preventing certain crustaceans such as *Thalamita* spp. and *Dardanus lagopodes* (pers. obs.) from peeling back the shell of prey starting at the lip (Hughes 1986; Vermeij 1978).

Episodic growth such as that observed in these *Cymatium* spp. provides the advantages of both determinate and indeterminate growth strategies described by Vermeij and Signor (1992). The formation of a lip or varix provides resistance to predators and may play a role in the recognition of mature mates and in maintaining stability on the substrate whilst a capacity for further growth allows an increase in body size, and thus fecundity, if favorable conditions are encountered.

Interestingly, the significantly reduced growth observed in *C. muricinum* that passed the first 2 to 9 weeks as parasites of large *T. gigas* resulted in the formation of the first varix significantly later, after 55 days (range 44-81, P = 0.012, t-test). However, these tritons were protected

by the shells of their "hosts" for the periods of initial growth and greatest vulnerability. Reasons for this reduced growth may be that interactions with the "host", such as evading defence responses, represent a significant energy drain or that tissues easily available to these tritons such as the clam mantle are poorer sources of energy (Hughes 1986) than the internal organs more often attacked by nonparasitic tritons.

Estimating somatic growth from shell growth assumes a direct relationship between the two (Hughes 1986). In the case of the study species the relationship between tissue weight and shell size is complex, depending on factors such as food availability, consumption rates and growth stage (Laxton 1970a and discussion below). The assumptions of the VBGF regarding growth of these species in terms of length are not met during the early stages of growth. This explains the better fit of the generalized VBGF to growth data when unrealistically (in terms of tissue growth) low values of "D" are used. The biphasic growth VBGF model of Soriano et al. (1990) could not be fitted to the present data presumably because it assumes that the change in growth is concomitant with changes in diet and metabolism. No evidence was found for such changes in the current study.

The fitting of these data to the VBGF is useful, however. Firstly it provides useful estimates of the average maximum length (L_∞) attained by the tritons. Secondly it allows comparisons between individuals and species in this work. Thirdly it allows comparisons with published gastropod growth parameters. Finally the VBGF does describe the stages of growth after the formation of the first varix at which time the assumptions of this model are met.

The estimated L_∞ of the four study species is in very close agreement with the maximum size of these species observed in experiments and in the field in Solomon Islands. However the estimated values are considerably lower (40-50%) than maximum reported values (Clench and Turner 1957; Springsteen and Leobrera 1986; Beu and Kay 1988).

The mean relative increment in shell length from one whorl to the next was calculated from the datasets. The means and s.e. obtained were: *C. muricinum*, 39.4% ±1.30; *C. aquatile*, 28.7% ±0.95; *C. pileare*, 35.7% ±2.06; and *C. nicobaricum*, 29.3% ±1.06. Thus the formation of one more varix would bring the maximum sizes of these four species in line with published values. However, the discrepancies are just as likely to be due to environmental or genetic differences resulting in increased growth in length between varices.

The mean initial linear growth rates estimated for *C. muricinum, C. aquatile* and *C. pileare* are very similar (Tables 3.3 and 3.4); however the parameters of the VBGF estimated for *C. pileare* are significantly different from those of the other three species (Fig. 3.9). This is principally due to the high value of L_∞ estimated for *C. pileare* (69 mm) as opposed to values of 45-48 mm estimated for the other three species. As *C. pileare* has a relatively low value of K, these differences are not apparent in the calculated values of ϕ'.

Perron et al. (1985) experimentally derived growth parameters for *C. muricinum* in Palau using a mark/recapture technique and Fabens (1965) routine to calculate the VBGF. An unspecified number of tritons were isolated in mesh bags with, presumably, large *T. gigas* (100 mm SL) and remeasured every 10 days. Values for L_∞ = 40.7 mm and K = 4.164 year^{-1} were obtained. The value of L_∞ is well within the range obtained in the present study but K is well below the mean although comparable to the minimum values. One explanation for this is that owing to the large size of *T. gigas* used throughout the work of Perron et al. (1985) the juvenile tritons fed parasitically at least initially. This reduced the initial growth rates of tritons in the current study to 0.3-0.4 mm·day^{-1} which is comparable to those obtained if the VBGF parameters of Perron et al. (1985) are applied. K was also reduced in the case of the single parasitic triton for which VBGF parameters could be calculated (c.f., Cm410, Table 3.2a).

The length:weight relationship for dry tissue of *C. muricinum* suggests that growth after the first varix is isometric. Further, all subsequent varices are invariably laid down after 2/3 of a whorl so growth is partially determinate. Thus it is not surprising that the second phase of growth in *C. muricinum* fits both models of the VBGF very well (Table 3.6) as demonstrated by the low values of rss obtained. The standard errors of the L_∞ values obtained are low and appear to fit the data much better than those obtained for the complete datasets. The values of K are much higher and still show large standard errors which may in part be due to the reduced amount of data available.

When the different growth models (linear and VBGF) are applied to the separate growth stages for individual tritons a very good fit is apparently obtained (Fig. 3.10). Unfortunately it appears difficult to estimate *a priori* the size or time when the first varix is formed and the duration of this process. This prevents the unification of both models into one that describes *Cymatium* growth through both phases. In common with Laxton (1970a), no evidence was found to suggest that growth rates varied between sexes.

The results obtained here suggest the following elaboration of the theory of Laxton (1970a) explaining the growth in stages and varix formation of these species of *Cymatium*.

Recently settled juvenile tritons faced with an abundant food supply grow rapidly with the effect of minimizing time spent at small sizes which are more vulnerable to predation. The bulk of secreted shell material consists of light organic material which is energetically costly to secrete (Hughes 1986). In fact Palmer (1983) estimated that the energetic cost of calcification is 7, perhaps 30, times less than that of protein synthesis. The perceived advantages of this growth mechanism are that the more costly processes of shell formation are performed while energy is available, the lighter shell material reduces energy expenditure on locomotion thus allowing more effective predatory action and that a heavier skeleton, that could limit the rate of body growth (Palmer 1981), is avoided.

The rate of increase in shell area is a function of the increase in mantle area (Wilbur 1964). Sometime during the period of initial rapid growth the energy absorbed becomes insufficient to support the rapid increase in mantle area required to secrete the, relatively much larger, shell area involved in the formation of each subsequent whorl. This point may be reached earlier due to an insufficient food supply (Laxton 1970a), but will inevitably be reached sooner or later even where food is super-abundant. When this stage is reached growth in shell area stops with the secretion of a varix and does not start again until tissue volume has grown sufficiently.

The rate of increase in shell thickness and weight is a function of the rates of secretion of calcium carbonate and the organic matrix (Wilbur 1964). Calcification depends, among other things, on the growth of calcium carbonate crystals (Wilbur 1964). This presumably slow process may be continuous or not but certainly becomes more obvious during the growth pause resulting in the visible strengthening of varix and shell.

When tissue volume is sufficient, growth recommences, often as fast as before. However, growth is determined by the formation of a subsequent varix after 2/3 of a whorl and so shortly growth slows and halts again. The predetermined distance between varices is probably genetically determined as it appears species specific such that this distance is every 2/3 of a whorl in the study species of *Cymatium* and *Charonia* spp. (Beu 1970) and every half whorl in *Mayena, Cabestana*, and members of the closely related family Bursidae (Laxton 1970a; Beu 1980).

The mode of growth of *C. muricinum* appears to favor the opportunistic predatory lifestyle of this gastropod (Perron et al. 1985). When food is abundant provision is made for the rapid

attainment of a large size whereas in the case of food shortage growth is consolidated at the current size and the shell is strengthened. This was the basis for the suggestion by Govan et al. (1993) that the feeding history of a triton could be determined by examination of the varices and growing shell edge. This allows clam farmers to determine whether *Cymatium* spp. found in clam cages entered as larvae or from the relatively food-scarce surrounding reef areas. Different methods of control could be applied accordingly (Govan et al. 1993).

Based on the above theory of growth and the observation that rates of consumption do not vary during varix formation (contrary to the predictions of Linsley and Javidpour 1980) it is possible that growth in tissue weight does follow a classic pattern of growth such as the VBGF. Unfortunately, without more information regarding the length:tissue weight relationship for the smallest tritons this cannot be tested nor can the complete growth pattern of these species be easily fitted to a single model.

Consumption Rates of Cymatium *spp.*

Perhaps the most striking feature of the consumption data presented here is the extremely high relative consumption by small juveniles of *Cymatium* spp., particularly evident in *C. muricinum* for which most data are available (Figs. 3.13 and 3.15). Although these results are not entirely surprising, based on published values (Edwards and Huebner 1977; Ansell 1982; Morton 1986; Morton 1990a, 1990b), examination of features of the experimental design will permit better interpretation of the data.

Firstly, as has already been pointed out, the tissue weight of small juvenile *C. muricinum* is much lower in relation to shell size than for larger tritons. To avoid this complication triton weights have been expressed as total wet weight (c.f., Broom 1982) but it is worth bearing in mind that tissue will form a relatively smaller part of this total in the smallest tritons.

Secondly, the smallest size of triton available for the determination of length:weight relationships was 11 mm and therefore errors may be introduced when using this relationship for tritons as small as 4-5 mm. However, based on visual observations of the smaller tritons it does not appear that these depart significantly from the general observations.

Lastly, the results could be skewed if smaller tritons were consistently incapable of finishing the first clams on which they were fed resulting in tissue wastage and an overestimate of initial consumption. This phenomenon was never observed during the experiments and seems unlikely to have significantly affected the results.

Morton (1986) points out that enhanced consumption by newly hatched juveniles is often overlooked in studies of predator consumption. Certainly such estimates are often omitted from consumption studies. Relative consumption rates of *Hemifusus tuba* feeding on bivalves declined exponentially with time, maximum daily consumption rates were calculated to be 27% of snail total wet weight within two weeks of hatching and Morton (1986) estimated that this might have been as high as 92% in terms of snail tissue weight. Consumption declined to presumably baseline values approximating those of adult *H. tuba* of 3-4% of tissue weight or 1% of total weight.

The scavenging Hong Kong neogastropods *Babylonia lutosa* and *Nassarius festivus* also showed an exponential decline in relative consumption rates from maximum values of 60% of dry tissue weight per day for 6-7 mm *N. festivus* to about 10% for 15 mm individuals (Morton 1990a). The larger *B. lutosa* showed a similar but less marked decline from 10-15% for 30-mm snails to around 4% for 50-mm individuals. Adult ranellid predators, *Linatella caudata*, also from

Hong Kong, were estimated to consume 3-6% of their dry tissue weight daily with a mean of 4.0% (Morton 1990b) when fed on their preferred bivalve prey, *Barbatia virescens*.

The relative daily consumption rates of the Malaysian muricid gastropod *Thais carinifera* feeding on the bivalve *Anadara granosa* (Broom 1982), declined from 16% of total body weight for 1-g individuals to 6% for adults (20 g). Interestingly the consumption rates of a naticid, *Natica maculosa*, in the same study did not vary with size, staying constant at around 7.5%.

Studies of temperate naticids have shown declining relative consumption rates in *Polinices alderi* (Ansell 1982) and *P. duplicatus* (Edwards and Huebner 1977). Daily relative consumption rates of *P. duplicatus* feeding on the bivalve *Mya arenaria* declined from 5.6% of ash free tissue weight for 1 year old (25 mm) snails to 3.7% in 2 year olds (39 mm). On an annual basis these values average 1% with peaks of 5-6% in summer. Adult *P. alderi* consumes 4.8% of its own body weight of the bivalve *Tellina tenuis* daily (at 25°C) although these rates increase to 15% when reproductively active and fall to 1.7% at 10°C (Ansell 1982).

Adult *C. muricinum, C. aquatile* and *C. pileare* had similar rates of daily consumption, between 2 and 7% of total wet weight and species means of 4-5%. Measured in terms of snail dry tissue weight the values for the above three species and *C. nicobaricum* were similar, around 3-7%. These results are in close agreement with similar studies on gastropod predators of bivalves around the world and support the observation of Morton (1986) that, in general, gastropod predators of bivalves consume 1-6% of their body weight per day under optimal feeding conditions.

Strikingly, the relative rates of consumption of juvenile *Cymatium* are extremely high, *C. muricinum* under 10 mm in size consume 100-250% of their total weight per day. Even if the sources of error discussed above are taken into account these values are outstanding and would be even higher if it were possible to calculate them in terms of snail tissue weight. Tritons as large as 18 mm length (well within the range of tritons used in the length:weight relationship of Table 3.1) consumed daily around 30-40% of their total weight in the case of *C. muricinum*, 60-90% in *C. pileare* and 50% in *C. aquatile*.

The high consumptions reported here in comparison to published values may in part be due to the fact that most authors have not examined consumption immediately after settlement or hatching although Morton (1986) reports values of only 27% for *H. tuba* 2 weeks after hatching. Morton (1986) reports relative consumption rates of juveniles of at least 10 times the basal rates of adults and suggests that this is related to the high energy requirements of initial rapid shell growth. The consumption rates of juvenile *C. muricinum* in the present study are 25-40 times those of adult tritons, perhaps even more. These exceptionally high rates may be required to support the also very high initial rates of shell growth which are 2-3 times those reported for *H. tuba*.

The relationship between body weight and consumption expressed as $(\text{body weight})^b = \text{consumption}$, would be expected to show values of $b = 2/3$ if proportions of the body were isometric throughout growth (Hughes 1986). Although values of $b = 0.67$ are occasionally reported, "b" appears to attain a range of values from 0.37 to 1.0 from species to species (Hughes 1986). Broom (1982) reports $b = 0.68$ for *T. carinifera* and $b = 1.01$ for *N. maculosa*. The temperate naticid *P. duplicatus* also showed high values of $b = 0.81$ in summer although the average year-round value was 0.53. Bayne and Scullard (1978) found $b = 0.43$-0.61 in *T. lapillus*.

The values of "b" reported herein of 0.55 for *C. muricinum* and 0.54 for *C. pileare* are both significantly less than 0.67 possibly due to the non-isometric growth and high consumption rates of juveniles. The value of $b = 0.72$ for *C. aquatile*, not significantly different from the other two

species, may be due to the scarcity of data points for tritons under 25 mm and the poor correlation obtained. Data presented by Morton (1986) for *H. tuba*, which presents similar growth and consumption patterns to the study species, allow the calculation of values of "b" falling in a 95% confidence interval from 0.36 to 0.44 (r^2 = 0.93), also much lower than 0.67.

Gross food conversion efficiency (K_1), which is equivalent to production efficiency or growth/food ingested is reported to decline with increased body size in several gastropods with the highest values recorded for veliger larvae (Hughes 1986). Broom (1982) reports values of K_1 falling from 26 to 0.4% with increased size for both *T. carinifera* and *N. maculosa*. Growth efficiencies have also been observed to decline with age in *P. duplicatus* from 51 to 16% and fluctuate widely with values between 104 and 0% (Edwards and Huebner 1977).

Estimated values of K_1 for *C. muricinum* in the present work fluctuated widely indicating that weekly consumption may not necessarily be linked to growth in the same week. High values of greater than 100% were recorded in the first week but these declined exponentially to values of 2-10% by week 4 and values close to 0% at maximum size. Interpretation of these results is hindered because snail growth in weight was based on calculated values derived from length:total weight relations not necessarily applicable to smaller tritons and probably a poor reflection of somatic growth. However, the high initial values could be explained by the fact that shell growth on a newly enriched diet may precede tissue growth, a fact which explained similar results in *P. duplicatus* (Edwards and Huebner 1977).

Implications for Giant Clam Culture

The study of gastropod consumption and growth rates in optimal laboratory conditions using flow-through aquaria and abundant prey may produce results higher than usually obtained in wild field conditions but, usefully, different workers' findings are consistent (Edwards and Huebner 1977; Morton 1986; Burrows and Hughes 1990 and above). Certainly *Cymatium* spp. on shallow tropical reefs in Solomon Islands will rarely encounter super-abundant prey but the purpose of this study was to ascertain the impact of these species on the culture of tridacnids under highly artificial conditions.

Floating and trestle ocean-nursery cages for juvenile clams present similar conditions of temperature (which did not vary greatly throughout the year), water flow, sunlight and prey abundance as in the experimental aquaria. Such cages are virtually isolated from the surrounding reef making it difficult for tritons to escape once settled and also for larger predators to enter.

Growth and consumption of the experimental ranellids may be reduced by handling and disturbances involved in prey replacement and measurement (Edwards and Huebner 1977). Snail growth and consumption may be adversely affected in clam cages by increased energy expenditure on locomotion, predator avoidance and intra-specific interactions. The most abundant prey in tridacnid cages was obviously *T. gigas* although occasionally fouling pearl oysters were quite abundant. As these are not the preferred prey of *C. muricinum, C. aquatile* or *C. pileare* their impact should be negligible. No experimental tritons and few wild tritons collected from cages were deemed to be reproductively active but care should be taken if consumption of tritons in this condition is to be considered. Overall the experimental data can be taken to represent a fair approximation to the growth and consumption of tritons in floating ocean-nurseries.

The results presented in this chapter have serious implications for clam farmers. Small and difficult to detect *C. muricinum* of say 11 mm in length can be expected to consume around 130 mg fresh weight of clam tissue per day equivalent to one 18-mm *T. gigas*. A full-sized *C.*

muricinum of say 43 mm may consume over the same time period 270 mg of clam tissue. Thus small tritons which are easily overlooked and very difficult to exclude from cages (Govan et al. 1993) have a disproportionately high impact on losses of clam biomass. Clam cages are rarely checked more frequently than every 3 days and heavy triton infestations could exact high mortality.

It is true that larger tritons are capable of killing larger clams than small ones (Perron et al. 1985; c.f., Chapter 2) but it is not necessarily correct to imply that emphasis should be placed on removing the large tritons (Perron et al. 1985; Govan et al. 1993). As relatively few small ranellids are capable of causing the same damage in terms of tissue consumption as a large triton it may well be worth placing more emphasis on controlling the former. Unfortunately this is much more difficult than excluding or removing large tritons (Govan et al. 1993).

CHAPTER 4

Reproduction and Recruitment of *Cymatium* spp.

4.1 Introduction

The capacity of larval ranellid predators of cultured bivalves to settle on or near their prey is undoubtedly the feature of most concern to aquaculturists. This behavior has been reported for at least seven species of ranellids, including *Cymatium muricinum, C. nicobaricum, C. aquatile*, and *C. pileare*, attacking cultured bivalves such as oysters (Ostreidae), pearl oysters (Pteriidae) and tridacnid clams (see Chapter 1).

This problem has not been generally associated with gastropod predators of cultured bivalves in temperate seas such as muricid and naticid drills (Hancock 1974; Jory et al. 1984; Gibbons and Blogoslawski 1989). The capacity of predators to settle in culture cages reduces or eliminates the effectiveness of commonly used off-bottom culture techniques, such as floating or trestle cages, and other devices designed to exclude benthic predators (Jory et al. 1984).

Considerable investments in manpower are routinely made at the various facilities culturing tridacnid clams in order to detect and remove recently settled ranellids (Heslinga et al. 1990; pers. obs.). The same is true for pearl oyster cultivation operations in Okinawa (Muramatsu, pers. comm.). Infestations of juvenile ranellids in culture cages are known to be episodic or seasonal (Perron et al. 1985) but otherwise little is known of the reproductive biology and factors affecting recruitment of these gastropods.

This chapter focuses on the reproductive biology of the family based on a review of published information and observations of reproduction and recruitment of *C. muricinum, C. pileare, C. aquatile* and *C. nicobaricum* in Solomon Islands. Factors affecting recruitment of these four species are examined further in Chapter 5.

Reproduction in the Ranellidae

Mesogastropods, to which the Ranellidae belong, generally transfer sperm through copulation and fertilization takes place internally (Webber 1977). Sexes of members of the Ranellidae are always separate (Kilburn and Rippey 1982). The anatomy of the genital systems of *Ranella australasia australasia, C. parthenopeum parthenopeum* and *Cabestana spengleri* from New Zealand was found to be relatively advanced, with the female reproductive system in particular, being comparable to that of neogastropods (Laxton 1969). The reproductive systems of *C. muricinum* and *C. nicobaricum* were found to be similar to those described for the New Zealand ranellids (Houbrick and Fretter 1969).

Pairing and copulation have been described wherever mating has been observed between ranellids, specifically: *C. nicobaricum* (Houbrick and Fretter 1969), *Charonia tritonis variegata* (Percharde 1972), *Ca. spengleri, R.a. australasia, C.p. parthenopeum* and *Ch. lampas rubicunda* (Laxton 1969).

Ranellids deposit their eggs in proteinaceous capsules (oothecae) as do other advanced mesogastropods and neogastropods (Webber 1977). The oothecae are relatively thin-walled compared to those of neogastropods and a pre-formed exit aperture is lacking (Houbrick and Fretter 1969; Laxton 1969). Two characteristic shapes of egg mass have been described, the most commonly reported is cup-shaped, consisting of a hemispherical sheath of tough gelatinous material attached at the base with the opening facing outwards. The internal surface of the hemisphere is covered by a single layer of elongated oothecae attached by their bases perpendicularly to the hemispherical sheath. These cup-shaped egg masses have been described for *C. nicobaricum* (Houbrick and Fretter 1969; Purtymun 1974), *C. corrugatum corrugatum* (Ramón 1991), *C. parthenopeum echo* (Arakawa 1960), *C. muricinum* (Boullaire 1953), *C. parthenopeum parthenopeum* (Laxton 1969), *Ca. cutacea cutacea* (Ramón 1991), *Ca. spengleri* (Anderson 1959; Laxton 1969; Riedel 1992), and *Linatella caudata* (Thangavelu and Muthiah 1983).

Ganapati and Sastry (1973) report a similar shaped egg mass from *C. pileare* attached to the operculum of the parent. However, this report is probably erroneous as the figured specimen is clearly not *C. pileare* but a member of the Bursidae which are also known to produce similar egg masses (D'Asaro 1970).

The other shape of egg mass reported consists of an irregular flat mass conforming to the shape of the substrate and in which the oothecae are deposited independently. The oothecae are generally larger than those of species which lay cup-shaped masses. Species producing irregular egg masses are *Ch. lampas lampas* (Cazaux 1972), *Ch.l. rubicunda* (Laxton 1969), *Ch. tritonis variegata* (Berg 1971; Percharde 1972), *Fusitriton magellanicus laudandus* and *R. australasia australasia* (Laxton 1969).

Tonnaceans, and in particular ranellids, are known to be aggressive brooders (D'Asaro 1970; Riedel 1992) and external brooding was reported in all species of *Cymatium* and *Cabestana* and also in *R.a. australasia, Ch.l. rubicunda* and *L. caudata*. However, Cazaux (1972) states that egg-laying in *Ch.l. lampas* occurs over approximately 15 days and that during this period the egg mass is partially covered by the parent's foot but warns that this should not be falsely interpreted as brooding and that the adult abandons the mass as soon as laying is completed. The possibility that this is the case with *Ch.l. rubicunda* cannot be totally rejected with careful reading of the work of Laxton (1969).

Data on fecundity of ranellids are sparse. Around 100 oothecae were deposited by single specimens of *C. nicobaricum* and *C. gemmatum* (Houbrick and Fretter 1969), *C. muricinum* (Boullaire 1953) and *Ch.l. lampas* (Cazaux 1972). The number of eggs per capsule reported varies considerably between and within species and although most authors checked for the existence of nurse eggs, none were observed.

Riedel (1992) found that the spawn of *Ca. spengleri* contains between 200 and 350 egg capsules and a single spawn houses around one million embryos. *L. caudata* was observed to deposit 271 oothecae containing an estimated 346,000 eggs (Thangavelu and Muthiah 1983). *Ch.l. lampas* deposited between 200,000 and 250,000 eggs (Cazaux 1972). An egg mass being brooded by *C. gemmatum* contained approximately 40,000 eggs (Houbrick and Fretter 1969) and roughly 660,000 larvae were reported to hatch from an egg mass laid by a specimen of *C. nicobaricum* maintained in an aquarium (Purtymun 1974).

Ca. spengleri develop inside the oothecae for 2-4 weeks (Anderson 1959; Laxton 1969) similar to *C.p. parthenopeum* but less than *R. australasia* (3 months) and *Ch.l. rubicunda* (2 months) (Laxton 1969). Hatching continues in *Ca. spengleri* over a period of 1 week before all the egg capsules are empty. Larvae of *Ca.c. cutacea* emerged from the oothecae after 27 days, 18 days in the case of *C.c. corrugatum* (Ramón 1991) and 38 days in the case of *Ch.l. lampas* (Cazaux 1972). In these three cases hatching took place over a period of several days. Hatching of *C. nicobaricum* larvae took place 21 days after spawning and all larvae emerged within a day (Purtymun 1974). Comparison of these published incubation periods is hindered because their duration can be expected to depend partly on temperature (Ramon 1991).

Early gastropod shell growth is usually defined in terms of growth before and after metamorphosis. The protoconch consists of shell growth that takes place before metamorphosis, subsequent shell growth forms the teleoconch (Lima and Lutz 1990). In planktotrophic larvae (including those of most Tonnoidea) two stages of protoconch formation may be observed. The protoconch I or embryonic shell consists of less than two whorls and is formed within the egg capsule before hatching. Shell growth after hatching and before metamorphosis comprises the protoconch II consisting of 2.5 to 4 whorls (Waren and Bouchet 1990).

Most ranellid larvae emerge from a hole in the tip of the oothecae as planktotrophic veligers (Laxton 1969; Cazaux 1972; Ramón1991) with a fully formed protoconch I. Larvae of *Ca. spengleri* and *L. caudata* have been reported to settle and crawl within a few days of hatching (Anderson 1959; Thangavelu and Muthiah 1983). Riedel (1992) re-evaluated the ontogeny of *Ca. spengleri* and concluded that there was no evidence of direct development, Anderson's results being attributed to either abnormal development or that the egg mass belonged to a different species. It is probable that the results of Thangavelu and Muthiah (1983) are also abnormal, possibly due to disturbance of the normal incubation periods or artifacts of the experimental techniques.

The larvae of *C.c. corrugatum* and *Ca.c. cutacea* measure 290 and 240 μm in shell length respectively on hatching (Ramon 1991) and *Ca. spengleri* measures 200 μm (Riedel 1992). Bandel (1975) described recently hatched larvae of *C. nicobaricum* and *C. martinianum* with lengths between 0.28 and 0.30 mm. *Ch.l. lampas* larvae measure 430 μm on hatching (Cazaux 1972) and recently hatched *Ch.t. variegata* are reported to measure 770-930 μm (Berg 1971). Nothing further appears to be known about the early planktotrophic stages of these ranellid larvae.

Larval ranellids make a reappearance in the scientific literature at a size of several millimeters floating amongst the plankton of ocean currents, hundreds or thousands of kilometers from land (Lebour 1945; Laursen 1981; Scheltema 1966, 1971a). Larvae of various species of *Cymatium* have received attention because they are "teleplanic", i.e., they are larvae of benthic, continental shelf, animals capable of a long larval development in which they disperse over long distances in the open sea (Scheltema 1971a).

Morphological adaptations of teleplanic larvae of *Cymatium* which increase buoyancy and otherwise facilitate a planktonic existence have been described. Work on *C. parthenopeum* suggests that after an initial (presumably nearshore) developmental period in which the protoconch II is formed, the larvae halt growth during transoceanic transport and shell calcification is greatly reduced (Pechenik et al. 1984) or calcified shell may even be resorbed (Richter 1984). These larvae are aided by four large velar lobes used for swimming and feeding (Scheltema 1971a, 1971b) which may extend up to a total diameter of 10 times the larval shell length (illustration in Lebour 1945).

Laursen (1981) described teleplanic larvae of 12 species of *Cymatium* from plankton tows in the North Atlantic including *C. nicobaricum* (4-5 mm in shell length), *C. muricinum* (3.50-3.75 mm), *Linatella caudata* (2.0-2.5 mm) and *C. pileare* (4-5 mm). This last species is probably actually *C. martinianum* which replaces *C. pileare* in the Atlantic (Beu 1985).

Based on the size of larvae from Atlantic plankton tows and rough estimates of larval growth, Scheltema (1971b) suggested that *C. nicobaricum* and *C. parthenopeum* may remain in the plankton for a minimum developmental period of around 200 and 150 days, respectively. Subsequent to this obligatory developmental period, larvae are capable of settlement but may delay settlement until an appropriate cue is encountered. This delay period may extend for over 100 days, during which little growth is experienced, giving a total planktonic life more than long enough to permit transatlantic transport.

Scheltema (1971a, 1971b, 1977) argues convincingly that such teleplanic larvae serve as a genetic link between geographically isolated populations of these benthic species explaining the wide distribution of ranellids in both the Atlantic (Scheltema 1971a) and the Pacific Oceans (Scheltema 1986).

Some teleplanic larvae captured in plankton samples have been observed to metamorphose in aquaria, specifically *C. nicobaricum* (Lebour 1945; Scheltema 1971b) and *C. pileare* (Lebour 1945). No field observations of metamorphosis or settlement have been reported but where recruitment is mentioned it is invariably reported to be episodic or seasonal (Thangavelu and Muthiah 1983; Villalobos and Baez 1983; Perron et al. 1985; Heslinga et al. 1990).

4.2 Methods

Reproduction of Cymatium *spp.*

Fully grown individuals of *C. aquatile, C. muricinum, C. nicobaricum* and *C. pileare* were placed, according to species, in wire mesh cages suspended inside an 80-l aquarium supplied with constantly running seawater, pumped directly from the nearby sea. During the 20-month course of the experiment usually at least four specimens of each species were contained in each of four cages but the number was sometimes reduced due to the removal of spawning animals. It was not always possible to establish the sex of the tritons and if no sexual activity was observed (courtship, copulation, egg-laying) over a couple of months then fresh tritons were introduced.

Tritons were fed regularly with mantle tissue from adult *T. gigas* previously sacrificed for other purposes and stored frozen. All tritons were observed to feed on this carrion but preferred live clams when available, especially *C. aquatile* and *C. pileare*. The only substrate suitable for egg-laying in each cage was a small, wide-necked glass jar. When egg-laying was observed to commence the other tritons were temporarily removed from the cage to avoid disturbances to the parent triton. When egg-laying was finished, the glass jar with egg mass and parent was removed carefully and placed in a separate, smaller aquarium until hatching.

Depending on factors such as time of hatching and whether the egg mass was kept in a static or flow-through aquarium, hatched veligers were collected, and at least one subsample was examined, measured, and counted under the microscope. Hatched veligers of each species were kept in a variety of hatchery facilities and a number of different, small-scale, attempts were made to feed and induce settlement of the larvae.

Dead veligers of each species in which the tissue had rotted away were rinsed in fresh water on fine mesh sieves and sun-dried. These samples were sent to Heather Winsor of James Cook University, Queensland, who performed scanning electron microphotographs using a Philips XL20 S.E.M.

Recruitment of Cymatium *spp. to Ocean-Nurseries*

Field data on occurrence of *Cymatium* spp. were obtained from the two major tridacnid ocean-nurseries run by ICLARM in Solomon Islands (Fig. 1.2). The first, where most ocean-nursery clam stock is held, is located just off the eastern shore of Nusatupe Island (NT) near Gizo in Western Province (8°06'N, 156°52'E). This site is generally well flushed with clear sea-water and is located on a sandy reef flat with coral outcrops and patches of seagrass. The number of cages increased over the study period, most being of the trestle type but also floating and benthic cages (c.f., Chapter 1). This ocean-nursery was gradually moved approximately 50 m offshore after February 1992.

The second ocean-nursery site was located less than 100 m offshore from the ICLARM Coastal Aquaculture Centre (CAC) at Aruligo on Guadalcanal Island (9°18'N, 159°48'E). This site is also well flushed with sometimes strong tidal currents and is exposed to wind-driven waves. The water is often turbid with strong influence from nearby rivers during the rainy season. The seabed shelves steeply and is composed of coral rubble and bommies giving way to sand with increased depth and distance from shore. During the study period virtually all cages were of the floating type.

During the course of routine and, usually, daily checks of ocean-nurseries for the purposes of cage maintenance and predator control, staff supervised by I. Lane (NT) and T. Shearer (CAC) were requested to record species, size and cage of origin of all ranellids. For this purpose specially designed forms were provided as well as containers for snail collection and plastic vernier calipers with which tritons were measured to the nearest 0.1 mm.

Recently settled ranellids present few if any of the characteristics of adult tritons and therefore may represent a problem for identification. Examination of sub-adult tritons of the four common species (c.f., Plates III and IV) suggested that the shape of the protoconch II was a distinctive feature of each of these species and this was confirmed by A. Beu (pers. comm.; Beu 1988). Samples, photographs and descriptions of relevant snails and their protoconchs were circulated to ocean-nursery staff.

Raw data were provided by I. Lane and J. Hambrey regarding details of cage types and deployment and also numbers and sizes of tridacnids in the ocean-nurseries at the regular censuses.

Data handling. All raw data were entered into the database program DataEase or Supercalc5 spreadsheets using MS-DOS operated computers. Data were processed and subsequently exported to an interactive statistical analysis program, Statistix (Analytical Software 1991). This program provides the same range of data analyses and manipulation techniques as the better known packages but has the advantage of being a single integrated system.

Biological data. Approximate settlement dates were calculated for *C. muricinum, C. aquatile* and *C. pileare* collected at NT and CAC by using the predictive regressions obtained for linear growth (Tables 3.3 and 3.4). Most *T. gigas* in ocean-nurseries during periods of heavy *C. muricinum* settlement were less than 60 mm SL, averaging around 30 mm SL. In the case of *C. muricinum*, which was found to grow slower when feeding on larger clams, a growth rate of 0.56

$mm \cdot day^{-1}$ (SE 0.05, n=9) was calculated resulting from the mean of growth rates of all tritons initially fed on clams less than 60 mm SL (mean: 28.1 mm SL).

The time taken for tritons to reach their size at collection was calculated as described by Sokal and Rohlf (1981) for estimation of X from Y in predictive regression:

$$\text{Time} = (\text{Size} - a)/b \qquad \textbf{...4.1)}$$

where "b" is the growth rate of juvenile ranellids (c.f., Table 3.3) and "a" is the size of the protoconch II of the species in question.

Subtracting this calculated time from the collection date of each triton gives an estimate of the date at which tritons started adding teleoconch shell material to the protoconch. For the purposes of this study and based on the literature reviewed in Section 4.1 this date is considered the "settlement" date. The settlement date could not be calculated for *C. nicobaricum* as data were lacking on juvenile growth rates of this species.

The estimated settlement data for each triton species in each cage type was converted to density of settlement by dividing the number of tritons settled in a given cage type (floating, trestle or benthic) and time period (months or weeks) by the available area of that cage type in the same time period. Settlement data were available for a period of 24 months at the CAC and for 20 months at NT. During the last 6 months of the experimental period the NT ocean-nursery was moved some 50-100 m offshore.

This approach makes a variety of assumptions, two major ones being:

1. Growth in the field follows approximately the same pattern and rates as obtained in aquarium experiments.
2. The ranellids settle with a complete protoconch II and commence growing immediately.

Field estimation of* C. muricinum *growth rate. The first assumption and the value for growth rate used in equation (4.1) were tested by analyzing length frequencies of collected *C. muricinum* during periods of peak settlement over subsequent days. Raw data were examined for datasets in which clear size-frequency peaks were observable over at least three consecutive sampling days. The size-frequency distributions of each sample were split into age groups using the Bhattacharya method (Sparre et al. 1989) which is included in the Compleat ELEFAN, a package of computer programs produced at ICLARM by Gayanilo et al. (1988) (see also Hilborn and Walters 1992).

As *C. muricinum* growth was expected to be linear for the small tritons which composed these samples the mean sizes of each age group for successive days were regressed against time using Model II or GM linear regression (c.f., Chapter 3) to estimate linear growth rate.

The second assumption is based on the limited reports in the scientific literature as discussed in Section 4.1. and also the size of recently settled *C. muricinum* as collected from ocean-nurseries around the Pacific.

Statistical Analyses

The time-series nature of the datasets, in which the random variables are not mutually independent, precludes analysis using standard parametric statistics in which mutual independence is a strong assumption (Diggle 1990). The serial dependence of both monthly and weekly datasets was examined using the autocorrelation function from Statistix, based on computations in Box and Jenkins (1976).

In order to examine whether fluctuations in recruitment between species or cage types were correlated it is first necessary to remove serial dependence from the data. This can be achieved in the case of the monthly data, which is only serially correlated at a lag of one month, by the process of first differencing (Thompson and Page 1989). First order differences were calculated for each variable using equation (4.2) (Diggle 1990; Pepin 1990).

$$X_d = X_t - X_{t-1} \qquad ...4.2)$$

where X_d represents the change in the value of the variable X_t from the previous time period. Correlations of these first-order differences were calculated using rank correlations. Spearman's rank correlation coefficient (r_s) was selected in preference to that of Kendall (tau) as r_s is more appropriate when there is less certainty about the reliability of close ranks (Sokal and Rohlf 1981). However both tests are expected to produce similar results (Bailey 1981; Analytical Software 1991).

The significance of estimated values of r_s can be tested as an ordinary product-moment correlation for $n > 10$ (Sokal and Rohlf 1981). Two tailed significance tests on r_s were carried out automatically using the Pearson correlation function in Statistix but in cases where $n \leq 10$, or significance levels were close to 0.05 or 0.01, specific tables for r_s were used (Kendall and Gibbons 1990).

Different overall numbers of each ranellid species were collected from cages at the CAC and different numbers of *C. muricinum* were collected in each cage type at NT. The significance of these differences was tested using a pairwise sign test of the monthly data. This test requires virtually no assumptions about the distribution of the paired samples (Analytical Software 1991; Sprent 1993).

4.3 Results

Reproduction of Cymatium *spp.*

The reproductive behaviour of *C. aquatile, C. muricinum, C. nicobaricum* and *C. pileare* was observed under aquarium conditions. As far as could be ascertained, mating, egg-laying, incubation, development and hatching followed the same general pattern regardless of species. Records pertaining to reproduction in the four study species are summarized in Table 4.1.

Pairing between males and females was observed and the male would accompany the female side by side or more usually, attached to the body whorl of the female shell. This behaviour continued for several days and occasionally copulation was observed. However, some tritons were observed to spawn when no copulation could have taken place for at least 1 month.

Female tritons laid egg capsules in the corners of aquaria or in the substrata introduced for that purpose, over a period of 2 to 4 days (Fig. 4.1). The egg mass formed a hemispherical cup-shaped mass as described in Section 4.1, achieved by laying egg capsules in a spiral starting from the center of the base and gradually tilting each new capsule towards the center of the hemisphere. The size of the egg masses was variable but never significantly wider than the parent's body whorl. The egg capsules were approximately cylindrical with a rounded apex and flattened base although the exact shape was variable. The size of the egg capsules was also variable, between 3 to 5 mm in length and 1 to 2 mm in diameter. The female tritons remained attached to the aperture of the egg

Table 4.1. Details of reproduction in captivity of four species of *Cymatium*. The size of parent snail, number of egg cases laid, number and size of hatched larvae are shown where measured. "Development" is the total number of days from commencement of egg-laying on the "spawning date" until hatching. The number of days from the spawning date to full moon. An asterisk indicates that the parent snail consumed its own eggs before hatching could take place.

Species	Snail size (mm)	Egg cases	Larvae (number)	Larvae size (μm)	Develop-ment (days)	Spawning date	Days from full moon
C. aquatile	-	-	200,000	-	19	18-Feb-91	-10
C. aquatile	50.6	168	-	230	15	21-May-91	-7
C. muricinum	-	-	-	-	11	18-Feb-91	-10
C. muricinum	-	-	30,000	-	10	18-Feb-91	-10
C. muricinum	-	186	28,000	240	11	19-May-91*	-9
C. muricinum	47.1	118	-	-	-	28-Aug-91*	+3
C. muricinum	48.4	137	-	-	22	12-Sep-91*	-11
C. muricinum	36.4	140	-	-	-	11-Nov-91*	-10
C. muricinum	47.0	186	-	-	-	13-Nov-91*	-8
C. muricinum	-	-	-	-	-	15-Nov-91*	-6
C. muricinum	43.4	200	-	-	-	20-Nov-91*	-1
C. muricinum	45.8	210	-	-	-	12-Dec-91*	-9
C. muricinum	45.9	-	-	-	-	06-Feb-92*	-12
C. muricinum	44.0	158	-	-	-	17-Aug-92*	+4
C. muricinum	41.9	-	-	-	-	31-Aug-92*	-12
C. nicobaricum	39.3	140	65,000	230	12	23-Jan-91	-7
C. nicobaricum	34.4	-	-	-	17	19-May-91	-9
C. nicobaricum	43.2	164	-	240	12	23-Aug-91	-2
C. nicobaricum		-	-	-	-	01-Oct-91	-4
C. nicobaricum	56.9	200	-	-	-	14-Jan-92	-5
C. nicobaricum	34.1	-	-	-	27	30-Apr-92	+13
C. nicobaricum	35.7	134	-	-	-	13-Aug-92*	0
C. nicobaricum	55.4	-	-	-	-	22-Aug-92*	+9
C. pileare	46.2	-	-	250	18	17-Sep-91*	-6
C. pileare	34.0	194	-	-	-	18-Dec-91*	-3
C. pileare	48.2	-	-	-	-	17-Aug-92*	+4

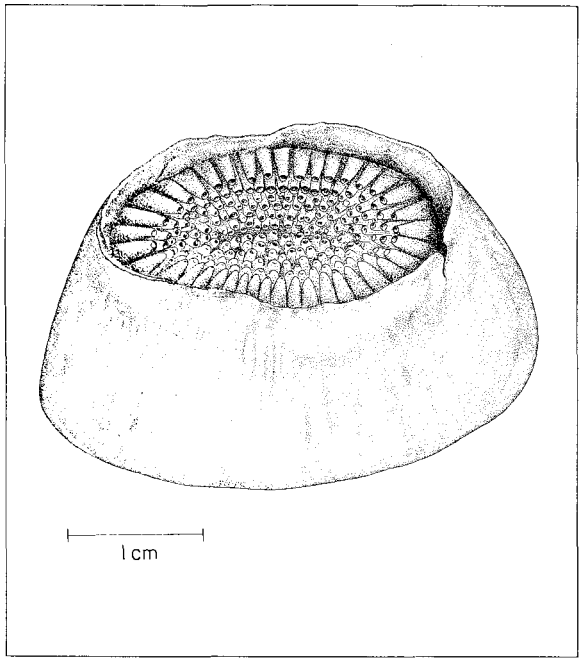

Fig. 4.1. Egg mass of Cymatium pileare. *Note the holes in the tips of individual egg capsules through which larvae escaped on hatching.*

masses during the whole incubation period, but tritons were observed to consume all their eggs and to abandon the egg mass if disturbed.

From the limited data available, no evidence of seasonal spawning in *C. muricinum* and *C. nicobaricum* could be detected, much less so for *C. aquatile* and *C. pileare* for which fewer observations are available. *C. muricinum* commenced egg-laying 6 to 12 days before full moon in 10 out of 13 cases while *C. nicobaricum* commenced egg-laying 0 to 6 days before full moon in 5 of 8 cases.

The duration of the incubation period varied greatly, from 10 to 22 days in the case of *C. muricinum* and 12 to 27 days for *C. nicobaricum*. Larvae hatched through a hole, approximately 0.5 mm in diameter, which formed in the apex of the egg capsules. When hatching took place during the day time and was observed directly, it occurred over a period of 20 minutes to several

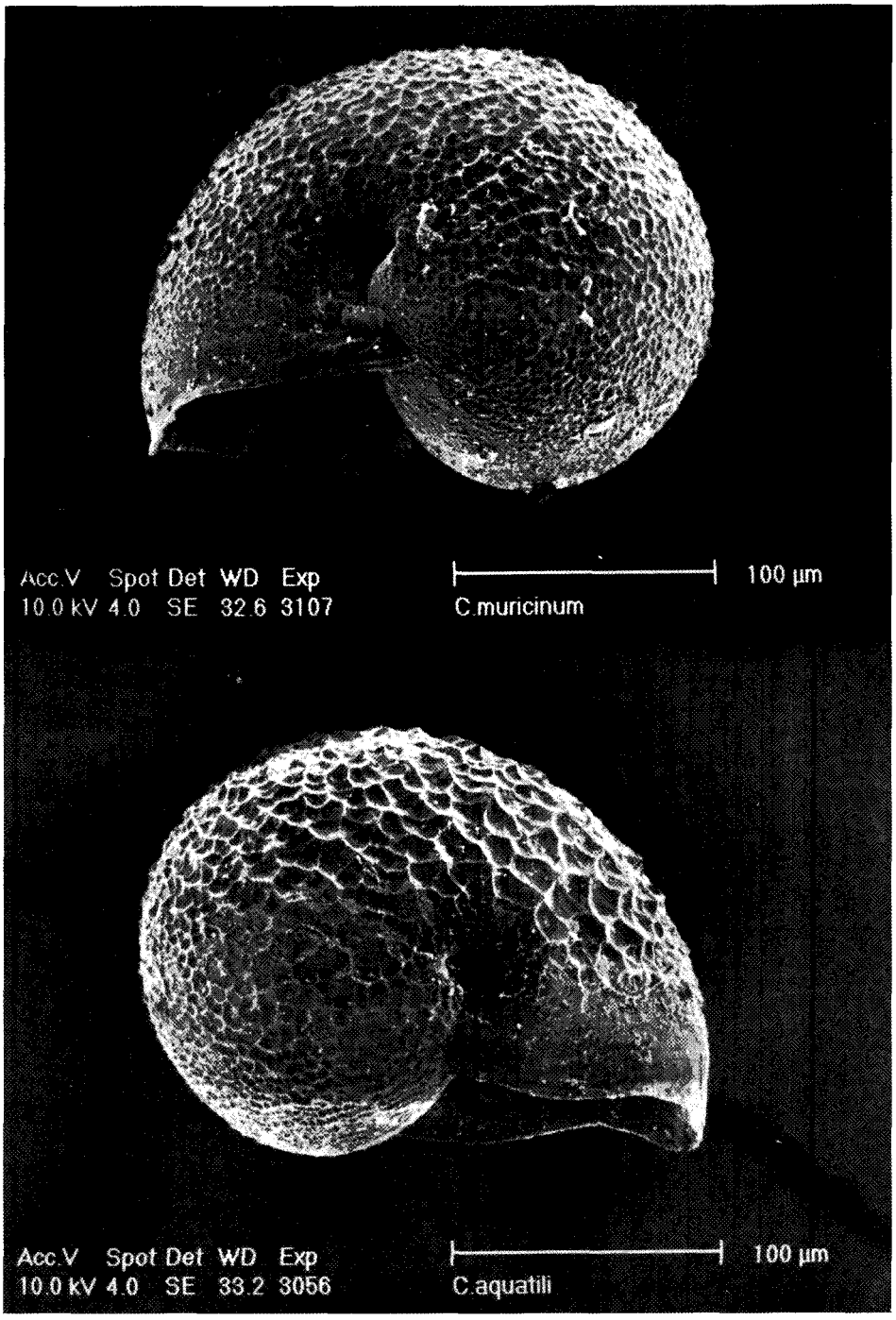

Plate VII. Scanning electron micrographs of larval shells (protoconch I) of recently hatched *Cymatium muricinum* (upper) and *C. aquatile* (lower). (Photos by H. Winsor).

hours. In one case a *C. nicobaricum* disturbed towards the end of the incubation period appeared to induce hatching.

From the data available, the larvae of all four species appear to be 230-250 µm in length on hatching, with an aperture of about 100 µm. The shells of recently hatched veligers (protoconch I) comprise roughly one whorl, the entire surface of which is covered with an interlacing network of sinuate ridges which describe small, irregularly sided polygons. The edge of

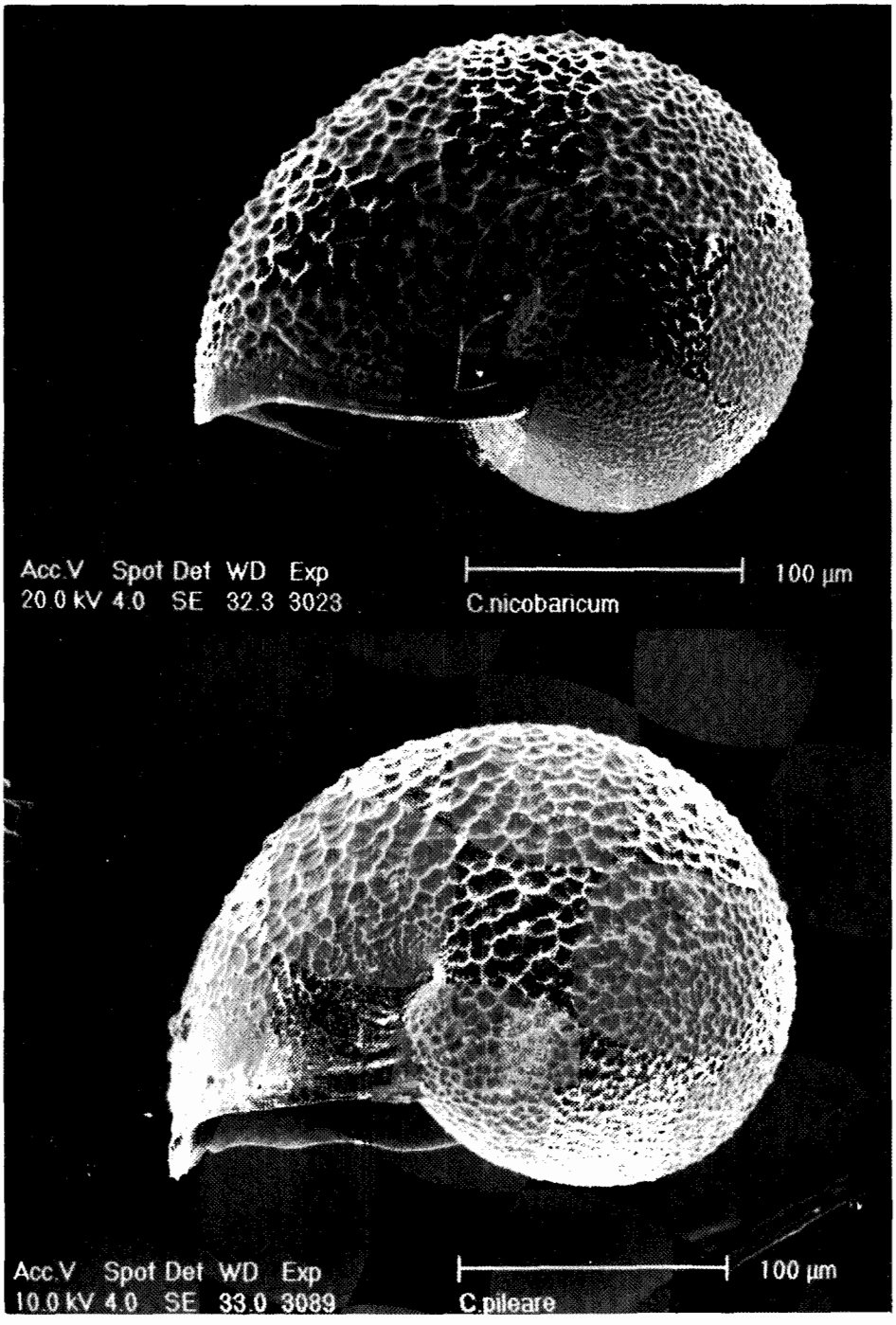

Plate VIII. Scanning electron micrographs of larval shells (protoconch I) of recently hatched *Cymatium nicobaricum* (upper) and *C. pileare* (lower). (Photos by H. Winsor).

the slightly thickened shell lip is smooth. No obvious features distinguished the larvae of the different species (Plates VII and VIII). The shells are colorless or faintly brown-tinged except those of *C. nicobaricum* which are a darker brown, sometimes purple-tinged.

A few aberrant shells of *C. pileare* and *C. nicobaricum* were observed, in which the embryonic shell had not formed a spiral but rather an extended sock-shape such as described by Bandel (1975) for *C. nicobaricum.*

The veligers possess a bilobate velum which is fringed with actively moving cilia approximately 50 μm in length, the foot and a small operculum are also visible. On hatching, the veligers actively swum upwards into the water column apparently by means of ciliary movements.

The numbers of larvae produced was recorded at 30,000-70,000 and, in one case, up to 200,000 per egg mass. Veligers were maintained in aquaria for up to 2 weeks but despite efforts including feeding with algal blooms, artificial diets and flow-through systems the veligers invariably died with little appreciable growth. The addition of various combinations of juvenile tridacnids, stones covered with encrusting algae, potassium chloride (Pechenik and Heyman 1987), fouling algae and pearl oysters did not increase growth, induce metamorphosis or increase survival as far as could be ascertained. The best survival was obtained using natural algal blooms from fertilized tanks of seawater and daily sieving of larvae and exchange of the water.

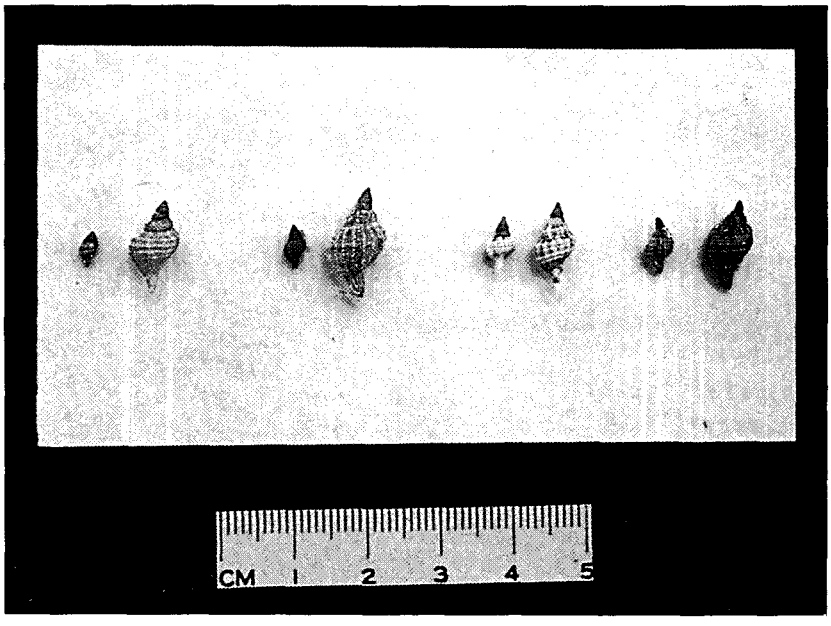

Plate IX. Juvenile shells of recently settled specimens of four species of *Cymatium*. Pairs of shells are from left to right: *C. muricinum, C. aquatile, C. nicobaricum* and *C. pileare*. Note the distinctive protoconch II of each species. (Photo by H.Govan).

Recruitment of Ranellids to Ocean-Nurseries

The following characteristics of the protoconch II were found to be most useful in distinguishing juveniles of the four ranellid species commonly found in ocean-nurseries (Plate IX). The protoconch of *C. aquatile* is the largest of the four species, conical in shape with very slightly convex sides. *C. muricinum* has a wide protoconch which although conical in shape has strongly convex sides and sits on the teleoconch at a slight angle to its axis of coiling giving the impression of being "crooked". *C. nicobaricum* has a very sharp protoconch conical in shape but straight or even slightly concave sides. The protoconch of *C. pileare* is the narrowest with virtually parallel sides for the oldest whorls and may also be situated at a slight angle on the teleoconch.

Abundance of recently settled* Cymatium *spp. Over 20 months 7,114 ranellids were collected from floating, trestle and benthic ocean-nursery cages at Nusatupe (Table 4.2). During the last 14 months, when records were kept for all species, 86% of ranellids collected consisted of *C. muricinum*, 6% *C. nicobaricum*, 5% *C. pileare*, 3% *C. aquatile* and less than 1% *C. mundum* and *C. comptum* combined. A maximum of 39 *C. muricinum* were collected per m^2 of

Table 4.2. Collection of four species of *Cymatium* gastropods from cages at the Nusatupe tridacnid ocean-nursery, Solomon Islands. Total numbers of snails collected and monthly densities measured as snails collected per m^2 of available cage space are shown for three consecutive periods of ocean-nursery operation. N/A = data not available.

Species	Cage type	January - April 1991		May 1991-January 1992		February - July 1992	
		Total	Density (range)	Total	Density (range)	Total	Density (range)
C. aquatile	Floating	N/A	N/A	78	0.87 (0.4-2.4)	17	0.27 (0.0-0.5)
	Benthic	N/A	N/A	5	0.18 (0.0-1.6)	1	0.02 (0.0-0.1)
	Trestle	N/A	N/A	73	0.25 (0.1-0.5)	46	0.11 (0.0-0.2)
C. muricinum	Floating	56	3.2 (1.5-4.8)	1,662	19.47 (3.7-39.0)	123	2.01 (0.1-4.8)
	Benthic	19	2.7 (0.0-5.0)	508	12.31 (1.2-31.5)	74	1.28 (0.0-2.6)
	Trestle	309	4.0 (0.9-6.9)	2,844	10.09 (0.7-24.1)	544	1.43 (0.0-2.4)
C. nicobaricum	Floating	N/A	N/A	181	2.08 (0.4-3.8)	14	0.23 (0.0-0.5)
	Benthic	N/A	N/A	10	0.19 (0.0-0.6)	7	0.12 (0.0-0.4)
	Trestle	N/A	N/A	149	0.50 (0.0-1.0)	36	0.09 (0.0-0.2)
C. pileare	Floating	N/A	N/A	53	0.63 (0.2-1.8)	24	0.34 (0.0-1.2)
	Benthic	N/A	N/A	12	0.25 (0.0-0.6)	15	0.25 (0.0-0.8)
	Trestle	N/A	N/A	69	0.24 (0.1-1.0)	134	0.33 (0.0-0.7)

Table 4.3. Collection of four species of *Cymatium* gastropod from cages at the Coastal Aquaculture Centre tridacnid ocean-nursery, Guadalcanal Solomon Islands. Total numbers of snails collected and monthly densities measured as snails collected per m^2 of available cage space are shown for a 2-year period from October 1990.

Species	Total	Density	(range)
C. aquatile	134	0.30	(0.0-2.6)
C. muricinum	421	0.80	(0.0-4.2)
C. nicobaricum	108	0.23	(0.0-0.8)
C. pileare	176	0.36	(0.0-2.2)

cage per month with a weekly maximum of 22.4. Ranellids were collected from cages within a few days of these being deployed.

Lower densities of ranellids were collected from floating cages at the CAC over 24 months (Table 4.3). A total of 839 ranellids were collected composed of *C. muricinum*, 50%; *C. pileare*, 21%; *C. aquatile*, 16%; and *C. nicobaricum*, 13%. A maximum monthly density of 4.2 *C. muricinum* per m^2 of cage was collected.

Field estimation of* C. muricinum *growth rate. Two sets of data from Nusatupe, appropriate for length-frequency analysis were found, corresponding to two 4-day periods in May and June 1991, respectively. In each of these datasets a single peak of *C. muricinum* recruitment appeared to have occurred that was clearly discernible in collections made over three subsequent days (Fig. 4.2). Model II regression of the modes of these peaks suggested a growth rate (± s.e.) of 0.579 mm·day^{-1} (±0.11, $r^2 = 0.931$) for the May data and 0.548 mm·day^{-1} (±0.06, $r^2 = 0.972$) for the June data. In all other datasets examined either clear peaks were not distinguishable or these were not detectable in subsequent samples.

Based on the above, the figure of 0.56 mm·day^{-1} for growth of *C. muricinum* obtained under laboratory conditions appeared to be a reasonable value to use for the back-calculation of the settlement date of collected juvenile tritons of this species.

The smallest *C. muricinum* collected from Solomon Island ocean-nurseries and also from nurseries in Kosrae (samples provided by S. Lindsay) and Palau (Perron et al. 1985) were never smaller than 3.2 mm in length. This suggests that the mean protoconch length used for this species in the present study of 3.5 mm is probably within the range of reasonable variation.

Variations in recruitment of* Cymatium *spp. Further analysis of data from the NT ocean-nursery concentrated on *C. muricinum* which was by far the most abundant species collected.

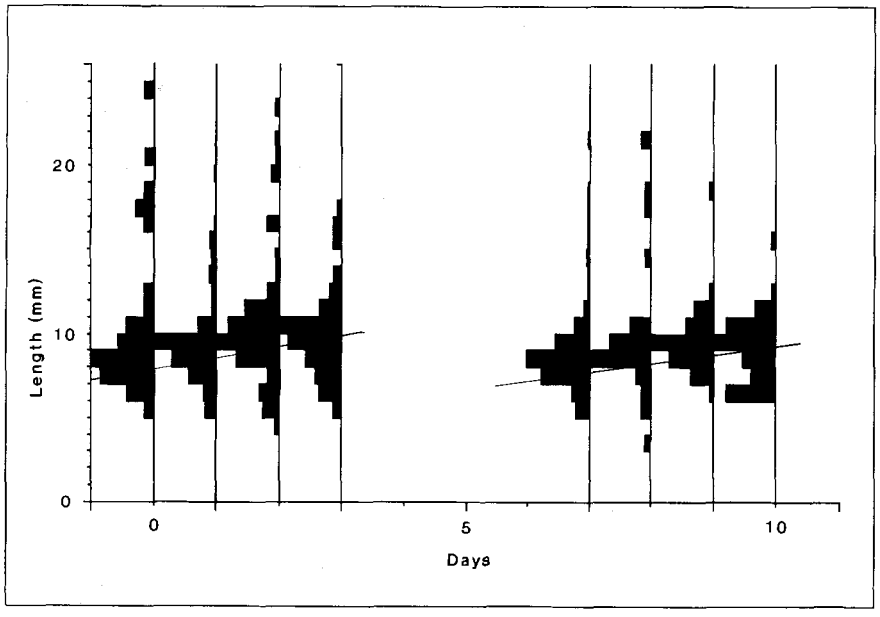

Fig. 4.2. Length-frequency samples of *C. muricinum* collected from the Nusatupe tridacnid ocean-nursery during two periods of four consecutive days. Oblique lines represent the growth of juvenile snails calculated by regressing the mode of the main component of each length frequency sample over time.

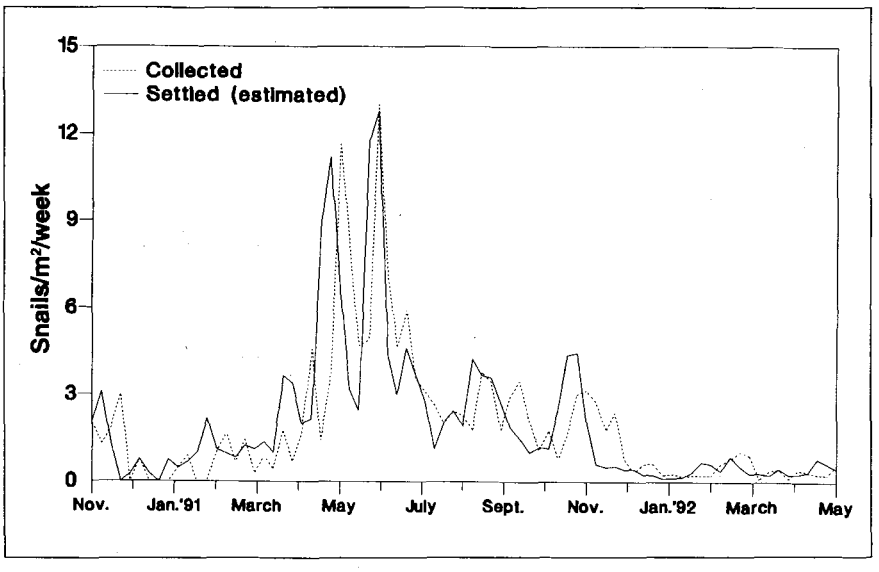

Fig. 4.3. Time-series of weekly densities of *C. muricinum* collected at the Nusatupe tridacnid ocean-nursery, Solomon Islands. Weekly densities of larvae settlement are estimated based on the size of collected snails and experimentally derived growth rates.

Weekly densities of *C. muricinum* collected at the NT ocean-nursery are shown in Fig. 4.3. The estimated settlement densities are also shown in Fig. 4.3 based on the methods and growth rates outlined above. Approximately 2.2% of tritons were considered to have exceeded the size at which their growth was described by the linear model and had to be excluded from this last analysis. These larger tritons may have been immigrants to cages from the surrounding habitat although this is extremely unlikely in the case of floating cages. More probably, the larger tritons had been overlooked during previous collections. The mean size of tritons collected from benthic cages was 11.0 mm and 2.0% of tritons were excluded from the analysis on the basis of size, the corresponding data for trestle cages were 11.8 mm and 2.4% and for floating cages 11.5 mm and 1.8%.

The plot of estimated settlement densities of *C. muricinum* (Fig. 4.3) eliminates much of the random noise apparent in the collection data and clearly defined peaks of settlement are apparent. Peaks of settlement occur every 1-2 months with maxima in May and June 1991. After February 1992, settlement appeared reduced, coinciding with the period when the ocean-nursery was moved offshore.

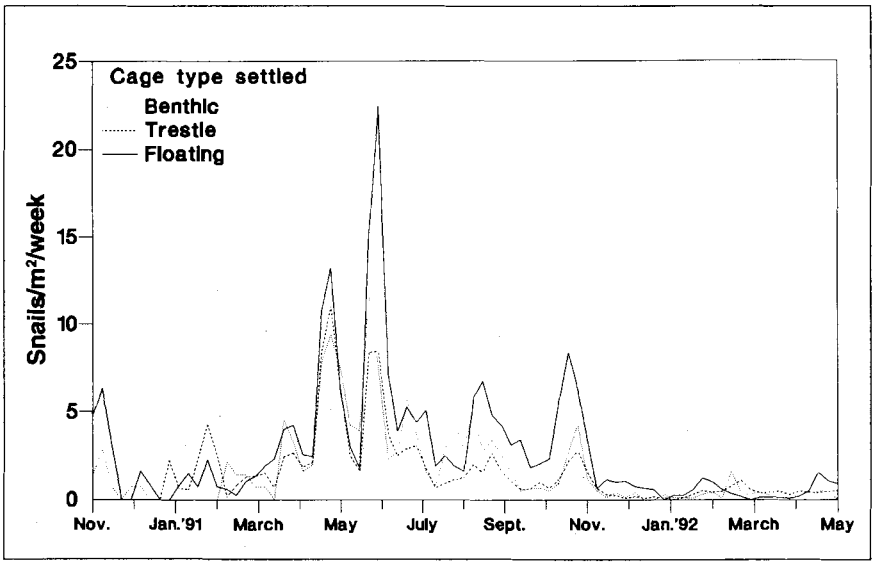

Fig. 4.4. Time-series of estimated weekly densities of *C. muricinum* settled in cages at three different depths at the Nusatupe tridacnid ocean-nursery, Solomon Islands. Cages were located on the seabed (benthic), on trestles raised off the seabed (trestles) and suspended just below the surface (floating). Densities of larval settlement are estimated based on the size of collected snails and experimentally derived growth rates.

Settlement data for *C. muricinum* in three different cage types are shown in Fig. 4.4. Paired sign tests of monthly data suggest that the density of settlement in floating cages is higher than that in benthic or trestle cages ($P < 0.05$) and that settlement is not significantly different between benthic and trestle cages ($P = 0.6$). Spearman rank correlations of the first order differences of settlement data suggest that changes in monthly settlement density are significantly correlated between cage types with r_s values between 0.635 and 0.689 ($P < 0.01$, $n = 19$).

The weekly densities of *C. muricinum* collected at the CAC are shown in Fig. 4.5 over a 2-year period. The estimated settlement density is shown, based on data from 350 of the 421 *C. muricinum* collected. The remaining 20% of tritons had exceeded the size at which their growth was described by the linear model. The mean size of all the *C. muricinum* collected at the CAC was 17.6 mm.

The estimation of settlement densities at the CAC produces more clearly defined peaks and less high-frequency fluctuations than apparent from the collection data alone. Particularly high settlement was recorded from January to April 1992 with very low levels in October and November 1991.

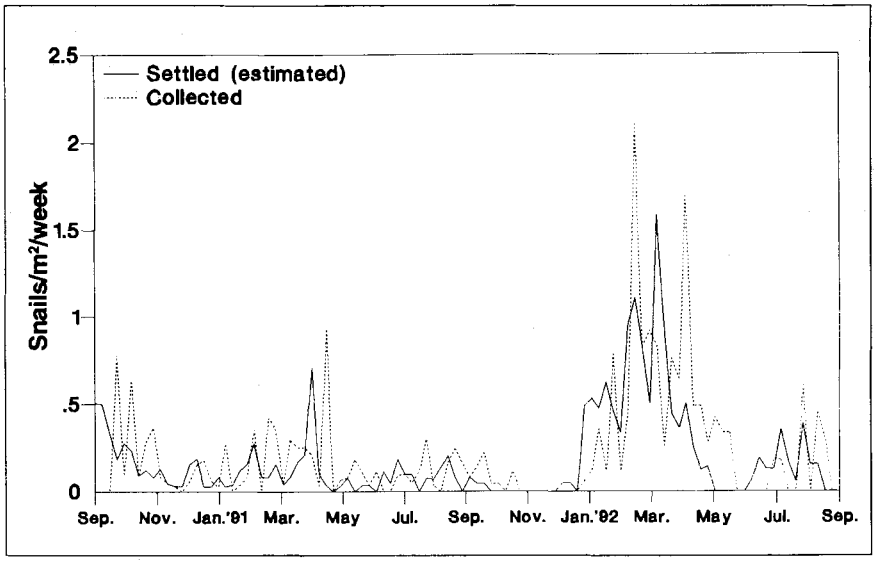

Fig. 4.5. Time-series of weekly densities of *C. muricinum* collected at the Coastal Aquaculture Centre tridacnid ocean-nursery, Guadalcanal, Solomon Islands. Weekly densities of larval settlement are estimated based on the size of collected snails and experimentally derived growth rates.

Fig. 4.6 shows the monthly settlement densities of the three species of *Cymatium*. A paired sign test suggests that significantly more *C. muricinum* settled than of the other two species ($P < 0.001$). Densities of settlement of *C. aquatile* and *C. pileare* were not significantly different ($P = 0.08$). Spearman rank correlations of the first- order differences of monthly settlement data for the three species at the CAC suggest that monthly changes in settlement density are correlated between species ($r_s = 0.500\text{-}0.678$, $n = 23$, $P < 0.015$). *C. nicobaricum* was excluded because the diet and growth of early juveniles is not known.

Autocorrelations performed on monthly settlement data from the CAC and NT showed that data were significantly autocorrelated at a lag of 1 month. First-order differencing of monthly data was found to remove any significant autocorrelation. Weekly datasets showed significant autocorrelations at lags from 1 to 4 weeks at the CAC and from 1 to 5 weeks in the case of *C. muricinum* at NT and 1 to 3 weeks in the case of *C. aquatile* and *C. pileare*.

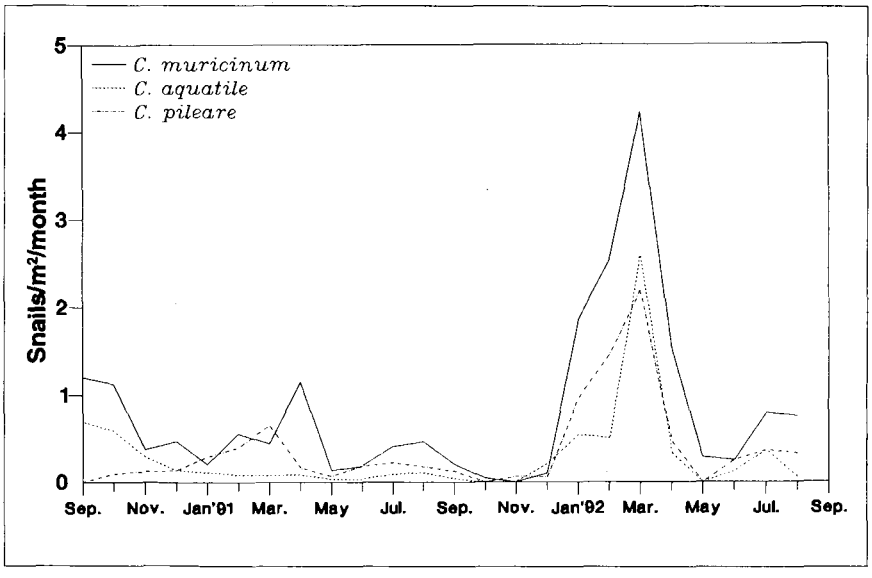

Fig. 4.6. Time-series of monthly densities of C. *muricinum*, *C. aquatile* and *C. pileare* settled at the Coastal Aquaculture Centre tridacnid ocean-nursery, Guadalcanal, Solomon Islands. Monthly densities of larval settlement are estimated based on the size of collected snails and experimentally derived growth rates.

4.4 Discussion

Reproduction in the Ranellidae

The four species of *Cymatium* studied in the present work are closely related (Beu 1985), all belonging to the subfamily Cymatiinae Iredale 1913, and *C. aquatile, C. nicobaricum* and *C. pileare* belong to the same subgenus, Monoplex. This close relationship may account for the lack of significant differences observed between the reproductive behaviors of the four species.

The egg masses were found to be cup-shaped and the female tritons were determined and aggressive brooders. Ramón (1991) suggests that three types of egg mass occur in the Ranellidae. The present work and the review by Henning and Hemmen (1993) suggest that only two types of spawn have been observed. Flat egg masses are produced by members of the genera *Charonia*, *Fusitriton* and *Ranella* while cup-shaped masses are produced by the genera *Cabestana*, *Cymatium* and *Linatella*.

Brooding appears to take place for the main purpose of protection, as development and hatching take place normally in the absence of the female (Laxton 1969). Cup-shaped egg masses are well suited to this brooding habit. Although the oothecae are thin-walled the external surfaces of the egg mass are protected by a thicker layer of horny material and the opening of the egg mass is small enough to be easily covered by the parent's foot. It is perhaps significant that the only report of a nonbrooding ranellid is that of *Ch.l. lampas* which lays flat egg masses (Cazaux 1972).

Perron et al. (1985) report that *C. muricinum* spawns throughout the year in Micronesia and no evidence was found in the present study for a yearly breeding cycle. Ranellids in more temperate latitudes such as New Zealand and Southern Australia are reported to spawn during the warmer season (Laxton 1969; Riedel 1992).

Synchronicity between spawning and lunar phase/tidal cycle is relatively common amongst tropical fish with pelagic larvae. Spawning around the time of new or full moon maximizes tidal transport of larvae on ebbing spring tides (Johannes 1978). Tidal rhythms of spawning are reported in a number of invertebrates including littorinid gastropods (Webber 1977; Giese and Kanatani 1987). Nothing is known about spawning cues of ranellids. Although there is slight evidence of lunar periodicity in the present study this may be an artifact owing to the aquarium conditions or the sparse data. It is reasonable to expect ranellids, with their long planktonic larval stage, to attempt to achieve optimum tidal dispersal although the time of hatching would be more significant in this respect than that of spawning.

The length of the incubation period for the four species of *Cymatium* studied of 10 to 27 days is within the range reported for other gastropods with planktonic larvae (Webber 1977) and similar to that of other species of *Cymatium* (c.f., Section 4.1). The duration of the incubation period varied greatly for members of the same species and did not appear to be linked to seasonal conditions such as temperature.

Female *C. muricinum, C. nicobaricum* and *C. pileare* were observed to consume their own egg masses if disturbed and sometimes spawn again subsequently. This behavior, if not an artifact of laboratory conditions, has not been reported in ranellids nor have any reports been found for other gastropods. Presumably this behavior improves the chances that energy expended on reproduction is not wasted.

The study species were observed to present a number of reproductive features which could potentially enable a high degree of control over the time veligers enter the water column. Female tritons were capable of storing sperm for more than a month, as also noted by Ramón (1991). Hatching of veligers from egg capsules takes place almost simultaneously and although the exact method of hatching is not known it is possible that in some cases this could be induced by the parent. However, whether these features and the possibly flexible duration of the incubation period really are adaptations in order to allow precise timing of the entry of veligers into the water column remains the subject of future research.

No data are available regarding the total fecundity of the study species although it is possible that two specimens of *C. muricinum* spawned twice in less than 4 months. *C. nicobaricum* in an aquarium in Hawaii was observed to spawn three times in less than a year, one of the egg masses releasing about 660,000 veligers. Captivity may cause gastropods to produce fewer eggs (D'Asaro 1970) and the number of eggs produced will depend on factors such as the age, size and nutritional status of the parent snail. It is probable that mature tritons of the species studied produce a minimum of 100,000 veligers yearly and the true figure may be as much as ten or twenty times higher.

Recently hatched larvae of *C. muricinum, C. nicobaricum, C. pileare* and *C. aquatile* share the same general features of shape and sculpture. The bilobate velum of these hatchlings bears little resemblance to the four large velar lobes reported for members of the genus during their teleplanic existence (Lebour 1945; Scheltema 1971b). Presumably these develop during the subsequent planktonic existence of the larvae.

Electron micrographs of the protoconch I have been published for the following ranellids: *C. cynocephalum, C. labiosum* and *C. parthenopeum* (Richter 1984), *C. martinianum* and *C. nicobaricum* (Bandel 1975), *C.c. corrugatum* and *Ca. cutacea* (Ramón 1991) and *Ca. spengleri* (Riedel 1992). These protoconchs and those of the species examined in this work are very similar in appearance and no distinguishing features are apparent. These protoconchs are also similar to those of certain members of the Tonnidae and Bursidae (photographs in Bandel 1975; Waren and Bouchet 1990) and it appears that the characteristics of these protoconchs although not sufficient to distinguish between species of these families are typical of planktonic larvae of the Tonnoidea (Riedel 1992).

In contrast to the findings regarding the use of the protoconch I in ranellid identification, the protoconch II was found to be sufficiently characteristic in each of the four species studied to enable species identification based on the protoconch II alone. Beu (1988) and Waren and Bouchet (1990) also found the use of the protoconch II to be important in identification of species of tonnaceans.

Ranellid larvae have never been reared to settlement or even to the stage of protoconch II formation. Most authors report total larval mortality within a few weeks of hatching, during which time the yolk supplies of *Ca. spengleri* larvae were observed to rapidly decrease. It is possible that mortality of larvae in culture occurs when the yolk supplies are finished and appropriate food is not encountered. The nature of food required is not known and live algal and artificial diets used in bivalve culture were tried unsuccessfully.

It is worth examining the obligatory developmental period estimated for ranellids by Scheltema (1971b) more closely, as this is thought to represent the minimum amount of time that the larval ranellids must remain in the plankton and will be a major factor influencing recruitment.

In calculating obligatory developmental periods (ODP) of 150 and 200 days for *C. parthenopeum* and *C. nicobaricum*, respectively, Scheltema (1971b) used a larval growth rate of 21-22 $\mu m \cdot day^{-1}$ obtained for the neogastropod *Nassarius obsoletus* over a 12-day larval phase (Scheltema 1962, 1967). The selection of this rate was due to the few data available for the growth of any gastropod larvae (Scheltema 1971b). Independently derived estimates of the duration of the larval life of the neogastropod *Thais haemostoma* were in close agreement with calculated values, a fact which increased the confidence in the rough estimates derived for other species (Scheltema 1971b).

Since 1971 more data have become available regarding the growth rates of larval gastropods which enable a reappraisal of Scheltema's (1971b) estimates for the ODP of the two *Cymatium* species. Dobberteen and Pechenik (1987) estimated larval growth rates of 27 $\mu m \cdot day^{-1}$ for *T. haemostoma* and 65 $\mu m \cdot day^{-1}$ for the mesogastropod *Crepidula fornicata*. Larvae of *Crepidula plana* grow at a rate 59 $\mu m \cdot day^{-1}$ under optimum conditions of full salinity at 29°C (Zimmerman and Pechenik 1991). *Strombus costatus* grew at a rate of 29 $\mu m \cdot day^{-1}$ over a 32-day period (Davis et al. 1993). The above larvae show linear patterns of growth but the mesogastropod *Strombus gigas* showed an increasing growth rate over the 21-day larval phase, with a mean of 39 $\mu m \cdot day^{-1}$ (Davis et al. 1993).

The larval growth rate of *T. haemostoma* (Dobberteen and Pechenik 1987) is similar to the figure used by Scheltema (1971b) and explains the close agreement he found between estimated and independently derived values of the ODP in this species. However the wide variation in larval growth rates at the generic (20-65 $\mu m \cdot day^{-1}$) and even specific level, coupled with possible variations in growth pattern suggest that Scheltema's estimates for *C. parthenopeum* and *C. nicobaricum* are unreliable.

If Scheltema's (1971b) calculations are repeated using a linear larval growth rate in the middle of the range of 20-65 $\mu m\ day^{-1}$ then ODP values of 81 and 107 days are obtained for *C. parthenopeum* and *C. nicobaricum*, respectively, just over half the values obtained by Scheltema. A more reasonable estimate of the ODP for species of *Cymatium* would therefore be something in the region of 3 months. It is possible that even these revised values represent a serious underestimate. Growth rates of postlarval *C. muricinum, C. pileare* and *C. aquatile* estimated in Chapter 3 are 8 to 35 times higher than those obtained by Taylor (1977) for other juvenile tropical carnivorous gastropods belonging to the families Muricidae, Naticidae, Columbellidae and Costellariidae. The possibility exists that larval growth of ranellids is also relatively fast in which case the ODP could easily assume values of a month or less.

The only information pertaining to the larval growth of a ranellid is an observation by Riedel (1992) based on the observed growth of larvae of *Ca. spengleri* during the first few days after hatching in which it is tentatively estimated that it could take 3 months for the larvae to construct a complete protoconch II and be ready to metamorphose.

It should be mentioned in closing that ODPs of as little as 1 month would still enable trans-atlantic transport of ranellid larvae as proposed by Scheltema (1966, 1971a, 1971b) owing to the capacity of these larvae to delay metamorphosis for over 100 days as determined experimentally by Scheltema (1971b).

Recruitment of Cymatium *spp. to Ocean-Nurseries*

Recruitment in most marine invertebrates is composed of three components: larval supply, settlement and growth and survival of newly settled juveniles. Recruitment is almost always measured as the end-product of these three components (Butman 1987; Harrold et al. 1991). In this study, recruited individuals are considered to be those collected from ocean-nurseries by staff. These data were used as a measure of larval settlement without accounting for postsettlement processes such as mortality due to predators, diseases and genetic causes, active or passive migration, and sampling error (c.f., Butman 1987). Factors affecting recruitment are the subject of Chapter 5.

Settlement of *C. muricinum* and other ranellids in the Solomon Island ocean-nurseries is episodic or sporadic (Figs. 4.2 and 4.4). Similar settlement patterns have been described for *C. muricinum* in tridacnid ocean-nurseries in Palau (Perron et al. 1985) and for *Linatella caudata* infesting oyster farms in India (Thangavelu and Muthiah 1983).

The factors triggering settlement of *Cymatium* larvae can only be speculated on. Juvenile *Cymatium* spp. were collected from floating ocean-nursery cages within days of these being deployed and settlement was estimated to have commenced at the time of deployment. Densities of ranellid infestation were observed to increase as the size of an oyster farm in Tuticorin, India, increased (Muthiah et al. 1985) and a similar phenomenon has been observed but not quantified in ocean-nurseries in Solomon Islands and the Philippines (pers. obs.). This suggests that settlement of these ranellids may be induced by cues associated with the presence of their bivalve prey.

The presence of prey has been reported to induce metamorphosis amongst predatory and parasitic opisthobranch gastropods and other marine invertebrate larvae (Franz 1972; Scheltema 1974). The existence of such a mechanism amongst larvae of these species of *Cymatium* would not be surprising given the indications of a high degree of chemoreception in juvenile and adult tritons (Laxton 1971; Govan et al. 1993; Chapter 2).

Data provided by A. Dalton (pers. comm.) on collection of recently settled *C. muricinum* from tridacnid cages at Mili Atoll, Marshall Islands, showed that individual clams suffering infestations by several tritons simultaneously outnumbered clams attacked by only one triton by a factor of 7-20. Some clams were infested by more than 30 tritons simultaneously. Heslinga et al. (1990) found large numbers of *C. muricinum* infesting individual tridacnids and suggest that the tritons are attracted by the dying clams. Similar patterns of infestation have been encountered in Solomon Islands and Western Samoa (pers. obs.). The heavy infestations suffered by specific clams strongly suggest that something is attracting the small *C. muricinum*. Cues inducing settlement or attracting recently settled tritons may be provided by the presence of other ranellids or features of the clam such as stress or injury. Given that ranellid larvae are capable of remaining in the plankton until suitable prey is encountered and that such prey in natural conditions may usually be ephemeral or patchily distributed it seems most probable that settlement cues are provided by the presence of prey, particularly if these cues are related to a state of greater prey vulnerability.

The high correlation found between variations in settlement densities of *C. muricinum* over time between cage types at Nusatupe suggests that essentially the same factors are involved at each depth. The correlation between the variations in settlement densities of *C. aquatile, C. muricinum* and *C. pileare* over time at the CAC site leads to a similar conclusion regarding the factors affecting recruitment of these species.

Despite the correlations, significantly higher densities of ranellids were estimated to settle in floating cages than in trestle and benthic cages at the Nusatupe ocean-nursery. Possible explanations for this difference include:

i) Presettlement conditions. The local hydrography may affect settlement owing to differences in current strength between the surface and seabed.

ii) Postsettlement conditions. After settlement the density of juvenile tritons may be reduced by factors such as emigration or predation which may occur preferentially near the seabed.

iii) Sampling error. Floating cages were more accessible to skin-diving staff than benthic cages making predator collection easier in the former.

Dalton (pers. comm.) found nearly four times higher settlement of *C. muricinum* in floating tridacnid cages suspended at 3-m depth than in those suspended at 0.3 m in the Marshall Islands and Bell (1992; pers. comm.) found 2.5 times more recently settled *C. muricinum* in benthic tridacnid cages than trestle cages in American Samoa.

It seems unlikely that juvenile *Cymatium* spp. would emigrate from cages that provide such an abundant supply of food and adequate shelter to the surrounding, relatively impoverished, habitat. If tritons were more easily overlooked in benthic cages then one would expect the mean size of tritons eventually collected to be larger than those collected from trestle or floating cages. However, the mean size of tritons from all cages types was not found to be significantly different (t-test, $p > 0.05$) which supports staff claims that all tritons were collected from cages regardless of type (I. Lane, pers. comm.).

The hydrography of ocean-nurseries and the effects of predation on recently settled ranellids appear to be the most likely candidates of those discussed to account for the differences in recruitment density observed. Possible differences in ease of access of other predators between cage types and sites is discussed further in Chapter 6 and hydrography is further discussed below.

Estimated settlement of *C. muricinum* in floating cages at Nusatupe reached high levels of 39 snails·m^{-2} per month and on one occasion 22.4 snails·m^{-2} were estimated to settle in 1 week. Average monthly densities of settlement in floating cages ranged from 0.8 to 19.5 snails·m^{-2} depending on site and season. Dalton (pers. comm.) reports even higher densities of *C. muricinum* recruitment, more than 400 snails·m^{-2} per month in cages suspended at a depth of 3 m at Mili Atoll.

The high densities of *C. muricinum* recruitment in tridacnid ocean-nurseries appear remarkable if this species has an obligatory planktonic phase of at least 3 months as discussed above. Before possible explanatory mechanisms are discussed it is worth examining exactly what planktonic densities of competent veligers would be required to account for the observed recruitment.

For the purpose of these calculations a square cage 1 m x 1 m is assumed. Floating cages in the Nusatupe ocean-nursery were usually suspended at a depth of roughly 0.4 m and cages are therefore assumed to present a 0.4-m^2 "window" to the prevailing current. Currents in the ocean-nursery were usually wind-driven or tidal and if a modest average current speed of 0.25 km·$hour^{-1}$ is assumed then approximately 7.3 x 104 m^3 of water can be estimated to pass over the cage every month.

The cage mesh and support structure probably cause mixing of inflowing water and reduced water velocities near the cage base and clams, both of which phenomena are likely to enhance the chances of floating larvae of receiving settlement cues from the cage substrate (Eckman 1983; Butman 1987). The competent larvae of the *Cymatium* spp. are large and well adapted to their planktonic existence with large velar lobes (Lebour 1945; Scheltema 1971b) and may be able to respond actively to settlement cues. If it is assumed that most of the larvae passing over the cage settle and that postsettlement losses are negligible then monthly recruitment densities of 10 *C. muricinum*·m^{-2} could be achieved with a planktonic larval density of 1.4 x 10^{-4} *C. muricinum*·m^{-3}.

The only data available on planktonic densities of teleplanic larvae of *Cymatium* spp. pertain to the North Atlantic and are those of Scheltema (1971b) for *C. parthenopeum* and *C. nicobaricum* and those of Laursen (1981) for nine species of *Cymatium* including *C. muricinum*. Scheltema (1971b) calculated that for a larva to be found in one of his plankton tows it had to be present in the ocean waters at a minimum concentration of 1.35 x 10^{-3} larvae m^{-3}. *C. parthenopeum* and *C. nicobaricum* were sampled at least once in 27% and 4%, respectively, of all plankton tows throughout the North Atlantic. This gives minimum planktonic densities of 4.0 x 10^{-4} larvae m^{-3} for *C. parthenopeum* and 0.5 x 10^{-4} larvae·m^{-3} for *C. nicobaricum*.

Plankton tows in the Central Pacific Ocean (including Solomon Islands) yielded ranellid larvae at 30% of stations (Scheltema 1986). *C. muricinum* is one of the more common ranellid species in the tropical Pacific (c.f., Chapter 1). If it is assumed that larval *C. muricinum* occur in oceanic waters bathing Solomon Islands at densities of a similar order of magnitude to those observed for *C. nicobaricum* and *C. parthenopeum* in the North Atlantic then a minimum value in the region of 1.0 x 10^{-4} larvae m^{-3} seems reasonable.

Data on capture of larvae of *C. muricinum* during plankton tows in the North Atlantic presented by Laursen (1981) allow the calculation of approximate planktonic densities. *C.*

muricinum larvae occurred at densities of up to 1.2 x 10^{-3} larvae·m^{-3} throughout the Caribbean and Gulf Stream. Considering only the plankton tows performed within 300 nautical miles of the tropical coast of America and the Caribbean, a mean value of 1.8 x 10^{-4} larvae m^{-3} is obtained.

Densities of 0.8 to 39.0 *C. muricinum*·m^{-2} settling in Solomon Island ocean-nurseries could be achieved with planktonic densities of 1.1 x 10-5-5.5 x 10^{-4} larvae·m^{-3} which, based on the rough calculations and assumptions outlined above, do not seem unreasonable. The high levels of *C. muricinum* recruitment could be explained by settlement of teleplanic larvae without recourse to more complex mechanisms.

If assumptions regarding settlement behavior or average current speeds are unduly optimistic, then higher densities of *C. muricinum* larvae must be found in the waters surrounding the island and lagoon ocean-nursery sites than in the open ocean in order to account for the high levels of recruitment observed, particularly those at Mili Atoll. Hydrographic mechanisms appear to be the most likely means of accounting for these increased densities.

A number of hydrographic mechanisms have been documented which would account for the often higher observed concentrations of plankton, including larvae, around tropical islands than in the nearby ocean (c.f., review by Young and Chia 1987).

Black et al. (1990, 1991) and Black (1993) modelled the dispersal of neutrally buoyant particles such as larvae around reefs in the Great Barrier Reef system. The authors concluded that subject to factors such as reef size, currents, tidal regimes, depth and residual currents, 50% of neutrally buoyant material may remain near the reef of origin after 12-14 days and more than 5% may remain indefinitely. The results suggested that retention of larvae could be further enhanced if larvae were negatively buoyant, if spawning occurs at high or spring tides and if reefs are found in complex groups or clusters (Black et al. 1991).

Oceanic Islands in major current systems often have eddies and turbulence associated with their downstream wakes (Young and Chia 1987). Mesoscale eddies and currents in the lee of the island of Hawaii can entrain larvae from reefs for several months during which time the larvae may be swept back over the same or nearby reefs a number of times (Lobel and Robinson 1986). Correlations have also been observed between the formation of these eddies and occurrence of trade winds (Patzert 1969 in Lobel and Robinson 1986).

The residence time of water in lagoons may be surprisingly long. Gallagher et al. (1970) calculated a residence time of at least 11 months for water contained in the lagoon of Fanning Island. In Bikini lagoon the circulation pattern is strongly influenced by the trade winds which drive the surface waters across the lagoon. The channels between islands on the leeward side are too small to allow the escape of most of the water which is obliged to proceed back to the windward side of the lagoon along the bottom (Von Arx 1948 in Young and Chia 1987). This and other mechanisms such as temperature mediated stratification probably retain larvae in many such lagoon systems particularly if the larvae can achieve a position in the deeper lagoon waters (Young and Chia 1987).

Hydrographic mechanisms such as these could account for the large differences in *C. muricinum* recruitment density observed between sites. The complex reef systems around the Nusatupe ocean-nursery would be expected to retain more larvae than the relatively open coastal site at the CAC (see map; Fig. 1.2) and extremely high densities of recruitment at Mili Atoll are not surprising given potentially very long residence times of the lagoon water. Interestingly, Dalton (pers. comm.) reports the presence of a thermocline between the shallow and less infested cages and the deeper and heavily infested cages.

Implications for Giant Clam Culture

The possibility that dying or wounded clams may attract larval or postlarval ranellids suggests that such clams should be removed from ocean-nurseries as soon as possible.

Current advice for the selection of ocean-nursery sites includes surveys for the presence of predators (Calumpong 1992). Ranellids are likely to be the most serious predator affecting ocean-nursery clams (this work; Govan 1992a), but the present work and experiences from other ocean-nurseries (Sims and Howard 1988; Heslinga et al. 1990; Govan et al. 1993) suggest that the threat is principally from the settlement of planktonic ranellid larvae.

The emphasis in site selection should be on the local hydrographic regime and, at least until more knowledge is gained, a certain amount of trial and error may be involved. Linear, open coasts such as that at the CAC are probably less likely to accumulate high densities of larval ranellids compared to more complex sites such as that at Nusatupe.

A factor that may be expected to influence settlement is the speed of currents over the settlement substrate. Although a faster current may be expected to bring more larvae into the proximity of a cage there is likely to be a maximum speed beyond which the larvae are unable to settle on the surface of the cage (c.f., Eckman 1983). If this is true, cages may act as traps for larvae by providing areas of turbulence and back-eddies which provide larvae with suitable conditions for settlement. Large areas of fine cage mesh would increase the effect. This may be the reason why settlement of *C. muricinum* appears to have been much reduced at Nusatupe in 1992, coinciding with the movement of cages to an outer and more current swept site.

The hydrographic processes discussed above should be considered and, when the ocean-nursery is established, ranellid recruitment should be monitored and evaluated in the light of these processes. Basic monitoring need only take the form of recording the approximate date of triton collection, the cage or cage type and whether the triton is juvenile or adult (Govan et al. 1993). Ocean-nurseries suffering unacceptably high ranellid recruitment may benefit by relatively minor adjustments in cage location, either horizontally or vertically. The structure of cages may have an impact on the hydrodynamic processes affecting recruitment (Eckman 1983) and cage design may be critical in some situations.

CHAPTER 5

Environmental Factors Affecting Recruitment of *Cymatium* spp.

5.1 Introduction

The recruitment of predatory ranellids to tridacnid ocean-nurseries in Solomon Islands shows high variability (c.f., Chapter 4) and *Cymatium muricinum* recruitment in tridacnid ocean-nurseries in Palau has been described as episodic (Perron et al. 1985; Heslinga et al. 1990). Similar patterns of recruitment have been observed for *Linatella caudata* (Thangavelu and Muthiah 1983) and *C. muricinum* and *C. martinianum* (Littlewood 1991) infesting farmed oysters (*Crassostrea* spp.).

The cultivation of bivalve species affected by ranellid predation would benefit if peaks of occurrence of these tritons could be predicted. Such predictions would enable bivalve spat to be moved from the safety of land-based nurseries, where ranellid incidence is usually negligible, to ocean-nurseries during periods when ranellid incidence is expected to be low. Furthermore, the intensity of control measures could be adjusted according to the intensity of predicted incidence resulting in savings in manpower and equipment.

Most authors do not mention seasonality or other factors correlated with ranellid recruitment which could enable predictions of recruitment. This is probably largely due to the short and incomplete datasets involved. However, Villalobos and Baez (1983) report that infestations of *C. corrugatum amictum* on stocks of cultured *Anadara tuberculosa* follow an annual cycle.

The only reports of factors thought to affect the recruitment of ranellids (*C. muricinum*) in ocean-nurseries come from the MMDC in Palau. Based on collection per unit effort data from ocean-nursery cages, the abundance of juvenile *C. muricinum* was observed to increase during periods of high rainfall (Heslinga et al. 1990). Adult tritons were found to breed throughout the year and the authors suggested that rainfall increases productivity through nutrient-rich run-off in lagoon waters which in turn enhances larval survival and/or metamorphosis and hence recruitment. The observations were not examined statistically and no other environmental or biological variables were considered.

The Study of Recruitment Variability

The study of recruitment variability in relation to fisheries has received much attention during the course of this century, in most cases with a remarkable lack of progress (Bakun 1985). For many years after the ground-breaking work of Ricker (1954) the emphasis was

placed on the relationship between parent stock and recruitment and the effects of environmental variability were largely neglected (Longhurst and Pauly 1987). This trend has now been reversed and environmental and ecological mechanisms are now widely accepted as perhaps the principal determinants of abundance variability in many stocks (Shepherd et al. 1984; Longhurst and Pauly 1987; Fogarty 1993).

Despite the above, attempts to relate recruitment variations with variability in the environment or biological community have been generally unsuccessful (Bakun 1986). Such studies have been hampered by the incredibly complex interactions of environmental and biotic factors on the, usually little known, early life stages of the study species (Bakun 1985). Other complications arise owing to the interference of annual or other periodicities, the usually short datasets available (particularly in the case of tropical fisheries) and serial correlations owing to the time-series nature of the data (Bakun 1985, 1986; Pepin 1990; Hilborn and Walters 1992).

The bulk of research on recruitment variability has been carried out on fish stocks but knowledge of the factors affecting the recruitment of benthic marine invertebrates has also expanded, especially since the seminal works of Gunnar Thorson (1946, 1950, 1966). Thorson's views have been broadly vindicated (Rumrill 1990) and wastage of marine invertebrate larvae with dispersive development may be a primary factor influencing recruitment into benthic populations (Thorson 1950).

Drinkwater and Myers (1987) tested environmentally based predictions of landings of invertebrates in the Northwest Atlantic and found them to be generally more accurate than those for fish stocks. Predictive models have been developed with varying degrees of success for the recruitment of tropical shrimps. An example is the banana prawn, *Penaeus merguiensis*, fishery of Northern Australia the volume of which appears strongly correlated with the rainfall of previous seasons and to a lesser extent with certain wind components (Staples et al. 1984; Vance et al. 1985). The recruitment of other commercially important invertebrates has also been the subject of predictive studies including the gastropod *Haliotis rubra* (McShane et al. 1988), the bivalve *Pecten maximus* (Thouzeau 1991 and references therein) and the crab *Callinectes sapidus* (Johnson and Hester 1989).

Factors Influencing Recruitment

The three potential causes of variations in recruitment listed by Shepherd et al. (1984) are:

i) Environmental factors such as variations in climate, tidal conditions etc.
ii) Variations in the abundance of the parent stock.
ii) Ecological interactions such as the variations in the abundance of predators or competitors or prevalence of disease.

In the case of tropical invertebrate larvae with an extended planktonic phase, environmental and ecological processes acting on the larvae are probably the strongest determinants of the magnitude of recruitment as has been reported for many coral reef fishes (e.g., Shulman 1985; Meekan et al. 1993).

The biological and environmental factors causing larval wastage of invertebrates proposed by Thorson (1950) include: failure of fertilization, inadequate food supplies, lethal and sublethal environmental extremes, absence of appropriate settlement substratum, offshore transport by currents and predation of larvae. To these factors, Rumrill (1990), in a recent review, added genetic abnormalities and larval diseases.

As pointed out by Johannes (1978), tropical marine environments differ substantially from those at higher latitudes. Seasonal variations in day length, temperature, nutrient levels and

oceanic plankton densities are relatively low. The seasonal cycle generally consists of two monsoonal or trade wind seasons distinguished on the basis of wind, precipitation and current patterns.

From the above it seems reasonable to assume that the following factors may be important causes of variability in ranellid recruitment to ocean-nurseries: environmental factors, such as wind direction and strength, current direction and strength, tidal cycles, rainfall and ecological processes, such as planktonic and postsettlement predation and competition.

Environmental Influences on C. muricinum *Recruitment*

Detailed time-series of information on planktonic ecological processes such as predation and competition which may affect ranellid recruitment will rarely, if ever, be available for most areas where tridacnid culture is practiced. On the other hand, meteorological data related to environmental influences on recruitment may often be available from local airports or weather bureaus and key parameters may even be monitored by the farmers themselves.

Heslinga et al. (1990) reported that rainfall is successfully used as a predictor of ranellid recruitment in Palau and that snail collection efforts are intensified in the ocean-nursery after periods of increased rainfall. However, no such mechanism has been reported from other tridacnid ocean-nurseries. The objective of the present chapter is to examine the relationship between a number of environmental variables and the recruitment of *C. muricinum* reported in Chapter 4 for two Solomon Island ocean-nurseries, with a view to assessing the potential of these variables as predictors of ranellid recruitment in tridacnid culture.

Relating variations in recruitment to environmental variability is notoriously difficult (Shepherd et al. 1984; Bakun 1986). This is not because correlations are difficult to obtain: on the contrary, where large numbers of variables or time lags are tested it would not be surprising to obtain a "statistically significant" correlation in 1 of every 20 cases when tested at the the standard 5% level of probability (c.f., Walters and Collie 1988). The interrelationship between variables may be very complex but also the relationships may not be linear. For example, the dome-shaped or parabolic relationships suggested between recruitment and specific environmental factors by Cury and Roy (1989) and Dalzell (1990).

Most recruitment and many environmental time-series are autocorrelated (Fogarty 1993), a factor which is not taken into account by ordinary correlation analysis and which increases the chances of obtaining spurious correlations (Shepherd et al. 1984). Time-series methods of analysis (which take account of the sequential nature of the data) have often been used in the study of recruitment. The two principal methods of analysis are spectral analysis and ARIMA (auto-regressive integrated moving average) analysis (Shepherd et al. 1984).

Spectral analysis essentially examines the existence of periodicities or deterministic cycles in the data and has found wide application in the fields of terrestrial and aquatic ecology (Platt and Denman 1975; Shepherd et al. 1984; Coull 1985; Diggle 1990). Methods of cross-spectral analysis have been developed which can handle multivariate series (e.g. Colebrook and Taylor 1984).

ARIMA analysis examines the data in terms of linear values of past values of the series and/or previous random shocks, respectively, auto-regressive and moving average processes (Box and Jenkins 1976). Multivariate series may also be objectively related and this type of analysis has been applied to a number of fishery-related problems (e.g., Fogarty 1988; Meekan et al. 1993).

Both the above time-series methods generally require many data points (more than one hundred or so) to generate meaningful results (Shepherd et al. 1984). First-differencing is a simple procedure (c.f., Section 4.2) commonly used to remove the long-term trend in time-series thus reducing the problem of serial correlation (e.g., Drinkwater and Myers 1987; Thompson and Page 1989; Meekan et al. 1993). Data thus transformed may be examined using standard correlation techniques and may yield useful insights into the processes involved (Drinkwater and Myers 1987; Pepin 1990).

The approach adopted in the present study was largely determined by the short datasets available. The work presented below represents an exploratory analysis which examined:

i) the presence and frequency of periodicities in the recruitment and environmental datasets using spectral analysis;
ii) correlations between environmental and recruitment variables before and after major trends were removed using differencing; and
iii) the variability accounted for by different environmental models and the independent effects of each environmental variable using simple path analysis.

5.2 Methods

Database

Recruitment data. Raw data regarding recruitment of *C. muricinum* were provided by I. Lane and J. Hambrey as described in Chapter 4 along with details of cage types and deployment.

Environmental data. Meteorological data were provided by the Solomon Islands Meteorological Service (SIMS) for Munda (daily) and Honiara (monthly). Munda is about 40 km east of the NT site and Honiara is some 25 km east of the CAC.

Rainfall records in $mm \cdot m^{-2}$ were grouped into monthly totals for Honiara and weekly and monthly totals for Munda. Complete datasets were available for Honiara and Munda.

Wind data for Honiara were only available as monthly per cent incidence of each wind direction at 1400 hours and the per cent incidence of different wind strengths regardless of direction. Daily wind data were available for Munda in the form of wind direction and speed (in knots) at 1400 hours. These data were expressed as mean weekly and monthly wind speed for each direction.

Solomon Islands is affected by two seasonal wind patterns; the monsoons or "Komburu" which blow from the northwest sector during the wet season from November to May and the southeasterly trade winds, "Ara", which predominate during the rest of the year (L. Tahani, SIMS, pers. comm.). Local topography modifies the direction of these predominant winds at the CAC and NT sites.

Wind incidence data for 16 points of the compass during the study period at both Honiara and Munda were examined to determine the main wind components (Vance et al. 1985). Graphic representation of the raw data resolved the major components and Spearman rank correlations were used to confirm these apparent relationships.

Honiara is on the north coast of Guadalcanal, a high island, thus the Ara blows from the east or southeast and Komburu from the north, northwest or west. Winds from these directions accounted for 30% of total wind incidence at 1400 hours in Honiara. Nonseasonal northeast

winds accounted for 62% of wind incidence at the same time but examination of data for 0800 hours suggested that this wind was a daily onshore wind which reversed in direction during the night. Similar conditions were observed at the CAC (pers. obs.).

The topography of the area surrounding Munda is complex but the wind components of the Ara were clearly distinguishable from the the east to southeast and Komburu from the west to northwest. These components accounted for about 60% of the wind incidence with occasional, nonseasonal, southerly and northeasterly winds accounting for the remainder. The NT site was only 40 km from Munda and should be affected by the same overall wind regime but the angle of incidence of these winds may be modified by the different topography of the area.

The wind data at each site were resolved into the main components detected above by adding the proportion of incidences (in the case of Honiara) or mean wind speeds (Munda) for each wind belonging to the component. All meteorological data were available for a period covering and exceeding the period for which settlement data were available.

Data on tides were obtained from tide tables published annually by the Solomon Islands Hydrographic Division for Honiara and a port 3 km from Nusatupe, Gizo. Weekly figures were obtained for the height of low and high tides and the tidal range was calculated from these. The tidal regimes of Honiara and Gizo were identical.

Statistical Analyses

All datasets were examined initially to determine what statistical tests and transformations were appropriate (Sokal and Rohlf 1981). Normality was tested using Wilk-Shapiro statistics and rankits (Sokal and Rohlf 1981; Analytical Software 1991). Variables were tested for independence or serial correlation using the Statistix autocorrelation program based on computations in Box and Jenkins (1976).

Most datasets only conformed to normal distributions after transformation. This was only an issue for the tests which require normality, specifically spectral analysis (Platt and Denman 1975) and the Pearson product-moment correlations (Sokal and Rohlf 1981) used in the path analysis. The remaining correlations were performed using Spearman's rank correlation technique as described in Chapter 4.

The *C. muricinum* recruitment data appeared log-normally distributed, as is often the case with such data (Shepherd et al. 1984; Thompson and Page 1989; Pepin 1990), and they were transformed as Log(X+1). Wind data from Honiara, expressed in per cent frequencies, corresponded better to a normal distribution when square root rather than arcsine (Sokal and Rohlf 1981) transformations were used. First differencing was performed as described in Chapter 4.

Each set of raw data was cross-correlated with an annual cycle represented by a sine wave with a 12-month period. This enabled identification of the timing of any regular seasonal maxima and minima, i.e., the months with the maximum significant ($P < 0.05$) positive and negative correlations, respectively (Robertson 1990).

Spectral analysis. The existence of periodicities or deterministic cycles in the recruitment data was examined using spectral analysis. The Statgraphics program was used to produce periodograms in which spectral density estimates were obtained using Fast Fourier Transformations (FFT) for transformed data with the mean removed (STSC 1985). Only the datasets consisting of weekly records contained enough data points ($n = 75$ to 105) to be suitable for analysis, i.e., those pertaining to *C. muricinum* recruitment in floating cages at the CAC and floating, trestle and benthic cages at Nusatupe, meteorological data for Munda and tidal data for Gizo and Honiara.

Spectral analysis is only appropriate for stationary data (Diggle 1990) and as the present datasets were short and therefore could easily present a trend, these were detrended where appropriate. Detrending was achieved by polynomial regression of the datasets and the resulting regression equation was removed from the data prior to spectral analysis (Diggle 1990; Janacek and Swift 1993). Sixth-order polynomials were used but the results were also compared with the results obtained using third-order polynomials, first-order differences and the original data. The environmental series presented little trend and were not detrended.

The resulting periodogram ordinates were smoothed using third-order moving averages. This process enabled the more important spectral peaks to be distinguished from erratic fluctuations although it does cause a small loss in terms of resolution (Diggle 1990).

The possibility that the time-series were "white noise" sequences (or sequences of mutually independent random variables) was tested using cumulative periodograms. Departures from the values expected for a white noise sequence were tested at the 95% level of significance using a Kolmogorov-Smirnov statistic (STSC 1985; Diggle 1990).

Confidence limits at the 95% level of significance were calculated for raw and smoothed spectral density estimates using the chi-squared method (Gottman 1981; Diggle 1990).

Correlations. Spearman rank correlations were used to test for relationships between monthly recruitment data and the environmental series available for each site. Lagged datasets were also tested and the whole analysis was repeated with the same data detrended by differencing.

Correlation matrices for the detrended and transformed data were constructed using Pearson's product-moment correlation in order to examine interrelationships between environmental variables and to provide coefficients for path analysis.

Path analysis. Simple models of interactions between environmental factors and the effect of these on recruitment were examined using path analysis (Asher 1976; Sokal and Rohlf 1981; Johnson and Wichern 1988; Pepin 1990). Models (path diagrams) were kept simple and only two or three predictor variables were included as suggested by Shepherd et al. (1984).

A path diagram is shown in Fig. 5.1, "X_i" represent environmental variables and "Y" represents recruitment. Path analysis separates the correlation between variables into the sum of the chain of path coefficients (p_{Yi}) or correlations (r_{ij}) along *all* the paths by which they are connected. Relationships which are considered to be cause and effect are depicted by one-headed arrows and correlated causes are depicted by double-headed arrows.

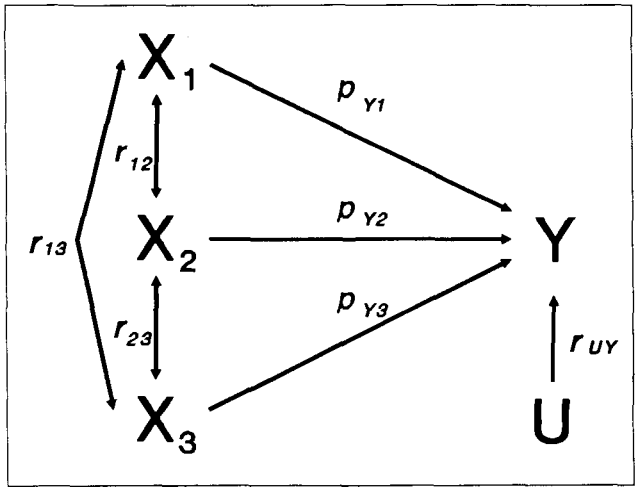

Fig. 5.1. Path diagram relating environmental variables and recruitment. "X_i" represents environmental variables and "Y" represents recruitment. Path coefficients are represented by P_{Yi} and correlation coefficients by r_{ij}. Relationships which are considered to be cause and effect are depicted by one-headed arrows and correlated causes are depicted by double-headed arrows. See text for details.

The direct association between recruitment and a given variable can be separated from the indirect associations due to the correlation of the independent variables of the proposed model. Thus the correlation between each variable and recruitment is determined by the combined direct and common causes. The unknown factors which determine recruitment are lumped together as a single, unknown, residual variable "U". The total determination of recruitment for each known variable are calculated using equation (5.1):

$$\sum_{i} p_{Yi}^{2} + 2\sum_{ij} p_{yi} p_{Yj} r_{ij} + r_{UY}^{2} = 1 \qquad \text{...5.1)}$$

where p_{Yi} is the standard partial regression coefficient between recruitment (Y) and direct cause (X_i), r_{ij} is the correlation between variables i and j and r_{UY} is the residual correlation. The first two elements on the left-hand side of equation (5.1) represent the coefficient of determination (r^2).

5.3 Results

Recruitment in this study refers to the density of *C. muricinum* collected from ocean-nurseries by staff. Because of the variation in sizes, and presumably ages, of collected tritons the approximate date of settlement was back-calculated based on experimentally derived growth rates (c.f., Chapter 4). The use of this estimated settlement data was deemed in Chapter 4 to eliminate much of the noise and variation due to the irregular collection technique and thus the recruitment dates used in the present chapter are back-calculated as well.

Time-series data. Monthly time-series of recruitment data and the available environmental data were compiled and plotted. The minimum value of each series was subtracted and the remainder were normalized between 0 and 1 to enable the graphical comparisons shown in Fig. 5.2 for the CAC and in Fig. 5.3 for the NT site.

Yearly cycles are apparent in the monsoon and trade winds and in rainfall at Honiara. The tidal data appear to follow a twice yearly cycle. Other cyclic patterns are not immediately apparent. The last 6 months of recruitment data at NT show a greatly decreased level of variance. This was the period when the ocean-nursery was moved offshore.

Cross-correlations confirmed the seasonality of monsoon and trade winds at Honiara and Munda (Table 5.1), the monsoons peaked around January-February and the trade winds around July-August. Wind strength and rainfall also show yearly peaks at Honiara but not at Munda although this may be due to the fewer data points available for analysis at the latter site. Recruitment analyzed by the same method did not show strong yearly cycles.

Recruitment, monsoon, trade wind and rainfall datasets showed significant first-order positive autocorrelations ($P < 0.05$). Nonseasonal winds and wind strength did not appear autocorrelated. Tidal range showed positive first-order autocorrelations and also negative autocorrelation of order 3, indicative of a twice yearly cycle. All autocorrelations were removed when the data were differenced with the exception of the third-order autocorrelation in the tidal data.

Spectral analysis. Cumulative periodograms of the *C. muricinum* datasets from CAC and NT confirmed the above findings that data were not serially independent and did not correspond to white noise sequences. The same was true for all Munda environmental data with the exception of rainfall and northeast winds for which the possibility could not be excluded using this test that the data corresponded to sequences of mutually independent variables.

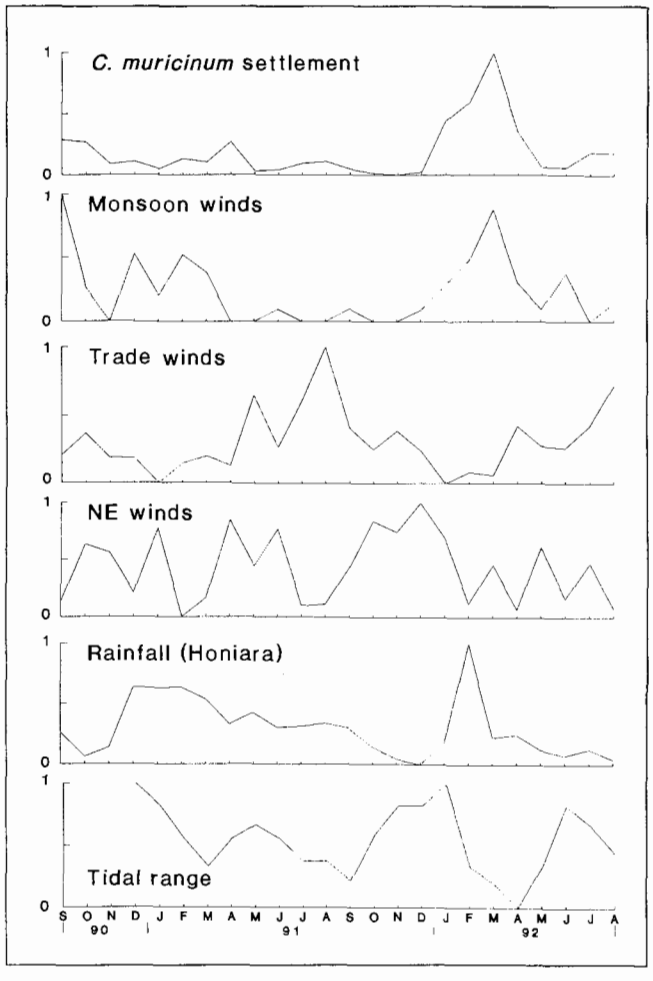

Fig. 5.2. Time-series of monthly *C. muricinum* recruitment in floating ocean-nursery cages at the Coastal Aquaculture Centre and environmental parameters measured at Honiara, Solomon Islands. The minimum valve has been subtracted from each series and the remainder normalized such that the series run between zero and one.

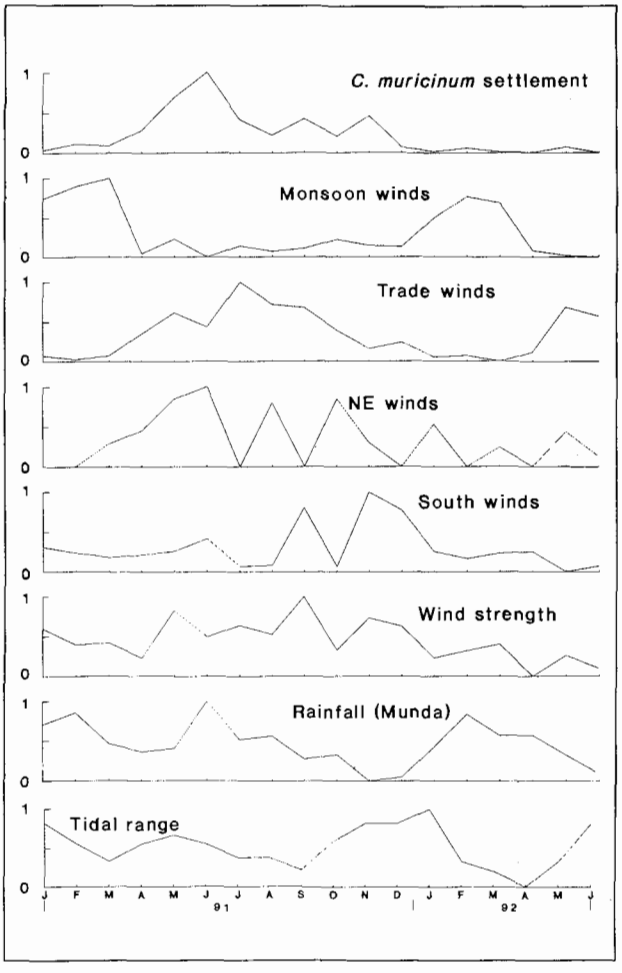

Fig. 5.3. Time-series of monthly *C. muricinum* recruitment in floating ocean-nursery cages at Nusatupe and environmental parameters measured at Munda, Solomon Islands. Tidal range is shown for Gizo. The minimum value has been subtracted from each series and the remainder normalized such that the series run between zero and one.

Table 5.1. The timing of seasonal weather patterns in Honiara and Munda, Solomon Islands over two years from 1990 to 1992. Dates and correlations represent the timing and significance of maxima and minima of phenomena correlated with a yearly cycle.

	Maximum	r_s	Minimum	r_s
Honiara				
Trade winds	July-August	0.700^{***}	January-February	-0.427^{*}
Monsoons	February	0.447^{*}	August	-0.587^{**}
Wind strength	June	0.582^{*}	December	-0.722^{**}
Rain	March	0.493^{**}	August-September	-0.488^{**}
Munda				
Trade winds	July-August	0.807^{***}	January-February	-0.754^{***}
Monsoons	January	0.606^{**}	July-August	-0.529^{**}
Wind strength	September	0.451^{*}	April	-0.350^{ns}
Rain	February-March	0.516^{**}	September	-0.387^{ns}

* $0.01 < P < 0.05$
** $0.001 < P < 0.01$
*** $p < 0.001$
ns not significant.

Confidence intervals for the periodograms were found to be extremely wide. This result is not entirely unexpected as these significance tests are known not to be very powerful unless based on a large number of observations and large bandwidth smoothing (Gottman 1981; Diggle 1990). The width of the confidence intervals warn against too precise an interpretation of the estimated spectra. For clarity the confidence intervals are not shown in graphs of the variance spectra (Figs. 5.4 and 5.5).

The results of spectral analysis for the detrended CAC and NT recruitment data are shown in Fig. 5.4. The periodograms all show a major peak in the region of 2 cycles·year^{-1} (a period of 26 weeks). The spectrum of CAC recruitment shows only minor peaks at frequencies above 3 cycles·year^{-1} (Fig. 5.4A).

The periodograms for recruitment in three cage types at NT (Fig. 5.4B-D) show a number of low frequency peaks up to about 13 cycles·year^{-1} although the number and magnitude of these peaks decline with cage type in the order floating > trestle > benthic. All three spectra show major peaks at 11-13 cycles·year^{-1} (4.0-4.5 week period) and, to a lesser extent, at 5-6 and 8-9 cycles·year^{-1}.

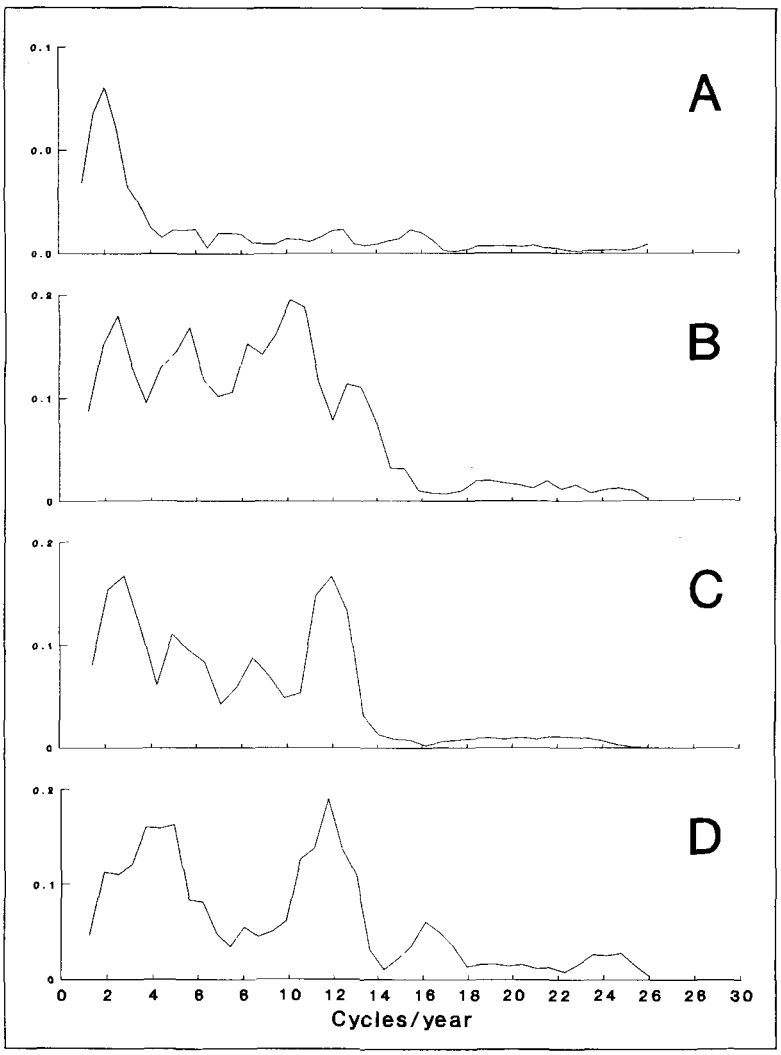

Fig. 5.4. Periodograms of the spectra of weekly recruitment of *C. muricinum* to tridacnid ocean-nursery cages in Solomon Islands from 1990 to 1992. Y axes represent spectural density in terms of periodogram ordinates. A: floating cages at the Coastal Aquaculture Centre, Guadalcanal. B: floating cages at Nusatupe near Gizo. C: trestle cages at Nusatupe. D: benthic cages at Nusatupe.

The effect of detrending the original datasets was examined. Periodograms of raw data and data detrended using third-order polynomials gave similar results to those presented above except that peaks at frequencies of 2 cycles·year^{-1} or lower were considerably enhanced. This was due to the existence of long-term trends, for the examination of which spectral analysis is inappropriate (Diggle 1990).

Spectra of environmental series were generally characterized by high peaks at frequencies lower than 2 cycles·year^{-1} due to the presence of long-term trends in the datasets (Fig. 5.5). These were the most important peaks in the case of seasonal winds but other winds and rainfall showed peaks at 4-22 cycles·year^{-1}.

Tidal range at Honiara and Gizo showed a relatively clear spectrum with a major peak at 24-26 cycles·year^{-1} reflecting the clear 2-week cycle observed in the raw

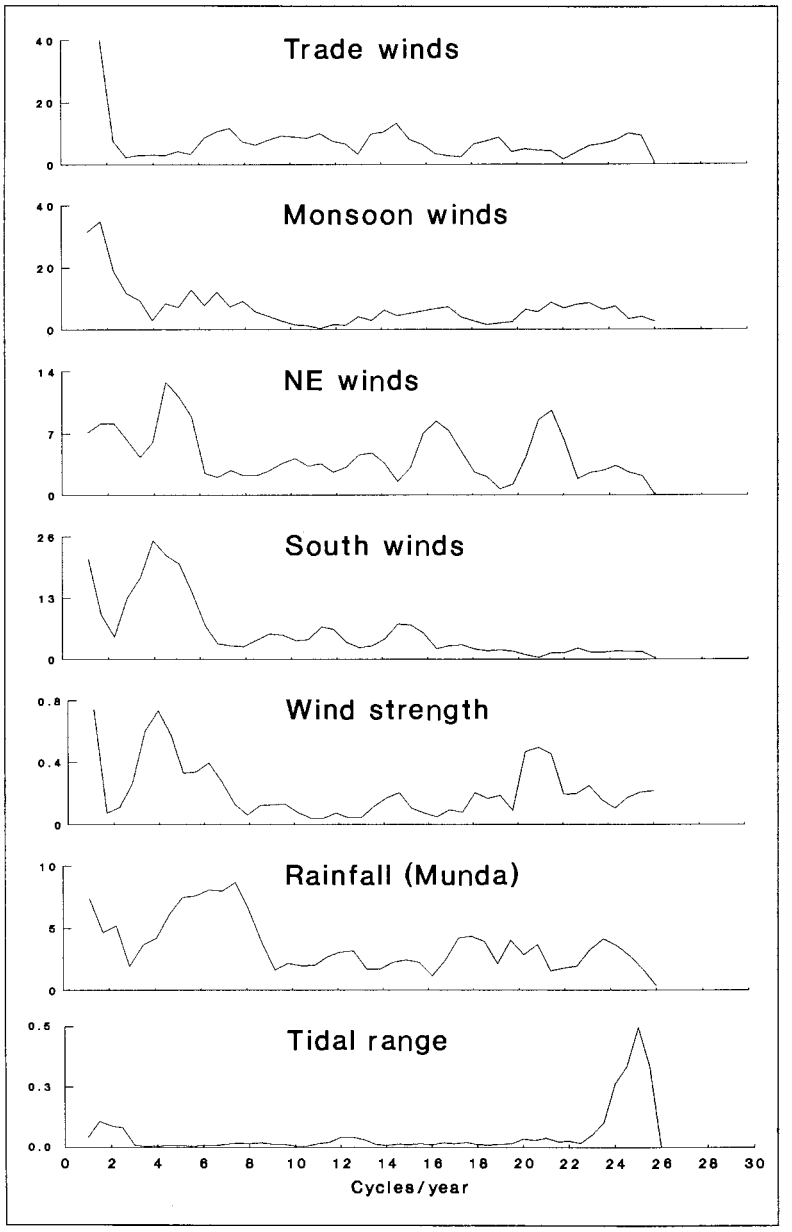

Fig. 5.5. Periodograms of the spectra of weekly environmental parameters measured at Munda (Gizo in the case of tidal range) in Solomon Islands from 1990 to 1992. Y axes represent spectral density in terms of periodogram ordinates.

data and also peaks at 2 and 12-13 cycles year^{-1} reflecting twice-yearly and monthly tidal rhythms. Examination of the raw data for tidal range showed that the variation in tidal range over the 2-week cycle was less than that for the other two cycles.

Environmental correlates of recruitment. Correlations between environmental factors at different lags and recruitment of *C. muricinum* at the CAC are shown in Table 5.2. Rainfall at Munda was included as a variable and a new variable was created for each wind direction consisting of a grouping of the incidence at lags of 0, 1 and 2 months weighted at a ratio of 1 : 0.5 : 0.25, respectively. This was intended to produce a more realistic measure in the case that wind was a transport mediating factor during the planktonic life of the larvae (several months).

Significant correlations with recruitment at the CAC were found for at least one lag of each raw time-series tested; positive correlations with monsoon winds and tidal range and negative correlations with northeast and trade winds and rainfall. The grouped wind data also showed significant correlations. The scenario is greatly simplified if the differenced time-series are considered. The only significant correlations in this case are those of the monsoon winds, tidal range lagged by 2 months and rainfall at Munda lagged by 4 months. This last, and the grouped monsoon wind data, are deemed highly significant ($P < 0.01$).

A similar procedure as above was followed to examine correlations between environmental factors and recruitment at NT (Table 5.4). Relatively few significant correlations were found especially in the case of the differenced time-series where only two of the 25 were significant; the prevalence of south winds and northeast winds lagged by 1 month.

The raw and differenced data for all correlations examined at NT and CAC were plotted graphically and examined for nonlinear relationships, but none were evident.

Table 5.2. Spearman rank correlations between monthly recruitment of *Cymatium muricinum* in floating tridacnid ocean-nursery cages at the Coastal Aquaculture Centre, Solomon Islands and environmental parameters measured at Honiara over 24 months from October 1990 to September 1992. Correlations are shown for the raw time-series and for the detrended time-series.

	Lag (months)	Raw time series	Differenced time-series
Winds (direction)			
Monsoons (N-W)	-	0.546**	0.457*
Monsoons (N-W)	1	0.525**	0.194
Monsoons (N-W)	2	0.250	0.109
Monsoons (N-W)	0+1+2[a]	0.650**	0.591**
Trade winds (E-SE)	-	-0.291	-0.004
Trade winds (E-SE)	1	-0.533**	-0.285
Trade winds (E-SE)	2	-0.398+	-0.134
Trade winds (E-SE)	0+1+2[a]	-0.506*	-0.128
NE winds	-	-0.418*	-0.147
NE winds	1	-0.193	-0.203
NE winds	2	0.125	0.006
NE winds	0+1+2[a]	-0.429*	-0.259
Rainfall (Honiara)			
Total	-	0.191	0.071
Total	1	-0.062	0.227
Total	2	-0.272	-0.100
Total	3	-0.513*	-0.211
Total	4	-0.499*	-0.360+
Rainfall (Munda)			
Total	-	0.327	0.161
Total	1	0.228	0.283
Total	2	-0.090	0.052
Total	3	-0.273	-0.099
Total	4	-0.663**	-0.586**
Tides (Honiara and Gizo)			
Range	-	-0.440	-0.182
Range	1	0.114	-0.003
Range	2	0.523*	0.509*
Range	3	0.565*	0.449+
Range	4	-0.003	0.084

\+ $0.05 < P < 0.1$
* $0.01 < P < 0.05$
** $0.001 < P < 0.01$
[a] Sum of wind incidence over months of lag 0, 1, and 2 in a ratio of 1:0.5:0.25.

Path analysis. The construction of the Pearson's correlation matrices for the path analysis reduced the number of degrees of freedom available owing to some variables being highly lagged. Thus, a usable correlation matrix was only available for the CAC data with 15 degrees of freedom. Data from NT showed only one significant correlation with recruitment, that of south wind ($r = 0.724$, $p = 0.012$), but was omitted from analysis having fewer than 10 degrees of freedom.

In the models to be examined it was assumed that the effect of winds on recruitment would be primarily that of larval transport through wind-driven currents and so the grouped and weighted wind data were used in the analysis as described above.

The correlation matrix for the differenced environmental and recruitment data for the CAC is shown in Table 5.3. Not surprisingly, the results are similar to those shown in Table 5.2; the monsoon winds are highly correlated with recruitment as is tidal range to a lesser extent. Lagged rainfall at Honiara and Munda show correlations with recruitment, negative in the case of 3 and 4 month lags and positive in the case of Honiara rainfall lagged by 1 month. This last is a result not expected from the Spearman correlations (Table 5.2).

The incidence of monsoon winds (northwest) in Munda are included as these may also be expected to influence larval transport from this direction. Although a correlation for this variable with recruitment exists, it is smaller than the correlation between it and monsoons in Honiara. A number of other correlations between environmental variables were observed, notably between monsoon winds, rainfall and tidal range.

Path analysis models were examined and are shown in Table 5.5. Partial correlation coefficients are shown for each of the variables contained in each model. These coefficients enable the effect of each variable on recruitment to be examined independently of the effects due to the

Table 5.3. Matrix of Pearson correlation coefficients between monthly recruitment of *Cymatium muricinum* in floating tridacnid ocean-nursery cages at the Coastal Aquaculture Centre, Solomon Islands and environmental parameters measured at Honiara from October 1990 to September 1992. Data were detrended using differencing. Number of cases = 17, degrees of freedom = 15.

	Lag	R	RH3	RH1	RM4	TR2	TR3	MM	NEH	TH
Recruitment	-									
Rainfall, Honiara	3	-0.512*								
Rainfall, Honiara	1	0.495*	-0.148							
Rainfall, Munda	4	-0.510*	0.103	-0.044						
Tidal range	2	0.600*	-0.358	0.471	-0.208					
Tidal range	3	0.360	-0.458	-0.005	-0.489*	0.175				
Monsoon, Munda	0+1+2[a]	0.488*	-0.374	0.413	-0.184	0.534*	0.490*			
NE wind, Honiara	0+1+2[a]	-0.064	0.396	-0.025	0.263	0.012	-0.745**	-0.433		
Trade winds, Honiara	0+1+2[a]	-0.397	0.249	-0.242	-0.141	-0.196	0.166	-0.292	-0.461	
Monsoon, Honiara	0+1+2[a]	0.643**	-0.583*	0.647**	-0.236	0.430	0.494*	0.752**	-0.377	-0.369

* $0.01 < P < 0.05$
** $0.001 < P < 0.01$
a Sum of wind incidence over months of lag 0, 1, and 2 in a ratio of 1:0.5:0.25.

Table 5.4. Spearman rank correlations between monthly recruitment of *Cymatium muricinum* in floating tridacnid ocean-nursery cages at Nusatupe, Solomon Islands and environmental parameters measured at Munda over 12 months from February 1991 to January 1992. Correlations are shown for the raw time-series and for the detrended time-series.

	Lag (months)	Raw time series	Differenced time-series
Winds (direction)			
Monsoon (N-W)	-	-0.490	-0.210
Monsoon (N-W)	1	-0.210	-0.227
Monsoon (N-W)	2	-0.073	-0.297
Trade winds (E-SE)	-	0.573+	0.000
Trade winds (E-SE)	1	0.459	0.182
Trade winds (E-SE)	2	0.123	0.527
NE winds	-	0.346	-0.049
NE winds	1	0.741**	0.709*
NE winds	2	-0.238	-0.503**
South winds	-	0.305	0.818
South winds	1	-0.546+	-0.355
South winds	2	-0.173	0.018
Wind strength	-	0.552+	0.315
Wind strength	1	-0.301	-0.127
Wind strength	2	-0.100	0.091
Rainfall (Munda)			
Tota	-	0.042	0.084
Total	1	0.182	-0.007
Total	2	-0.049	-0.525+
Total	3	0.497+	0.420
Total	4	0.350	0.070
Tides (Honiara and Gizo)			
Range	-	-0.198	0.084
Range	1	-0.274	0.284
Range	2	-0.693*	-0.378
Range	3	-0.281	-0.535
Range	4	0.454	-0.238

\+ $0.05 < P < 0.1$
* $0.01 < P < 0.05$
** $0.001 < P < 0.01$

other variables in the model (Sokal and Rohlf 1981). Model A shows the effects attributable to the prevailing winds. Only the monsoon wind has any appreciable effect. Model B shows that the effect of monsoons in Munda on recruitment was due entirely to the correlation of this variable with monsoons in Honiara.

Model C suggests that rainfall in Honiara lagged by 1 and 3 months and in Munda lagged by 4 months have an effect on recruitment. This was examined further in Models D, E and F where the effects of rainfall in Honiara appear to be due to correlations with monsoon winds but rainfall in Munda lagged by 4 months still appears to have an effect. This is confirmed again in Models G, H and I where a third variable is introduced; tidal range. Tidal range appears to have an important effect on recruitment (see also Models J and K).

Most of the models explain more than 50% of the variability in recruitment (see r^2 values in Table 5.5). The best three-variable model is that including monsoon winds at Honiara, tidal range and rainfall in Munda lagged by 4 months, this accounts for 65% of variability. The best two-variable model includes only the monsoon and rainfall variables, accounting for 55% of recruitment variability.

Table 5.5. Partial correlation coefficients and coefficients of determination (r^2) of path models relating recruitment of *Cymatium muricinum* in floating tridacnid ocean-nursery cages at the Coastal Aquaculture Centre, Solomon Islands and environmental parameters measured at Honiara over 17 months from 1991 to 1992. Results were calculated using the correlation coefficients estimated for differenced data in Table 5.3. The lag of variables is shown in brackets. The coefficient of determination is equivalent to the proportion of the variation explained by the variables in the path model.

	Model										
Variable (lag)	A	B	C	D	E	F	G	H	I	J	K
Monsoon winds[a]	0.53	0.48	-	0.49	0.49	0.63	0.46	0.42	0.53	0.53	-
Trade winds[a]	-0.07	-	-	-	-	-	-	-	-	-	-
NE winds[a]	0.14	-	-	-	-	-	-	-	-	-	-
Monsoons, Munda[a]	-	0.01	-	-	-	-	-	-	-	-	-
Tidal range (2)	-	-	-	-	-	-	0.46	0.45	0.47	0.47	0.59
Rainfall (1)	-	-	0.52	0.14	-	-	0.01	-	-	-	-
Rainfall (3)	-	-	-0.55	-	-0.22	-	-	-0.18	-	-	-
Rain, Munda (4)	-	-	-0.60	-	-	-0.48	-	-	-0.48	-	-0.49
r^2	0.45	0.41	0.64	0.42	0.44	0.55	0.54	0.56	0.65	0.54	0.52

[a]Sum of wind incidence over months of lag 0, 1, and 2 in a ratio of 1:0.5:0.25.

5.4 Discussion

Environmental factors affecting *C. muricinum* recruitment are the subject of this chapter but it is worth bearing in mind other major factors affecting the planktonic larvae and recently settled juveniles. This is especially so as these processes will also be influenced to some extent by environmental processes.

Postsettlement processes include predation, active or passive migration and sampling error. Ocean-nursery cages are designed to exclude predators (Govan et al. 1993) and by concentrating on data from floating cages in this chapter it is hoped that the effect of these processes is minimized.

Planktivorous predators are abundant on coral reefs and predation is considered a major cause of mortality of invertebrate larvae in temperate seas (Young and Chia 1987). Presumably predation pressure is reduced in the open sea, away from reefs, because many spawning reef fish have been shown to release their eggs in locations where they will be carried offshore to avoid intense nearshore predation. Hydrographic processes regulate this transport and enable the fish to return to shallow water at the end of their larval development (Johannes 1978).

Environmental Influences on C. muricinum *Recruitment*

The environmental factors examined in this chapter were those for which measurements are usually available from local meteorological services, namely: wind incidence, rainfall and tidal range.

Wind-driven water movements, seasonal or other currents and tides will be instrumental in transporting larvae to suitable settlement habitats (e.g., Johnson and Hester 1989) or areas of more abundant food supply (Rumrill 1990). However, these water movements may also be related to other processes such as turbulence, mixing and upwelling, which may affect larval survival (Bakun 1985; Cury and Roy 1989).

Rainfall and associated river discharges may affect larval survival directly by decreasing the salinity of confined waters below tolerable limits (Pechenik 1987) or indirectly by increasing terrestrial run-off. Increased terrestrial run-off may raise nutrient levels thereby boosting planktonic productivity but may also increase turbidity with adverse effects on productivity and pelagic species (Dalzell 1990).

Apart from the effects of tides in dispersal and transport of larvae over ocean-nursery cages, tidal or lunar cycles may influence spawning in marine invertebrates (Giese and Kanatani 1987). In Chapter 4, it was shown that the possibility of a lunar spawning cycle in *C. muricinum* could not be discarded.

One environmental factor not hitherto mentioned is the presence of suitable habitat for the parent stock. Although the larvae of *C. muricinum* may survive in the plankton for many months it seems reasonable to expect that planktonic densities of these larvae will be increased in the vicinity or downstream of nuclei of parent abundance. Demond (1957) reports *C. muricinum* to be most abundant in sandy lagoons and seaward reef flats to depths of 50 m (c.f., Chapter 1). Such habitat is most abundant in Solomon Islands in Western Province (from Gizo and Munda to Marovo) and to a lesser extent Northwest Isabel Province (UNEP/IUCN 1988 and see Fig. 1.2).

Exploratory Analyses

Spectral analyses of *C. muricinum* recruitment in floating cages at the CAC and NT ocean-nurseries showed evidence of six-monthly cycles of recruitment. While little other evidence of periodicities was visible for the CAC data, several cycles between 1 and 6 months in period were a feature of recruitment in data for all NT cage types with monthly cycles being the most prominent.

The cut-off or absence of peaks above 12-13 cycles·year^{-1} in the NT data suggests peak settlement at this frequency (Platt and Denman 1975) and indeed, approximately monthly peaks of recruitment were observed in weekly plots of these data in Chapter 4 (Fig. 4.2).

Monthly and semiannual rhythms are suggestive of tidal and/or lunar periodicities (Giese and Katani 1987; Halberg et al.1987) and peaks at these frequencies in recruitment data are matched by peaks in the spectral analysis of tidal range for Honiara and Gizo (Fig. 5.5).

The spectra of environmental variables such as wind incidence and rainfall from Munda present peaks between 2 and 8 cycles·year^{-1} which is the range in which a number of periodicities are apparent in the spectra of NT recruitment, particularly in floating cages (Fig. 5.4). Supposing that these common periodicities are indicative of a relationship between fluctuations in these environmental variables and recruitment, the difference in the spectra from different cage types could be explained. The spectrum of recruitment in benthic cages has fewer and smaller peaks between 2 and 8 cycles·year^{-1} than that of floating cages and the spectrum from trestle cages shows a pattern intermediate between the two. Wind incidence would be expected to have the greatest influence on surface waters where floating cages are located and the least influence on benthic cages; trestle cages, being located in midwater, falling somewhere in between.

The overall impression is that variability in recruitment at the CAC is governed by relatively few, low-frequency periodicities operating at periods of 6 months or more or by noncyclic fluctuations. Recruitment at NT is more complex, particularly in floating cages, with several cyclic phenomena apparent at periods of 1 month or more. Similar patterns of variability to this have been reported for the temporal distribution of tropical zooplankton (Lewis and Boers 1991).

The structure of the spectra of these recruitment time-series could arise from a number of internal or external mechanisms. If external, environmental, forcing was responsible for the structure of the recruitment spectra then, of the variables examined, tidal cycles show the clearest association. However, the exploratory nature of the analyses do not permit firm conclusions in this regard.

The rank correlation analyses of the relationship between environmental variables and recruitment illustrate the risk of finding spurious correlations between strongly autocorrelated datasets (Walters and Collie 1988). The large number of significant correlations found among the raw datasets were considerably reduced when the data were detrended. Only the correlations between detrended variables are considered in the discussion below, bearing in mind that correlations between differenced datasets are a measure of the association between monthly fluctuations rather than absolute quantities (Pepin 1990).

Four correlations of the 27 performed between lagged environmental variables and *C. muricinum* recruitment at the CAC were found to be significant, two of these at less than the 1% level of significance. This is more than would be expected if the data were random and lends support to the significance of these results.

Variations in monthly tidal range are correlated with fluctuations in recruitment at the CAC with a lag of between 2 and 3 months. This result is consistent with the results of the spectral analysis discussed above. However, the detrended tidal data showed some evidence of serial correlation owing to a 6-month cycle still remaining after first-differencing and this may affect the significance of observed correlations.

Fluctuations in rainfall at Honiara showed little correlation with recruitment at the nearby CAC. In contrast, rainfall at Munda showed strong negative correlation with recruitment at the CAC with a lag of some 4 months. The incidence of monsoon winds also seems associated with recruitment particularly if data from the previous 2 months are included.

Fewer significant correlations were observed in the case of recruitment in floating cages at NT. Neither tidal range nor rainfall showed significant correlations with recruitment, the only two significant correlations being those of the nonseasonal northeast and south winds. Several variables showed relatively high, albeit not significant, correlations. This confused picture is similar to the spectrum for recruitment in floating cages where variability seemed complex, determined by phenomena over a range of different frequencies.

Environmental Forcing of Recruitment

A number of possible relationships between recruitment and environmental variables are apparent from the exploratory analyses. Rainfall was not found to be positively correlated with recruitment but rather showed strong negative correlation with a lag of 4 months at the CAC and slight negative correlation at NT lagged by 2 months. This is in contrast to the work of Heslinga et al. (1990) who found recruitment of *C. muricinum* was enhanced some weeks after periods of heavy rain.

The most likely mechanism by which rainfall could affect recruitment in Solomon Islands based on the above analyses is through increased river discharges. The main islands are large and relatively high and heavy rainfall would be expected to produce significant inputs of freshwater and terrestrial run-off after a certain lag period. These discharges result in a great increase in turbidity in coastal and enclosed sea areas (pers. obs.) which may hinder larval survival or development.

Palau is comprised of small islands and terrestrial run-off is presumably much reduced. Rainfall may have the effect, as suggested by Heslinga et al. (1990), of slightly increasing productivity without greatly increasing turbidity thereby enhancing survival and recruitment of *C. muricinum*. However, rainfall in the tropics is usually seasonal and may be accompanied by seasonal winds as is the case with the monsoons in Solomon Islands. Heslinga et al. (1990) did not examine other environmental parameters but it may be the case that the correlation they observed was due to seasonal wind or current patterns rather than rainfall itself.

Recruitment at both Solomon Island sites was strongly correlated with the prevalence of certain winds. The fact that this correlation was stronger if the prevalence of the monsoon wind over the previous 2 months was included at the CAC and that there was no correlation between recruitment and wind strength at Nusatupe suggest that wind affects larval transport rather than mixing or turbulence.

The effect of variation in tidal range is not so clear. At the CAC, recruitment appears to be correlated with peaks in tidal range 2-3 months previously. As spectral analysis showed little evidence of monthly cycles at the CAC, the correlation with tidal range is probably due to the twice-yearly tidal cycle although the possibility that the correlation is due to other phenomena of similar frequency cannot be discarded.

Based on the data from the CAC, the most likely influence of peaks in tidal range on recruitment is on spawning or hatching periodicity and/or dispersal of the recently hatched larvae from parent reefs. This is not supported by data from NT as no significant correlations between tidal range and recruitment were observed, although these may have been masked by the other complex processes occurring at similar frequencies as shown by spectral analysis. Correlations with the 30-day cycle would not have been picked up as data were lumped into monthly totals.

A synthesis of the possible effects of the environmental processes on recruitment at the CAC may be constructed as follows:

The obligatory planktonic phase of *C. muricinum* larvae may be about 3 months (c.f., Chapter 4). Thus environmental factors operating about 3 months prior to recruitment at the CAC would be influential. This is the case of tidal range which may be related to hatching and dispersal of larvae. Periods of heavy rain prior to hatching would result in adverse nearshore or lagoonal conditions for the recently hatched larvae due to increased river discharge over subsequent weeks.

Recently hatched larvae which had successfully dispersed from their parent reefs drift at the mercy of the currents. Particularly high densities of larvae might be expected in the vicinity of the complex lagoon systems of Western Province where adult *C. muricinum* should be relatively very abundant. Thus, periods of sustained northwesterly winds such as the monsoons might cause significant numbers of these larvae to be transported towards the CAC ocean-nursery in Guadalcanal. Other winds such as the northeast or southeasterly winds would tend to drive water masses which are relatively poor in *C. muricinum* larvae, towards the CAC from the open Pacific or from islands with comparatively little suitable habitat for adult *C. muricinum*.

A similar model relating environmental processes and recruitment at the NT ocean-nursery does not appear applicable. The effect of tides and rainfall on recruitment is not significant and few significant correlations are visible overall.

Analysis of data from NT was hampered by the short datasets available. Other reasons why environmental forcing may not be readily apparent at NT may include:

i) environmental data with the exception of tidal range was taken from Munda, some 40 km distant and located on the south coast of a high island, a very distinct topography from that of Nusatupe;
ii) the systems of lagoons and islands surrounding Munda and Nusatupe are extensive and very complex.
iii) Nusatupe is in an area where parent stocks of *C. muricinum* are expected to be high and therefore larval densities may be relatively high most of the time.

The above suggests that the major influence on recruitment at NT would be that of hydrographical factors impinging directly on ocean-nursery cages. These factors, such as current direction and strength or local winds, would have to be measured in the ocean-nursery itself.

Walters and Collie (1988) warn about the ease of rationalizing observed correlations between environmental variables and recruitment. Their caution is justified as it would have been similarly easy to explain other combinations of results in the present study but their recommendation not to report biological rationalizations unless supported by a variety of independent measurements seems too strict for the present case.

By formulating a model to explain the correlations between environmental factors and recruitment observed at the CAC and NT it was possible to discuss mechanisms that could be involved to varying extents at these ocean-nurseries and others throughout the Pacific.

The models tested for recruitment at the CAC and the correlation observed at NT statistically explained more than 50% of the recruitment variability. Of course, the acid test of recruitment-environment correlations is the ability to forecast data not available at the time of the original analysis (Shepherd et al. 1984) and this was not possible in the current case.

Implications for Giant Clam Culture

This work and that of Heslinga et al. (1990) suggest that practicable predictors of the timing of peaks of ranellid recruitment may be found at certain ocean-nurseries. For the purposes of most tridacnid mariculturists, recruitment of *C. muricinum* and other ranellid predators need not be predicted with great quantitative accuracy.

Therefore major ocean-nurseries will probably find it useful, at least initially, to combine the collection of ranellid recruitment data recommended in Chapter 4 with the collection of basic environmental information. If any environmental correlates become apparent within the first few years these could be tested subsequently.

The year-round breeding strategy of these ranellids and the constant background levels of recruitment suggest that regular checks for these predators in ocean-nurseries will always be a feature of tridacnid culture.

CHAPTER 6

Impact of *Cymatium muricinum* on the Ocean Culture of Tridacnids

6.1 Introduction

The success of an aquaculture operation generally depends on optimizing the growth and survival rates of the cultured organisms. In this context it is evidently very important to determine the causes of poor survival so that effort can be concentrated on the major and/or most easily tackled causes, thus maximizing profitability.

Despite many centuries of experience (e.g., Grizel 1993), predation on commercially cultivated molluscs during ocean culture remains one of the major hindrances to successful mariculture in many areas of the world (see review by Jory et al. 1984).

In temperate seas predation is recognized as a critical limiting factor in the culture of mussels, *Mytilus edulis* and oysters, *Crassostrea* spp. (Dare and Edwards 1976; Dare et al. 1983); hard clams, *Mercenaria mercenaria*, soft shell clams, *Mya arenaria* and Manila clams, *Venerupis* spp. (Gibbons and Blogoslawski 1989) and a number of other species including abalone, *Haliotis* spp. and conchs, *Strombus* spp. (Jory et al. 1984). Consequently, the prevention of predation has traditionally constituted a major component of the culture operations (Nelson 1931; Davies et al. 1980; Jory et al. 1984).

Molluscan culture in developing nations, and thus tropical seas, is less documented than that in temperate areas. Nevertheless, predation is reported to be a problem in the cultivation of oysters, *Crassostrea* spp. and *Saccostrea* spp. (Brohmanonda et al. 1988; Littlewood 1991); cockles, *Anadara granosa* (Thamasavate et al. 1988); mussels, *Perna* spp. (Vakily 1989) and juvenile pearl oysters, *Pinctada* spp. and *Pteria penguin* (Gervis and Sims 1992). However, in most cases the importance of predation compared to other sources of mortality is not recorded.

Ranellid predation has been reported from a number of culture operations of nontridacnid bivalves (c.f., Chapter 1) but generally the importance of the losses caused by these predators is not estimated. Ranellid predation has been reported as a major problem in the cases of *Cymatium pileare* preying on *Crassostrea gigas* in the Red Sea (Hughes-Games 1977) and of *Cymatium* spp. preying on *Pinctada* spp. in Okinawa (Muramatsu, pers.comm.).

Mortality and Predation of Tridacnids in Ocean-nurseries

Mortality of tridacnid clams cultivated in ocean-nurseries around the Pacific is relatively high even at the well-established nurseries of the Micronesian Mariculture Demonstration

Centre (MMDC) in Palau and Orpheus Island (OIRS) near Townsville, Queensland (see Fig. 1.1 for geographic locations). At the MMDC, mortality of *T. derasa* juveniles is 25-50% over the 16- to 22-month ocean-nursery phase, which starts when clams are 8-9 months old (30-40 mm SL). Nearly all of the mortality was attributed to predation by *C. muricinum* (Heslinga 1989).

Barker et al. (1988) calculated a survival rate of around 40% for juvenile *T. gigas* from 6 months to 3 years old in intertidal ocean-nurseries at OIRS. Mortality was not attributed to predation but rather overcrowding, algal overgrowth or gear failure.

Other, smaller ocean-nurseries invariably report problems with high mortality often attributed to predation (c.f., Chapter 1). In American Samoa, mortality of *T. derasa* juveniles (80-160 mm SL) was reported to be in the region of 20-30% per year, 45% of which was ascribed to predation by *C. muricinum* (Ponwith 1990).

One thousand 13- to 18-month old *T. derasa* introduced to the Cook Islands suffered 24.6% mortality in the first 2 months. This mortality was attributed to predation by *C. muricinum* and exacerbated by an ineffectual maintenance regime (Sims and Howard 1988).

Over 16% mortality was experienced in a batch of 15-month old *T. derasa* juveniles (84 mm mean SL) transferred to Yap, in the Federated States of Micronesia, over the first 6 months. This mortality was largely ascribed to *C. muricinum* infestations (Perron et al. 1985; Price and Fagolimul 1988).

Mortality of five species of juvenile tridacnids in Central Visayas, Philippines, over periods of up to 24 months were between 5 and 100%. Part of this mortality was attributed to various predators (Estacion 1988). Up to 90% mortality of juvenile *T. squamosa* was observed at an ocean-nursery site near Bolinao, Philippines. The causes are not known (Gomez and Belda 1988) although potential ranellid, buccinid and muricid predators have been found in this area (Perio and Belda 1988).

At most ocean-nurseries, predation by *C. muricinum* was implicated in the mortality of juvenile clams based on the presence of this gastropod in culture cages and the presence of dead clams. Virtually no attempts have been made to quantify the contribution of ranellids to the mortalities suffered.

The main problem in assessing the proportion of mortality due to different predators appears to have been the difficulty in establishing the numbers and residence times of predators in cages as most culture systems employed did not prevent snails from accessing cages at will from the seabed. Snails recovered may not represent the true levels of infestation experienced, at night time for instance.

Clams dying of other causes such as adverse environmental conditions, diseases or genetic abnormalities may attract scavengers. As discussed in Chapter 4, dead or moribund clams may attract *C. muricinum* which may be assumed to be the cause of death by clam farm operators despite the possibility that they are acting merely as scavengers.

The present study offered a good opportunity to assess the impact of predatory ranellids on cultured *T. gigas* for several reasons:

a) comprehensive records regarding predator collection and clam stocks were available for an ocean-nursery, that at Nusatupe;
b) most ranellids collected were thought to have settled in the ocean-nursery cages;
c) postlarval growth and consumption rates were known for the ranellid species in question; and
d) the extensive use of floating cages allowed predation owing to ranellids settled in culture cages to be examined in a situation where immigration and emigration of

these tritons in cages could be considered negligible and losses of clams and juvenile ranellids due to other predators were expected to be greatly reduced.

Perron et al. (1985) noted that dead or dying clams attract a variety of scavenging organisms but did not speculate on the potential impact of these animals on clam culture. Govan (1992a) proposed removing scavenging organisms from ocean-nursery cages where possible as these animals may compete with ranellids or other predators in the consumption of their prey thereby forcing the predators to kill more clams.

Although competition by gastropods such as *Cronia ochrostoma* and *Nassarius* spp. (known to scavenge on but not kill, tridacnids, Govan 1994) with predatory ranellids has occasionally been observed in ocean-nurseries (pers. obs.), evidence for the significant impact of such a mechanism is lacking.

This chapter examines the relationship between mortality of *T. gigas* in the Nusatupe ocean-nursery and incidence of *C. muricinum* and an attempt is made to quantify the clam production lost to this predator. The potential consumption rates of some gastropod scavengers is also examined as is the possibility that these animals could account for some of the unexplained losses in clam production.

6.2 Methods

Data used in this chapter for the estimation of tridacnid mortality and the impact of *C. muricinum* are those described in Chapter 4 for the Nusatupe ocean-nursery. Records were available of the number and size of clams in each cage at censuses carried out at 2- to 3-month intervals over 1.5 years from January 1991. Cages for which complete records were not kept, dubbed "production cages" by ocean-nursery staff, were omitted from this analysis. Records were available of the number and size of ranellids and the number of other gastropods and dead clam shells removed from cages on an approximately daily basis during the same period.

All the above records were incorporated in a computerized database (DataEase) and sorted such that at the date of each three-monthly census the following data were presented for each cage: number of clams present in the cage and the difference from that in the previous census (clam losses), the number of dead shells recovered since the previous census (dead shells recovered), the mean size of clams and the difference of this since the previous census (clam growth), number of *C. muricinum* and other gastropods recovered since the previous census and the time elapsed since the previous census.

Estimated values were also derived for the following parameters:

Dry tissue weight of clam losses and of the dead shells recovered. These were calculated using the length:weight relationships for *T. gigas* shown in Appendix 2. The size of clams used in this calculation was the average of the sizes at the previous and present census, a procedure which probably underestimates the total weight of a normally distributed sample because larger clams may be expected to contribute relatively more than the smaller clams (Beyer 1987). More precise computations given by Beyer (1987, 1991) were not possible as the standard deviations of mean clam sizes were not available. However, as mortality may be expected to be higher amongst smaller clams, the mean size of dead clams is probably smaller than that used above, a factor which probably causes the total tissue weight of clam losses to be overestimated. Thus, although the factors discussed above probably compensate for each other to a certain extent, the calculated values only represent rough approximations which are adequate for the purposes of the present study.

Dry tissue weight of T. gigas *consumed by juvenile* C. muricinum *in order to attain the sizes recorded on collection from cages.* These data together with 95% confidence limits were calculated using the results of aquarium-based studies shown in Table 3.8.

Daily mortality rates. Instantaneous mortality rates were calculated based on clam losses and dead shells recovered using an exponential decay function (equation 6.1).

$$S_i = e^{-Z_i} \qquad \text{...6.1)}$$

where "S_i" is the survival in time period "i", "Z_i" is the instantaneous mortality rate and "e" is the base of natural logarithms.

All parameters were summed to give an overall impression for the Nusatupe ocean-nursery and were also sorted and grouped by cage type and initial clam stocking size to examine the effects of these variables. The stocking size intervals (< 15 mm, 15-40 mm, 40-60 mm and > 60 mm SL) were set in an attempt to achieve approximately equal numbers of cases in each interval.

In order to examine the relationship between *C. muricinum* abundance and clam mortality over all censuses the data were analyzed using Spearman's rank correlations as discussed in Section 4.2. Because mortality and *C. muricinum* abundance increase as a function of time it was necessary to attempt to reduce the significance of the time element. This was achieved by converting all the parameters tested to daily rates. Correlations were calculated for all data grouped together and for datasets sorted by cage type and initial clam stocking size.

The possible impact of gastropod scavengers of dead or dying *T. gigas* on clam mortality in the Nusatupe ocean-nursery was examined. A variety of different gastropods were collected from ocean-nursery cages and the most common of these were kept in a variety of static and flow-through aquaria for 1-2 weeks and offered mantle tissue of *T. gigas* on at least three separate occasions to test their capacity to consume clam carrion. Animals not found to consume clam carrion and those found to be predators on *T. gigas* are reported in Govan (1994). A similar method was employed by I. Lane at Nusatupe who provided the observations concerning *Mitrella albina*, *Peristernia ustulata* and *Vexillum exasperatum.*

The gastropods known to consume clam carrion were removed from ocean-nursery cages and counted as part of the routine daily predator removal activities during the final 11 months of the experimental period at the Nusatupe ocean-nursery.

Rank correlation analyses were performed on the data for this 11-month period in order to examine the relationship between clam mortality and the presence of scavenging gastropods as compared with the abundance of *C. muricinum.*

Rates of *T. gigas* tissue consumption were measured for three species of gastropod scavengers available at the CAC. The protocol followed was that described by Morton (1990a) in a similar study of feeding in gastropod scavengers.

Five groups of five *Cronia ochrostoma* (mean size = 15.5 mm, mean blotted live weight = 0.77 g), two groups of five *Pyrene scripta* (mean size = 9.9 mm, mean weight = 0.43 g) and three groups of five *P. turturina* (mean size = 10.3 mm, mean weight = 0.49 g) were kept in the multichambered flow-through tank described in Section 3.2. Only adult snails were used. Snails were starved for 12 days and then offered pieces of clam mantle previously blotted dry in a standard manner and weighed.

The experiment ran overnight (17 hours) after which the tissue was removed from the chambers, reblotted and reweighed. A reduction in weight represented the amount of tissue eaten by the snails. To determine the error due to natural weight loss to (or gain from) the seawater, control mantle tissue was established and tissue variations recorded. Dry weights were obtained using the microwave oven drying technique described in Section 3.2. The amount of tissue, in terms of dry weight and wet weight, eaten by the snails in a standard time was obtained.

6.3 Results

The total number of clams of all sizes which died or were lost from the Nusatupe ocean-nursery are shown in Table 6.1. The clam losses represent the reduction in stock between

Table 6.1. Mortality of *T. gigas* in the experimental ocean-nursery at Nusatupe, Solomon Islands. 105,000 clams from 2 to 90 mm in shell length were placed in the ocean-nursery over 18 months. Daily mortality rates are based on clam losses in each cage over the 2.5-month period between each stock-taking. Total numbers of the major predator, *Cymatium muricinum*, collected in the ocean-nursery over the 18-month period are shown along with an estimate of clam tissue which the snails would have needed to consume to grow from their size at settlement to their size on collection. Numbers in brackets represent the 95% confidence interval of this estimate. The proportion of clam losses in terms of biomass which is accounted for if it is assumed that *C. muricinum* settled in cages as larvae and consumed only *T. gigas* until collected is given.

Total clam losses	41,930	
Total dead shells recovered	11,350	
Mean daily mortality rate (%)	0.45	
Estimated dry tissue weight of clam losses (g)	2,222	
Estimated dry tissue weight of dead shells recovered (g)	1,699	
Total *C. muricinum* recovered	3,187	
Estimated dry tissue weight of clams consumed by *C. muricinum* (g)	586	(427-804)
Proportion of clam losses accounted for (%)	26	(19-36)
Proportion of dead shells accounted for (%)	35	(25-47)

censuses including those clams found as dead shells and clams which disappeared. The large number of clams unaccounted for (73% of total losses) is worthy of note.

Approximately 105,300 clams were stocked in the Nusatupe ocean-nursery, however these were stocked at different times throughout the experimental period and at sizes ranging from 2 to 91 mm in shell length. Thus mortality was calculated as the average of the daily loss rates calculated for each cage and each intercensus period (2.5 months on average). This information was of value chiefly for comparative purposes.

In the region of 2.2 kg of clams were lost during the experimental period in terms of dry tissue weight and the estimated weight of the dead clams was 1.7 kg. The unaccounted for clam losses were far smaller in terms of tissue weight than in terms of numbers, giving the first indication that the missing clams were probably smaller than the dead shells retrieved.

More than 3,000 *C. muricinum* were recovered from the cages during the experimental period (Table 6.1) and, assuming similar consumption and growth rates to those observed in

aquaria, these tritons would have consumed between 0.4 and 0.8 kg of clam tissue (dry weight) to have achieved their size at collection. Thus, these tritons could have directly accounted for 25% of the missing clam biomass and about 33% of the biomass of the dead shells recovered.

A similar analysis is presented for four different stocking sizes of clam in floating, trestle and benthic cages (Tables 6.2a, 6.2b and 6.2c, respectively). Stocking size refers to the size of clams in a cage at the beginning of the period from previous census to the current census. As would be expected, mortality is highest amongst the smaller clams and is reduced as a function of increasing clam size in all three cage types. Comparison of the values given in Tables 6.2a to 6.2c for total clam losses and dead shells recovered shows that the large number of clams unaccounted for, as noted above, is almost entirely attributable to losses amongst the clams smaller than 15 mm SL (2-15 mm).

Table 6.2a. Mortality of *T. gigas* in floating cages at the experimental ocean-nursery at Nusatupe, Solomon Islands. Data are shown for clams grouped into four size ranges representing the initial mean size of the clams during the period for which mortality is estimated in each cage. "Initial number of clams" represents the sum of all clams present in each cage at the start of each experimental period. Other parameters are as described in the caption for Table 6.1.

	Size of clams							
	<15 mm		15-40 mm		40-60 mm		>60 mm	
Initial number of clams	30,920		14,070		6,418		-	
Total clam losses	22,787		3,599		1,645		-	
Total dead shells recovered	1,239		3,158		1,352		-	
Mean daily mortality rate (%)	1.44		0.37		0.36		-	
Estimated dry tissue weight of clam losses (g)	161		295		583		-	
Estimated dry tissue weight of dead shells recovered (g)	14		261		463		-	
Total *C. muricinum* recovered	242		864		465		-	
Estimated dry tissue weight of clams consumed by *C. muricinum* (g)	31	(23-41)	134	(98-180)	124	(89-173)	-	
Proportion of clam losses accounted for (%)	19	(14-26)	45	(33-61)	21	(15-30)	-	
Proportion of dead shells accounted for (%)	100+	(164-293)	51	(38-69)	27	(19-37)	-	

Table 6.2b. Mortality of *T. gigas* in trestle cages at the experimental ocean-nursery at Nusatupe, Solomon Islands. Data are shown for clams grouped into four size ranges representing the initial mean size of the clams during the period for which mortality is estimated in each cage. "Initial number of clams" represents the sum of all clams present in each cage at the start of each experimental period. Other parameters are as described in the caption for Table 6.1.

	Size of clams							
	<15 mm		15-40 mm		40-60 mm		>60 mm	
Initial number of clams	9,268		10,980		9,007		3,070	
Total clam losses	7,344		2,897		1,850		126	
Total dead shells recovered	417		2,214		1,270		137	
Mean daily mortality rate (%)	1.99		0.38		0.23		0.05	
Estimated dry tissue weight of clam losses (g)	49		265		524		108	
Estimated dry tissue weight of dead shells recovered (g)	4		196		342		123	
Total *C. muricinum* recovered	91		667		355		134	
Estimated dry tissue weight of clams consumed by *C. muricinum* (g)	15	(11-20)	93	(69-126)	85	(62-118)	47	(33-66)
Proportion of clam losses accounted for(%)	31	(22-41)	35	(23-48)	16	(12-23)	44	(31-61)
Proportion of dead shells accounted for(%)	100+	(275-500)	47	(35-64)	25	(18-35)	38	(27-54)

Table 6.2c. Mortality of *T. gigas* in benthic cages at the experimental ocean-nursery at Nusatupe, Solomon Islands. Data are shown for clams grouped into four size ranges representing the initial mean size of the clams during the period for which mortality is estimated in each cage. "Initial number of clams" represents the sum of all clams present in each cage at the start of each experimental period. Other parameters are as described in the caption for Table 6.1.

	Size of clams							
	<15 mm		15-40 mm		40-60 mm		>60 mm	
Initial number of clams	-		2,846		1,374		1,459	
Total clam losses	-		1,487		175		157	
Total dead shells recovered	-		1,263		143		105	
Mean daily mortality rate (%)	-		0.80		0.19		0.09	
Estimated dry tissue weight of clam losses (g)	-		163		63		70	
Estimated dry tissue weight of dead shells recovered (g)	-		138		52		106	
Total *C. muricinum* recovered	-		219		40		110	
Estimated dry tissue weight of clams consumed by *C. muricinum* (g)	-		23	(17-31)	11	(8-15)	25	(18-34)
Proportion of clam losses accounted for (%)	-		14	(6-19)	18	(13-24)	36	(26-49)
Proportion of dead shells accounted for (%)	-		17	(12-22)	21	(15-29)	24	(17-32)

Clams smaller than 15 mm SL are unusually small to be placed in ocean-nurseries (Munro et al. 1993) and such small shells could easily be swept out of cages by water movements, alive or dead. Small clams are often observed to actively change location inside cages or tanks by crawling with the foot (pers. obs.) and such clams may fall out of cages. Furthermore, even very occasional incursions by mobile predators such as fish or crabs would be expected to take an extremely high toll in terms of numbers of these clams. For these reasons the data pertaining to this size range are not considered further.

The estimates of tissue weight lost and consumed (Tables 6.2a to 6.2c) show a trend in which *C. muricinum* from floating cages could have accounted for up to 51% of the clam mortality in terms of biomass, while this figure is reduced in trestle cages and further reduced in benthic cages where *C. muricinum* consumption was only in the region of 20% of clam losses. A similar trend is observed with increasing clam sizes in each cage type except benthic cages. Consumption was about 50% of the tissue corresponding to dead clams recovered in the 15-40 mm size range at stocking, whereas this was considerably reduced for clams larger than 40 mm.

Clam mortality, measured as dead shells retrieved, is correlated at a high level of significance with the presence of *C. muricinum* both in terms of numbers and tissue weight consumed (Table 6.3). Clam losses, however, are not so highly correlated with the presence of *C. muricinum*, a fact probably due to these losses being caused by migration or other factors as mentioned above.

Table 6.4 gives a breakdown of correlations between *C. muricinum* and clam mortality for each cage type and three ranges of stocking size. The number of degrees of freedom for the data grouped by cage type and clam size varies between 5 and 33 with only the data for benthic cages having less than 10 degrees of freedom. Thus the relative values of r_s may only be compared for data pertaining to the same clam size and cage type and not between groups. Several trends are apparent, however; mortality in trestle cages tends to be more highly correlated with

Table 6.3. Spearman rank correlations between *C. muricinum* recovered from cages at the Nusatupe ocean-nursery expressed as either daily abundance or estimated daily tissue consumption and mortality of juvenile *T. gigas*. Mortality is presented in terms of the reduction of clam numbers between stock-takings in each cage or in terms of number of dead shells recovered in the same period divided by the length of the period. Only data from cages in which clams were stocked at a size greater than 15 mm are included, a total of 144 cases. With one exception, all correlation coefficients are significant at $P < 0.0001$.

	A	B
Daily clam losses (as % of initial stock)	0.467	0.233[1]
Daily dead shells recovered (as % of initial stock)	0.712	0.542
Estimated dry tissue weight of clam losses (g/day)	0.528	0.473
Estimated dry tissue weight of dead shells recovered (g/day)	0.641	0.623

A: *C. muricinum* recovered/day.
B: Estimated dry tissue weight of clams consumed by *C. muricinum*·day^{-1}
1: $P = 0.003$

Table 6.4. Spearman rank correlations between *C. muricinum* recovered from floating, trestle and benthic cages at the Nusatupe ocean-nursery and clam mortality in terms of dead shells recovered. The impact of *C. muricinum* is expressed as total *C. muricinum* recovered per cage/day between stock-takes (A) and estimated dry tissue weight of clams consumed by *C. muricinum*/day between stock-takes (B). Data are shown for clams grouped into three size ranges representing the initial mean size of the clams during each period for which mortality is estimated.

	Size of clams					
	15-40 mm		40-60 mm		>60 mm	
	A	B	A	B	A	B
Floating cages						
Daily dead shells recovered[1]	0.79*	0.68*	0.38^{ns}	0.33^{ns}	-	-
Estimated dry tissue weight of dead shells recovered[2]	0.60*	0.66*	0.55	0.60*	-	-
Trestle cages						
Daily dead shells recovered[1]	0.54*	0.35^{ns}	0.47*	0.40	0.44^{ns}	0.38^{ns}
Estimated dry tissue weight of dead shells recovered[2]	0.81*	0.72*	0.56*	0.53*	0.48	0.46^{ns}
Benthic cages						
Daily dead shells recovered[1]	0.86	0.93*	0.60^{ns}	0.21^{ns}	0.78	0.87*
Estimated dry tissue weight of dead shells recovered[2]	0.89	0.86	0.60^{ns}	0.30^{ns}	0.80*	0.95*

1: Calculated as number of dead shells collected from each cage between stock-takes as a % of initial stock/days between stock-takes.
2: Calculated as estimated tissue weight of the dead shells from 1 above/number of days between censuses.-: Not available.
ns: Not significant at $P > 0.05$
*: $P < 0.01$

numbers of *C. muricinum* recovered than with the biomass that these tritons were estimated to consume but mortality in floating cages shows highest correlations between the estimated tissue weight of dead shells and the estimated triton consumption. The results from benthic cages are not so clear but this may be due to the small datasets involved.

Gastropods collected from the ocean-nursery, and which were observed to consume dead clam tissue, are listed in Table 6.5. These gastropods were generally most abundant in benthic

cages and to a lesser extent in trestle cages, some were also found in floating cages. The most common scavengers were the muricids *Cronia margariticola* and *Muricodrupa fiscella* and the columbellids *Pyrene turturina* and *P. scripta* although other snails from these families and the Nassariidae, Costellariidae and Fasciolariidae were also found. These snails were all relatively small and, with the possible exception of floating cages, were able to enter and leave cages at will. Therefore the counts of scavenging gastropods are more indicative of frequency of access to cages of these animals than of total numbers.

Correlations between the total abundance of all scavenging gastropods and clam mortality in the ocean-nursery are lowest in the case of floating cages and highest in benthic cages.

Table 6.5. Gastropods collected from floating (Flo), trestle (Tre) and benthic (Ben) cages in the Nusatupe ocean-nursery which were observed to scavenge dead *T. gigas*. Snails were collected over a period of 341 days and data are presented as total number and as densities of snails m^{-2} collected from each cage type.

	Total collected			Total m^{-2}		
	Flo	Tre	Ben	Flo	Tre	Ben
Cronia margariticola	50	230	268	4.6	4.7	32.3
Cronia ochrostoma	10	24	14	0.9	0.5	1.7
Mitrella albina	22	69	150	2.0	1.4	18.1
Muricodrupa fiscella	11	138	43	1.0	2.8	5.2
Nassarius albescens	2	4	9	0.2	0.1	1.1
Nassarius echinatus	29	22	4	2.7	0.5	0.5
Peristernia ustulata	2	11	43	0.2	0.2	5.2
Pyrene scripta	37	327	73	3.4	6.7	8.8
Pyrene turturina	61	473	89	5.6	9.7	10.7
Vexillum exasperatum	6	36	55	0.6	0.7	6.6
Totals	230	1,334	748	21.2	27.3	90.2

Table 6.6. Spearman rank correlations between numbers of gastropods known to scavenge clam tissue and dead clam shells recovered in the Nusatupe ocean-nursery over 341 days. Data from the periods between stock-takes for each cage were converted to daily rates by dividing by the length of the period in days. Data are shown for clams grouped into three size ranges representing the initial mean size of the clams during each period for which collections were made.

	Size of clams		
	15-40 mm	40-60 mm	>60 mm
Floating cages			
C. muricinum recovered/day	0.749^{**}	-0.051^{ns}	nc
Other gastropods recovered/day	-0.152^{ns}	0.329^{ns}	nc
Number of cases	19	14	3
Trestle cages			
C. muricinum recovered/day	0.235^{ns}	0.488^{**}	0.512^{*}
Other gastropods recovered/day	0.204^{ns}	0.583^{**}	0.349^{ns}
Number of cases	15	35	20
Benthic cages			
C. muricinum recovered/day	nc	0.458^{ns}	0.850^{**}
Other gastropods recovered/day	nc	0.698^{*}	0.915^{**}
Number of cases	5	9	10

nc: Not calculated owing to insufficient number of cases
ns: Not statistically significant ($P>0.05$)
*: Significant at $0.05 > P > 0.01$
**: Significant at $P < 0.01$

Table 6.7. Consumption rates of three species of gastropod scavengers: *Cronia ochrostoma* (mean size = 15.5mm, mean live weight = 770 mg), *Pyrene turturina* (mean size = 10.3 mm, mean live weight = 490 mg) and *P. scripta* (mean size = 9.9 mm, mean live weight = 430 mg). Scavengers were offered mantle tissue of *Tridacna gigas* over 17 hours. An asterisk indicates samples that were not constantly available to snails due to floatation. See text for more details.

Species	n	Consumption/snail/hour (mg)	
		dry weight	wet weight
C. ochrostoma	5	0.41	2.16
C. ochrostoma	5	0.36	1.90
C. ochrostoma	5	0.31	1.63
C. ochrostoma	5	0.26*	1.37*
C. ochrostoma	5	0.41	2.15
P. turturina	5	0.12	0.63
P. turturina	5	0.13	0.68
P. turturina	5	0.00*	0.00*
P. scripta	5	0.13	0.69
P. scripta	5	0.05*	0.26*

Correlations also tend to increase with increased clam size (Table 6.6).

An estimate of the amount of tissue consumed by three species of gastropod scavenger is shown in Table 6.7. While determining the consumption rates of these scavengers, control clam tissue was found to increase in wet weight (presumably due to the absorption of water) and decrease in dry weight compared to tissue dried immediately (presumably due to decomposition and leaching). The figures shown in Table 6.7 are corrected for these variations.

The consumption figures may represent underestimates as the size of the pieces of tissue were too small to allow easy access by all snails in a compartment at the same time and in three instances tissue was observed to float to the surface of compartments at the end of the experiment due to the presence of gas bubbles.

Groups of five *C. ochrostoma* were capable of consuming up to 35 mg dry weight (DW) of tissue over the 17-hour test period and the smaller *Pyrene* species up to 11 mg DW. To put this in perspective, 35 mg DW of clam tissue is approximately equivalent to that of one 24-mm SL clam.

6.4 Discussion

Mortality of *T. gigas* smaller than 15 mm in shell length at the Nusatupe ocean-nursery is in general very high. Clams as small as 2 mm were placed in floating cages as part of innovative attempts to reduce the period during which such clams must remain in land-based tanks (Munro et al. 1993). Mortality of clams of this size is also relatively high in tanks (Munro et al. 1993) and considering the small numbers of *C. muricinum* and dead shells recovered it is likely that causes other than ranellid predation were responsible such as disease, overcrowding or, most likely, escape from the cages. Mortality of clams smaller than 15 mm SL in these experiments is not considered further.

Migration from cages and miscounts are probably the reasons for the discrepancy between estimated clam losses and numbers of dead shells recovered (c.f., Table 6.2). Dead shells probably provide a clearer indicator of predation-related mortality in cage culture.

Comparisons with survival rates achieved at other ocean-nurseries in the region are not straightforward owing to differences in husbandry techniques, such as stocking size and species cultivated. Based on mortality rates in Table 6.2 and an average growth rate of 5 mm·month^{-1} (Munro et al. 1993) it appears that 35% survival could be achieved 2 years after stocking with 15-mm clams or 50% survival if 40-mm clams are used. These estimates are comparable to values of 50-75% obtained at MMDC using *T. derasa* stocked at 30-40 mm over less than 2 years (Heslinga 1989) and of 40% for *T. gigas* stocked at a similar size but over 2.5 years at OIRS (Barker et al. 1988).

As a first step in determining the impact of *C. muricinum* on *T. gigas* production at the Nusatupe ocean-nursery the amount of clam tissue consumed by the tritons in order to attain their size on collection was calculated. This approach relies on the following assumptions being met:

i) *C. muricinum* have spent their entire postlarval lives in the cage from which they were collected. In Chapter 4, this was concluded to be the case for virtually all *C. muricinum* collected at Nusatupe and especially those from floating cages.

ii) Consumption and growth rates of *C. muricinum* in ocean-nursery cages are similar to those observed under laboratory conditions. No independent estimates regarding consumption rates are available although evidence was presented in Chapter 4 suggesting that the growth rate of *C. muricinum* in cages at Nusatupe was similar to that observed in aquaria.

iii) *C. muricinum* in the ocean-nursery cages at Nusatupe consume only the cultured *T. gigas* and not other organisms present in cages. Relatively few wild organisms were recovered from clam cages with the possible exception of periodic settlement of fouling pearl oysters, *Pinctada maculata*, in floating cages. However, results from Chapter 2 suggest that *T. gigas* was the preferred prey of *C. muricinum*, compared with these oysters and other commonly occurring animals.

iv) *C. muricinum* kill each clam attacked. It is possible that small tritons feed on *T. gigas* in ocean-nurseries but do not kill them before being removed or moving on to other clams. This would result in a loss of production but not necessarily increased mortality. Based on the work presented in Chapter 3 this sort of behavior seems unlikely and the size of most of the tritons collected was sufficiently large to account for the consumption of several clams from the cages from which they were collected. However, in some cases more than one small *C. muricinum* may feed on the same clam with the reduced effects on mortality described above.

v) *C. muricinum* consume the whole of each clam attacked. As soon as the feeding activities of a *C. muricinum* seriously weaken or kill the prey clam this will be attractive and vulnerable to scavenging organisms which may compete to consume the clam tissue. Dead clams become byssally detached and may represent too unstable a habitat for the tritons to cope with, especially in floating cages. Such processes would tend to result in an underestimate of the clam mortality associated with the presence of *C. muricinum*.

vi) Most *C. muricinum* occurring in the ocean-nursery cages are collected. Possible reasons why *C. muricinum* may not be collected from the ocean-nursery examined in Chapter 4 were the precollection loss of tritons due to migration (active or passive) or predation and difficulties experienced by staff in locating all tritons in certain cages. These processes are deemed more likely to occur in benthic and, to a lesser extent, in trestle cages; although they were thought not to be important, with the possible exception of predation on juvenile *C. muricinum*. Underestimation of the numbers of *C. muricinum* occurring in the ocean-nursery would obviously result in an underestimate of the clam mortality associated with this species.

From the above it appears that estimation of the amounts of clam tissue consumed by the *C. muricinum* collected from the Nusatupe ocean-nursery may be expected to provide a useful measure of the contribution of these tritons to losses in clam production although this measure may constitute an underestimate. The reliability of the method may be reduced in cages more

closely associated with the seabed. Low numbers of other ranellids were collected at Nusatupe and as the abundance of these was correlated with that of *C. muricinum* other ranellids were not considered in the analysis.

In floating and trestle cages *C. muricinum* consumption would appear to be the major cause of mortality in clams between 15 and 40 mm SL at Nusatupe. However, tissue consumption by *C. muricinum* would only account for 25-38% of dead shells of larger clams in these cages and 17-24% of dead shells of all sizes in benthic cages. This raises the question of whether *C. muricinum* has indeed less impact on the mortality of these clams or whether processes described in v) and vi) above come into play.

Larger sizes of juvenile *T. gigas* protected by cages are expected to suffer little predator-related mortality with the exception of that caused by ranellids (Govan 1992a; Govan 1994). The fact that insignificant numbers of predators other than ranellids were collected from cages containing larger clams or benthic cages in general warrants an examination of the possibility that scavenging organisms contribute to mortality caused by ranellids.

It seems reasonable to suppose that the effect of scavengers would be most noticeable in cases where *C. muricinum* attack larger clams as these will take a long time to consume, giving scavengers a better chance of detecting and finding the moribund clam. Also, cages located close to the seabed would be expected to afford greater ease of access to these scavenging organisms. These suppositions could explain the relatively low impact of *C. muricinum* estimated for larger clams and benthic cages.

One would expect mortality in terms of the estimated biomass of dead shells recovered to be correlated more highly with the estimated biomass consumed by *C. muricinum* than with the numbers of *C. muricinum* collected, only if this triton was chiefly responsible for the consumption of the dead clams.

Supposing the main effect of *C. muricinum* infestation was the killing or weakening of clams which were subsequently consumed by scavengers, the abundance of *C. muricinum* may be expected to bear more relation to clam mortality than the amount this species was estimated to consume. This would be reflected by greater correlations between clam mortality (particularly number of dead shells) and numbers of *C. muricinum* collected than with consumption.

Table 6.4 reflects the scenario depicted above as well as showing high correlations between *C. muricinum* infestations and clam mortality in general. In floating cages the salient correlations are between estimates of dead clam biomass and *C. muricinum* consumption whereas the salient correlations in trestle cages are with numbers of *C. muricinum* collected. The situation is not so clear in benthic cages but this may reflect the reduced datasets available, greater precollection losses of *C. muricinum* or the effects of other benthic predators on the smaller clams. Such benthic predators may include adult ranellids which may hide on the seabed during the day and attack clams in benthic cages nocturnally (c.f., Chapter 2) thus accounting for their absence in the routine, daytime, collections.

Further evidence supporting the hypothesis linking the activities of scavenging organisms to the impact of *C. muricinum* predation on cultured *T. gigas* is provided in the form of correlations between numbers of scavenging gastropods recovered and clam mortality (Table 6.6). Whereas these correlations are insignificant in floating cages they are generally high in trestle and benthic cages and in three cases out of four are higher than the correlation between mortality of larger clams and *C. muricinum* abundance. It is appropriate, however, to exercise the usual caution when interpreting correlations as cause-effect relationships (Sokal and Rohlf 1981). Increased clam mortality, whether scavenger mediated or not, may have the effect of attracting more scavengers.

The scavenging organisms collected during this study were all gastropods, probably owing to their relatively low mobility. More mobile scavengers such as fish and crustaceans are possibly abundant in cages but will rarely be collected as they are fast and probably nocturnal in habit (I. Lane, pers. comm.). Nevertheless these scavengers are probably also more abundant near the seabed.

Scavenging gastropods were collected far more frequently from benthic cages, as might be expected, but small numbers were also found in floating cages. Examination of these snails suggested that most may have settled in the floating cages during their larval phase but the possibility exists that some of the larger snails managed to find their way up the mooring ropes of these cages (about 5 m in length). However, once in the cages these snails were virtually trapped and may overrepresent the incidence of these snails in floating cages compared to cages of easier access such as those on trestles.

The consumption rates of the scavenging gastropods *Pyrene scripta, P. turturina* and *Cronia ochrostoma* are in the range of 1-7% of total wet body weight per day which was found for adult ranellids in Chapter 3 and also suggested by Morton (1986) to be generally characteristic of predatory gastropods under ideal feeding conditions. Specifically, the two species of *Pyrene* consumed 3-4% of their blotted live weights calculated on a daily basis and *C. ochrostoma* consumed 5-6%.

Morton (1990a) studied the consumption rate of the intertidal scavenging gastropod *Nassarius festivus* in Hong Kong and found that individuals 10 mm in length consumed about 0.78 mg wet weight of fish carrion·hour^{-1} while 15 mm individuals consumed 1.75 mg·hour^{-1}. Although not strictly comparable, owing to the use of clam mantle as carrion, these rates are similar to those of the two species of *Pyrene* (9-10 mm in length) which consumed 0.66 mg wet weight·hour^{-1} and of *C. ochrostoma* (15.5 mm mean size) which consumed 1.84 mg·hour^{-1}.

Nassariid and buccinid scavengers have been shown to be acutely sensitive to chemical stimuli emanating from food. These stimuli are used to locate the food rapidly rather than the slower and more laborious process of foraging (c.f., Morton 1990a). It is reasonable to expect that gastropods found in the Nusatupe ocean-nursery which rely heavily on carrion in their diet will be equally adept at locating food and it is likely that dying clams in benthic and trestle cages are rapidly infested with scavengers. Personal observation suggests that such activity takes place mostly at night.

Based on *C. muricinum* consumption rates estimated in Chapter 3 and those calculated for three species of scavenger in this chapter it is apparent that relatively small numbers of scavenging gastropods could easily double or triple the impact of ranellid predators in terms of biomass consumed.

For example, a recently settled *C. muricinum* may consume approximately 1 mg dry weight of clam tissue in a night and 10 and 15 mm specimens may consume, respectively, 8.4 and 11.4 mg in the same period. By comparison, a group of five 10-mm *Pyrene turturina* may consume 7.8 mg in a night and a group of five 15-mm *Cronia ochrostoma* may consume 24.7 mg. Larger gastropods present in the ocean-nursery which are capable of scavenging, such as *Cronia margariticola* and *Muricodrupa fiscella*, would have an even greater impact.

Implications for Giant Clam Culture

Examination of clam mortality and *C. muricinum* infestation rates in floating cages allows the impact of this triton to be studied in conditions where other predators and competitors of *C. muricinum* are greatly reduced. Most mortality in floating cages at the Nusatupe ocean-nursery

appears to be directly attributable to *C. muricinum* infestation in the case of *T. gigas* smaller than 40 mm SL. Somewhat circumstantial evidence suggests that this triton also causes most of the mortality of larger clams and in clams in other cage types although much of the tissue may actually be consumed by scavengers.

Mortality rates at the Nusatupe ocean-nursery are similar to others reported in ocean-nurseries in the Pacific region. With the exception of one ocean-nursery (Orpheus Island), ranellids are reported to be found in ocean-nursery cages at these sites and the present results support suggestions that tritons of the genus *Cymatium* are the principal predators (c.f., Perron et al. 1985; Price and Fagolimul 1988; Sims and Howard 1988; Ponwith 1990; Govan 1994).

The results raise a further worry for clam farmers. Attempts to control ranellid predators need to be complemented by the control of scavenging organisms by, for example, limiting the access of scavengers to ocean-nursery cages and removing all animals that are not exclusively herbivorous, as suggested by Govan (1992a).

CHAPTER 7

Prospects for the Control of Ranellid Predation on Cultured Tridacnids

7.1 Introduction

More than fifteen years of intensive research into tridacnid mariculture technology are beginning to bear fruit in the appearance of numerous experimental and even a few semi-commercial and commercial giant clam farms throughout the South Pacific (Copland and Lucas 1988; Fitt 1993a, Tisdell et al. 1993). This progress has been accompanied by many technological advances particularly in hatchery and land-based nursery procedures (c.f., Braley 1993) and ocean-nursery design (e.g., Munro et al. 1993).

Virtually no advances have been made in the methods employed to control ranellid predators of ocean-nursery clams since Perron et al. (1985) first advocated manual removal of the tritons (Govan 1992a, but see Govan et al. 1993). Recent economic analyses of giant clam farming suggest that the high cost of hatchery-produced clam seed and the high mortality experienced in ocean-nurseries represent the greatest constraints to the economic viability of tridacnid farming systems (Hambrey and Gervis 1993; Tisdell and Tacconi 1993). Work presented in Chapter 6 showed that a major proportion of the mortality experienced in Solomon Island ocean-nurseries was caused by ranellid predation and suggested that a similar scenario probably exists in other ocean-nurseries.

Survival of ocean-nursery clams could obviously be greatly enhanced if more effective means of ranellid control could be developed (Hambrey and Gervis 1993). Methods of ranellid control may be classed into the following broad areas: manual collection, exclusion and isolation, features of clam deployment (location and timing), chemical control and biological control. Most of these areas have been examined to some extent in this work or by previous authors with the exception of chemical and biological control.

In this concluding chapter actual and potential methods of control are discussed in the light of present knowledge of the biology of *Cymatium* spp. and experimental results regarding potential biological control agents are presented.

Ranellid Predation of Cultured Tridacnids: A Dual Problem

The ocean culture of tridacnid clams is affected by two overlapping forms of ranellid predation as discussed in Chapter 2:

i) Predation caused by postlarval and juvenile ranellids which enter cages as planktonic larvae.

ii) Predation caused by adult or subadult ranellids generally entering cages from the surrounding seabed.

The two forms of predation may overlap because tritons entering cages as larvae may rapidly grow to adult size if not detected and removed by clam farmers.

In this chapter these two forms of predation will be referred to as postlarval and adult according to the size of the triton when predation takes place. It is very important for clam farmers to distinguish between the two forms as they require different control methods (c.f., Govan et al. 1993). For instance, Heslinga et al. (1990) suggested that the use of off-bottom culture for tridacnids was not cost-effective owing to the capacity of ranellids to settle in cages at any depth. But Govan et al. (1993) found that the use of trestles to raise cages above the sea-bed reduced the incidence of adult ranellids and increased the survival of cultured tridacnids in Western Samoa.

Predation by postlarval ranellids is characterized by the small size and thin shells of the tritons which makes them difficult to detect but relatively vulnerable. These tritons may take refuge within the clams' valves and their feeding activities are almost parasitic although they usually seriously debilitate or kill their juvenile tridacnid prey. Postlarval ranellids are virtually impossible to exclude from cages and have very high consumption rates for their size.

Adult ranellids are relatively large and thick-shelled and are capable of killing juvenile clams very rapidly. These tritons appear to detect clams at some distance and enter cages from the surrounding seabed but may be excluded from cages by small aperture meshes or off-bottom culture techniques.

Biological Control in Bivalve Culture

Biological control of agricultural pests is receiving ever more attention and is clearly an attractive option both in terms of efficacy and reduced environmental impact. However, there are few records of the use of biological control agents (BCAs) in molluscan mariculture and most attempts have proven unsuccessful (Jory et al. 1984; Gibbons and Blogoslawski 1989).

Biological control of algal fouling in suspended culture of oysters has been successfully achieved using littorinid snails (Hidu et al. 1981). Toadfish, *Opsanus tau* (family Batrachoididae), have been used successfully to reduce crab predation on juvenile hard clams, *Mercenaria mercenaria*, in tray culture in Virginia, USA (Gibbons and Castagna 1985; Bisker and Castagna 1989).

Algal fouling is routinely controlled using a variety of fish and gastropods in both land-based (Heslinga et al. 1990; Govan 1992c; Braley 1993) and ocean-nursery culture (Munro et al. 1993) of tridacnid clams. Pyramidellid parasites are controlled in land-based nurseries in Netherlands Antilles using spiny lobsters (J.L. Munro, pers. comm.) and wrasse in Guam (R. Myers, pers. comm.). These same gastropod parasites are thought to be controlled naturally by benthic predators (probably crustaceans) in the ocean-nursery at Orpheus Island (Cumming 1988; Lucas et al. 1988). So far there are no records of biological control of tridacnid predators in giant clam ocean-nurseries.

The present study concentrated on selecting possible BCA candidates as a first step towards the development of methods of biological control of ranellid predators. Selected organisms were then screened for predatory behavior towards ranellids or juvenile tridacnids in aquaria.

Selection of Potential Biological Control Agents of Ranellid Predators of Tridacnids

The following criteria were developed for the selection of BCAs to be used in giant clam ocean-nurseries:

1. *Availability.* Organisms must be readily available in sufficient quantities for commercial clam farming, either by collection from the wild or through culture.
2. *Specificity.* Potential BCAs must consume or deter the target predators without negative impact on the cultured clams.
3. *Ease of handling.* The potential BCAs must be easy to manipulate and contain within clam cages.

Following these criteria the search for potential BCAs at the CAC could be narrowed down to gastropods and crustaceans (hermit crabs in particular) as these organisms were common and easily handled.

Gastropods. References used to gain a general understanding of the diets of tropical Pacific gastropods included: Paine (1963); Taylor (1978, 1984, 1986); Kilburn and Rippey (1982) and Reichelt and Kohn (1985). Neogastropod families contain members with highly specialized diets and attention was focused primarily on members of the Buccinidae, Conidae, and Fasciolariidae as well as common species from other families for which dietary preferences were not known. Promising but rare families at the CAC such as Olividae, Marginellidae and Volutidae could not be examined.

Crustaceans. Most decapod crustaceans are capable of carnivory and there is little rigid specificity in the diet of decapods (Barnes 1980). Many of the common decapods at the CAC have been found to kill juvenile *Tridacna gigas* (Govan 1994). The principal factor determining the decapod's capacity to kill juvenile clams is usually the relative sizes of the clam's shell and the crab's chelae (e.g., Dare et al. 1983) although this does not apply to crabs such as portunids that may attack through the valve gape or byssal orifice.

Based on these factors only decapods with relatively small chelae were screened as potential BCAs and their potential prey limited to juvenile *Cymatium.* Tests also had to be carried out to determine the maximum size of clam vulnerable to these decapods. The easiest decapods to handle and restrain were hermit crabs due to the relatively large bulk of their gastropod shells.

Other promising crustacean candidates not tested owing to lack of availability were spiny lobsters (Paniluridae), callapid crabs and stomatopods (*Gonodactylus* spp.). Spiny lobsters are known to be important predators of gastropods and tropical callapid crabs are reported to be specialized predators on gastropods (Vermeij 1978). *Gonodactylus chiragra* shows promise because its method of preying on juvenile *T. gigas* (cracking the shell with sharp blows from its modified chelae) is clearly limited to small clams (up to about 12 mm, Govan 1994) but liable to be effective against relatively large tritons. Also this species builds nests and is likely to be territorial and easy to confine in clam cages.

7.2 Methods

All organisms to be tested as potential BCAs were collected from the fringing reef near the CAC. Prey *Cymatium* spp. were collected from floating cages at the CAC.

Screening of Biological Control Agents

The predatory activity of potential BCAs on ranellids were examined in 2.5-l static aquaria provided with aeration. Complete water changes were performed three times every week. Depending on availability, test organisms were exposed to a size range of *Cymatium muricinum, C. aquatile, C. pileare* or the locally abundant cerithiid gastropod *Cerithium tesellatus.* Consumed prey were replaced. *C. nicobaricum* was not used as prey as this species is capable of consuming gastropods (c.f., Chapter 2). If it was not already known whether a potential BCA was capable of preying on juvenile tridacnids (c.f., Govan 1994) then these organisms were confined in aquaria with juvenile *T. gigas* over a period of at least 1 week and observed.

Small-scale Trials

Trials were performed in circular land-based nursery tanks (1,500 l). Equal numbers of *T. gigas* (15-55 mm SL) were confined in 32 x 32 x 14 cm cages with cement bases. The cage mesh was rectangular (12 x 25 mm). Ten *C. muricinum* snails of 26 mm maximum size were introduced into the tank (larger tritons would not have been able to get through the cage mesh).

In the first experiment five cages contained an individual *Conus textile* and five cages served as controls over a period of 2 weeks. Mortality of clams and *C. muricinum* was monitored and dead animals were replaced. The experiment was repeated using three cages containing *Pleuroploca filamentosa* and three controls over a period of 3 weeks.

The results of these trials were analyzed using the nonparametric Mann-Whitney U test (Sprent 1993) in the Statistix 4 suite of programs (Analytical Software 1991).

In order to examine interactions between BCAs and ranellids more closely, four cages containing equal numbers of clams were suspended in nursery tanks with continually running seawater. Two individuals of *D. lagopodes* previously observed to consume *Cymatium* spp. were introduced into each of two cages. Small *Cymatium* spp. were introduced into all four cages. The same procedure was repeated with *P. filamentosa* as a BCA but using two size ranges of *Cymatium* spp. Cages were examined at frequent intervals during the day and dead animals were removed and replaced with live ones.

7.3 Results

A problem throughout all experiments was a shortage of potential BCAs and prey *Cymatium* spp. Only one or two individuals of most potential BCAs were obtained and tested. There was some indication, especially in the small-scale trials that handling of the test organisms disturbed them sufficiently to affect their behavior for up to 1 week, some results may be affected by this bias.

Screening of Biological Control Agents

Results of the screening of BCAs are shown in Table 7.1. The gastropods *Conus textile* and *Pleuroploca filamentosa* consumed large numbers of gastropods and *Conus marmoreus, Latirus lanceolatus* and *Peristernia ustulata* also consumed test prey but to a lesser extent. None of the gastropods screened were observed to consume *T. gigas.*

Table 7.1. Gastropods and crustaceans screened as possible biological control agents (BCA) for gastropod predators of juvenile tridacnids. Average individual daily consumption is shown for comparative purposes. Test prey organisms were *Cymatium muricinum* (Cm), *C. aquatile* (Ca), *C. pileare* (Cp) and *Cerithium tesselatus* (Ct).

	BCA			Prey			
Species	Size(mm)	Days tested	Indi-viduals	Test prey	Number consumed	Size range(mm)	Mean con-sumption
Gastropoda							
Bursa sp.	30	12	2	Cm	0	5-35	-
Conus cf. *imperialis*	48	15	1	Ct	0	-	
Conus cf. *lividus*	27	29	1	Ct	0	-	
Conus cf. *rattus*	30	29	1	Ct	0	-	
Conus ebraeus	22	29	1	Ct	0	-	
Conus marmoreus	71	57	1	Cm,Cp,Ca	8	18-31	0.14
Conus textile	32,45,61	11	3	Ct	18	0.54	
Conus textile	32,45,61	1	3	Cm	2	20-27	0.67
Conus textile	32,45,61	8	3	Ct	23	0.96	
Cymatium comptum		15	22	1	Ct	0	-
Latirolagena smaragdula	35	15	1	Ct	0	-	
Latirus gibbulus	86	12	1	Cm	0	-	
Latirus lanceolatus	46	29	1	Ct	4	12-38	0.14
Mitra sp.	12	29	1	Ct	0	-	
Peristernia cf. nassatula	31	9	1	Ct	0	-	
Peristernia ustulata	26	29	1	Ct	1	0.03	
Pleuroploca filamentosa	134	12	1	Cm,Cp,Ca	20	16-40	1.67
Pleuroploca filamentosa	134,105	20	2	Cm,Ca,Cp	18	14-26	0.45
Pleuroploca filamentosa	134,105	28	2	Ct	147	2.63	
Pleuroploca filamentosa	134,105,99	22	3	Ct	64	0.97	
Crustacea							
Dardanus guttatus	-	12	3	Cm	0	-	
Dardanus lagopodes	-	20	6	Cm,Ca,Cp	26	up to 22	0.22
Dardanus megistos	-	3	1	Cm	6	up to 31	2.0
Calcinus sp.	-	5	1	Cm	0	-	
Clibanarius sp.	-	5	1	Cm	0	-	

The hermit crab *Dardanus lagopodes* consumed juvenile *Cymatium* spp. up to 22 mm in length. Table 7.2 shows the maximum size of ranellid consumed by each individual *D. lagopodes* tested as well as the smallest size of ranellid not consumed. The size of ranellid consumed by these hermit crabs varies widely between individuals probably relating to factors such as hermit crab cheliped size and ranellid shell thickness.

D. megistos consumed *C. muricinum* up to 31 mm in length but was observed to consume *T. gigas* over 50 mm SL. *D. lagopodes* consumed *T. gigas* occasionally but never over 20 mm SL. Other observations include the fact that *C. textile* only attacked gastropods at night whereas *P. filamentosa* and *D. lagopodes* attacked regardless of time of day.

Small-scale trials

Placing the gastropod-predators *C. textile* and *P. filamentosa* inside cages exposed to *C. muricinum* significantly ($P < 0.05$) reduced the mortality of *T. gigas* (Table 7.3). *C. muricinum* appeared to enter cages regardless of whether or not these contained BCAs. The BCAs consumed *C. muricinum* but not enough to prevent the ranellids from killing some clams. Reasons for this may include the exclusively nocturnal activities of *Conus textile* and the fact that *P. filamentosa* did not become active until 8 days into the experiment probably due to the disturbance caused by handling and the unfamiliar conditions of the tanks and cages.

Table 7.2. Sizes of juvenile *Cymatium muricinum* killed and alive after confinement in aquaria with different specimens of the hermit crab and potential biological control agent *Dardanus lagopodes*.

	Dead		Alive		
	Number	Maximum size	Number	Minimum size	Days tested
Dardanus lagopodes	4	12.2	3	14.6	11
D. lagopodes	5	21.8	3	17.2	11
D. lagopodes	4	14.8	1	17.4	11
D. lagopodes	6	16.9	2	17.2	11
D. lagopodes	4	16.9	6	11.6	11
D. lagopodes	2	10.8	3	11.2	11
D. lagopodes (juvenile)	1	6.6	1	12.0	10
D. lagopodes (juvenile)	0	0.0	2	7.0	10
D. lagopodes (juvenile)	0	0.0	2	5.9	6

Table 7.3. Reduction of mortality of *T. gigas* (25-55 mm SL) using biological control agents in cages placed in a nursery tank containing 10 *C. muricinum* (16-26 mm). Each cage contained 20 clams but half contained one *Conus textile* (32-61 mm) or, in a subsequent experiment, *Pleuroploca filamentosa* (99-134 mm). Dead clams and ranellids were replaced. Treatments were found to be significantly different ($P < 0.05$) using a Mann-Whitney U test.

Conus textile	Present		Absent	
Dead *C. muricinum* (SD)	2.2	(2.4)	0.0	
Dead *T. gigas* (SD)	1.2	(0.6)	2.4	(1.4)
n	5		5	
days	14		14	
Pleuroploca filamentosa	Present		Absent	
Dead *C. muricinum* (SD)	2.0	(0.0)	0.0	
Dead *T. gigas* (SD)	3.3	(5.8)	8.0	(4.3)
n	3		3	
days	21		21	

Observations of *D. lagopodes* in the suspended cages suggested that the hermit crab did not readily acclimate to cage conditions and either did not locate or did not attack juvenile ranellids. The hermits expended considerable energy in attempting to escape from cages and were observed feeding on fouling algae or associated fauna.

P. filamentosa took about a week to acclimate to the suspended cages. These snails appeared not to be able to locate or handle the smaller *C. muricinum*. When larger ranellids were substituted these were readily consumed.

7.4 Discussion

The control of ranellid predation should be a major consideration when planning ocean-nursery culture of tridacnids. A number of factors should be taken into account before the first clams enter the sea such as the location of the ocean-nursery and the design and placement of cages. When the ocean-nursery is operational visual inspection of cages and manual removal of predators will probably always be necessary but an understanding of the biology of these

ranellid predators gleaned in the present work may alleviate the burden. The following section enumerates the factors to be considered with a view to optimizing control of ranellids in the ocean-nursery culture of tridacnids.

Considerations in the Deployment of Ocean-nursery Tridacnids

C. muricinum is pantropical in distribution (c.f., Chapter 1) and may be expected to occur wherever the ocean-nursery culture of tridacnids is biologically feasible. The incidence of ranellids may be reduced or eliminated at certain locations such as Orpheus Island in Queensland probably owing to a combination of environmental factors such as high turbidity and nearby freshwater influence (c.f., Chapter 1). Many such sites will be unfavorable for tridacnid culture but it is worth conducting trials at likely locations.

The incidence of ranellid predators may be reduced at certain ocean-nursery locations and in particular seasons or meteorological circumstances. Large variations in the average density of recruitment of ranellids to ocean-nursery cages were reported in Chapters 4 and 5 depending on the location of ocean-nurseries or cages. Local hydrographic conditions may account for these differences and clam farmers may profitably experiment with different horizontal or vertical cage locations.

Kohn and Leviten (1976) found higher population densities and species richness of predatory gastropods in more topographically complex habitats at Eniwetok in the Marshall Islands. Coral rubble-filled depressions were found to provide the best refuge for these predators.

In more temperate seas, Auster et al. (1989) found that predation of benthic bivalves was more intense around shelter sites and occurred throughout the day. Further away from shelter sites predation was less intense and only occurred nocturnally, when the predators had less chance of being preyed on themselves.

Ocean-nurseries placed on or near the seabed are vulnerable to incursions by adult ranellids. These incursions may be reduced by placing cages in areas where these predators are expected to be less abundant either due to the topography or the general habitat (c.f., Chapter 1). Possibilities include mangrove areas, seagrass beds or the intertidal zone.

The local population of ranellids at long-established ocean-nurseries may become greatly increased owing to the escape of recently settled tritons from clam cages or the attraction of adult tritons from the surrounding environment. Where such a mechanism is suspected it may well be worth relocating the ocean-nursery or considering regularly rotating the location of the ocean-nursery.

In areas where ranellid recruitment is seasonal or at least partly predictable such as Palau (Heslinga et al. 1990) small clams may be transferred from the land-based nursery to ocean-nurseries during expected periods of low recruitment giving the clams the best chances of growing to a size less vulnerable to predation.

Exclusion and Isolation

Ranellid predation may be reduced by excluding these snails from cages either by using meshes or by elevating cages from the seabed. These methods are most effective against adult predation as larval ranellids are practically impossible to exclude from cages using meshes without greatly reducing water exchange.

Tridacnid clams in ocean-nursery culture are routinely placed in mesh cages which not only serve to contain the clams but also to exclude large predators (Calumpong 1992; Govan

1992a). The mesh sizes used in most ocean-nurseries are too large (25-50 mm) to exclude adult ranellids from the cages. Govan et al. (1993) suggested that reducing the mesh size by half, to around 12 mm, would exclude *Cymatium* larger than 26.7 mm or approximately two-thirds of the ranellid predators commonly found in benthic ocean-nurseries. Unfortunately, such a reduction in mesh size would increase the cost of the cages and also increase the area available to algal fouling and thus maintenance costs. Chemical means of reducing fouling appear impractical (Lucas 1988b) but the use of algal grazers may be a possibility.

The use of rectangular meshes of 12 x 25 mm or 12 x 50 mm should be tested in benthic ocean-nurseries where adult ranellids are a problem. These meshes would appear to combine the advantage of small mesh sizes in excluding adult ranellids and the reduced surface area for algal fouling of the larger mesh sizes.

Off-bottom culture may be an effective method of excluding adult ranellids. These large tritons are never recovered from floating cages unless the cages have touched the bottom or the tritons have settled in the cages as larvae and been allowed to grow therein for a number of months. Elevation of cages on trestles has been shown to reduce, but not eliminate, the incidence of adult ranellids (Govan et al. 1993) as these are still capable of locating their prey and climbing the trestle legs.

A device resembling a trap has been tested which greatly reduces the number of ranellids successfully climbing trestle legs under experimental conditions but the use of this device on all trestle legs in ocean-nurseries may not be cost-effective (Govan et al. 1993). A possible solution that has not been tested so far is the construction of frames resting on the seabed that emerge above sea level. Cages could be suspended from the emergent portions of the frames and would be free of adult ranellids as these would be unlikely to climb any distance out of the water.

Manual Collection

Manual removal is used at all giant clam farms to control predation and accounts for a major proportion of the labor requirements of ocean-nurseries (c.f., Heslinga et al. 1990; Hambrey and Gervis 1993).

The prospects of developing mechanical methods to remove predators such as employed by the oyster industry in the USA (Jory et al. 1984) are low and efforts should be concentrated on making manual removal more efficient.

For example, the floating ocean-nursery at the CAC was situated further from shore than the one at Nusatupe and in much deeper and more turbulent water. Workers at the CAC complained that they were not able to locate snails very easily owing to the movement of the cages and effort involved in working on them. The end result in terms of ranellid collection was that ranellids were more easily overlooked at the CAC, the mean size of *C. muricinum* recovered from the CAC was 17.6 mm whereas the mean size of tritons of this species recovered from Nusatupe was 11.7 mm. Based on calculations from Chapters 3 and 6 this means that tritons at the CAC, which were only 50% larger on average than those recovered from Nusatupe, had remained in cages 70% longer and may have consumed 174% more *T. gigas* tissue.

The accessibility of cages to clam farmers should be taken into account when designing them and ocean-nurseries in general. Benthic and trestle cages should be easy to open and, if at all possible, not placed at depths which make examination laborious.

Fouling organisms, dead clam shells and debris should be removed from cages whenever possible as these provide refuge for ranellids. Recently dead shells also provide the clearest indication of the activities of predators (Govan 1992a).

Clams at a number of ocean-nurseries are placed on gravel substrates to facilitate subsequent manipulation of the clams (Barker et al. 1988; Heslinga et al. 1990). At the CAC, flat cement substrates are used which provide no refuge for predators and therefore allow these to be much more easily detected than in cages containing gravel substrates (Govan 1992a, 1992b and see Chapter 1).

Traps have been used with varying degrees of success to control oyster drills in the USA (Nelson 1931; Galtsoff 1964; Jory et al. 1984) and the UK (Hancock 1974). Baited traps to control ranellid predators of tridacnids do not appear very promising because cages full of clams will probably be far more attractive than the bait.

The device designed to prevent ranellids from climbing the legs of trestles mentioned above does tend to function as a trap but has not been tested in ocean-nurseries yet (Govan et al. 1993). Preliminary experiments in which artificial refuges were placed in benthic ocean-nursery cages at the CAC with the idea of removing predators found sheltering inside were not successful (Govan, unpubl. report) as no snails were found.

Chemical Control

The application of chemical substances to control predators, such as copper sulfate and chlorinated oils used on clam and oyster beds in the USA (Jory et al. 1984; Gibbons and Blogoslawski 1989), has not been attempted in giant clam culture. The prospect for such methods of control are poor considering the negative impact such substances may be expected to have on clams and the environment.

Scope exists for research into chemical stimuli that attract adult ranellids to their prey or induce larval ranellids to settle. Such knowledge would allow the design of repellents or chemically baited traps.

Dead juvenile *C. muricinum* were removed from cages which had been dipped in freshwater at the CAC. Subsequent attempts to repeat these results under experimental conditions were not successful possibly because of the larger size of triton. However freshwater dips should probably be avoided as instances of high clam mortality were recorded (Govan, unpubl. data).

Biological Control

Preliminary screening of organisms available at the CAC yielded three potential BCAs:

i. The gastropod *C. textile* is common at the CAC and only consumed other gastropods. This snail was not effective against smaller ranellids and had to be handled with care as it is capable of inflicting a painful and even lethal sting (Kilburn and Rippey 1982).

ii. *P. filamentosa* is a relatively rare gastropod at the CAC which voraciously consumed other gastropods in aquaria but again it was not effective against smaller sizes of ranellid.

iii. The hermit crab *D. lagopodes* is common at the CAC and problems of availability are not envisaged. This hermit was only capable of consuming juvenile ranellids but was also able to kill small tridacnids. The size of prey consumed depends on the the size of the hermit crab's chelipeds and it may be possible to select crabs as BCAs for specific sizes of tridacnid.

These results suggest that *D. lagopodes* would be more useful in controlling recently settled *Cymatium* spp. whereas the gastropod BCAs would be useful in controlling adult and subadult *Cymatium* spp. and other gastropod predators and scavengers.

The BCAs were relatively easy to retain in cages. Adult *C. textile* and *P. filamentosa* are retained by normal meshes used at the CAC of either 12 x 25 mm or 25 x 25 mm. Larger individuals and most hermit crabs would be retained by even larger meshes.

However, small-scale trials suggest that in an ocean-nursery situation these BCAs may be able to fulfill their dietary requirements with other organisms that enter or grow in cages (such as fouling organisms, recently settled bivalves and cowries in the case of *D. lagopodes* and other abundant gastropods in the case of the two gastropod BCAs). This would result in reduced pressure on marauding ranellids and consequently no great reduction in clam mortality. Assuming that BCAs do not indulge in cannibalism, it may be possible to combat this problem by increasing the density of BCAs although a balance would have to be achieved to prevent BCAs starving to death. These parameters would be site- and cage-specific as is the incidence of predators.

Cultivation of the gastropod BCAs would be useful as it would provide an abundant source of such organisms without depleting local wild populations. Furthermore, juvenile BCAs would be available which could be introduced to cages at a small size and, assuming similar dietary preferences to those of their parents, may help control the incidence of juvenile ranellids. *C. textile* has been reared successfully under laboratory conditions (Perron 1980, 1981) and experience with *P. trapezium* suggests that it may be possible to culture species of this genus (Arakawa 1960; Govan, unpubl. data).

Biological control of ranellid larvae does not appear feasible considering the relatively low abundance of these larvae compared to that of other planktonic organisms (c.f., Chapter 4). While the exact nature of the cues that induce settlement of the ranellid larvae are not known it appears likely that these are related to the presence of tridacnid prey. Thus it is possible that settlement may be reduced by stocking clams in ocean-nurseries at lower densities. Such density-dependent effects were discussed in Chapter 4 and may operate on both adult and larval snails. There may be a case for encouraging the proliferation of a large number of small ocean-nurseries rather than concentrating on a few large ones, as suggested by Heslinga et al. (1986) with regard to problems with predatory fish.

Lucas et al. (1988) suggested that pyramidellid parasites were less abundant in benthic cages at Orpheus Island than in off-bottom cages and land-based tanks (Cumming 1988) because they were controlled by benthic predators. The possibility was raised in Chapter 4 that the lower densities of *C. muricinum* recovered from benthic cages at Nusatupe were due to the action of benthic predators which did not have ready access to off-bottom cages.

The action of such wild BCAs may have to be taken into account when selecting the mesh sizes to be used on ocean-nursery cages. It may pay to use the largest possible mesh size in benthic cages depending on the size of clams and the abundance and nature of other clam predators on the seabed (for example adult ranellids, as mentioned above).

Certain species of tridacnid such as *T. gigas* and *T. derasa* appear more vulnerable to ranellid predation while others such as *H. hippopus* are relatively resistant (Perron et al. 1985; Govan et al. 1993; c.f., Chapter 2). In certain circumstances it may be feasible to cultivate more resistant species in preference to others.

Conclusions

The control of ranellid predation in tridacnid ocean-nurseries depends on maintaining a comprehensive program of visual inspection and manual removal of predators as originally suggested by Perron et al. (1985). Tridacnid farmers should also be aware of the different aspects of ranellid predation and, in the light of the present work, that much can be done to reduce losses to *C. muricinum* and its allies.

The operators of ocean-nurseries seriously affected by ranellid predation must first determine to what extent the problem is due to recently settled juvenile ranellids or to adult tritons, as the control options vary accordingly.

Perhaps the first control option to be considered is whether the particular type of predation will be reduced by relocating the affected cages. In the absence of further advances in biological control every effort should be made to exclude large ranellids from cages. Large tritons are capable of killing clams in a few hours and leaving cages before their presence is detected, often at night. However, the impact of small and hard to detect postlarval ranellids must not be underestimated. Careful vigilance must be sustained in order to detect the first signs of sporadic, and possibly highly destructive, infestations by these juvenile tritons.

Given the experiences and results recorded in this work, predation by ranellid predators such as *C. muricinum*, *C. aquatile, C. pileare* and *C. nicobaricum* clearly has the potential to prevent tridacnid culture from becoming economically viable at many locations. In order to reduce the risk of failure of tridacnid farming ventures it is vital that clam farmers be aware of all aspects of the problem and the range of predator control options available.

Acknowledgements

Funding is gratefully acknowledged from the following sources: Australian International Development Assistance Bureau, International Center for Living Aquatic Resources Management (ICLARM), The Carnegie Trust for the Universities of Scotland and Voluntary Services Overseas.

I am grateful for the technical support provided by my assistant and good friend Henry Rota and also the staff involved in ocean-nursery work: Idris Lane and his team at Nusatupe and Tom Shearer and his team in Guadalcanal. I am also grateful for the support provided by G. Usher, Dr. J.L. Munro, M. Gervis, Dr. J. Hambrey, H. Tafea, F. Leung and all the other ICLARM staff during various stages of the work involved in this project. Thanks are also due to Dr. A. Beu, Dr. H. Mair, Dr. D. Pauly, Dr. M.G. Poxton, Dr. R. Scheltema, Dr. J.D. Taylor and Dr. T. Whitehead for valuable correspondence and comments on sections of drafts of this manuscript. I am extremely grateful to the then Director of the Coastal Aquaculture Centre in Solomon Islands, Dr. J. L. Munro, for more than eight years of support and encouragement.

My warmest gratitude goes to my family for everything and also to my dear Dee for her constant support and affection. It remains only to apologize to people whom I have inadvertently omitted from this list and to thank the people of Solomon Islands for six years of cherished memories and the opportunity to carry out this work.

References

Abdon-Naguit, M. R. and S.N. Alcazar. 1988. Notes on predation on giant clams (Bivalvia: Tridacnidae), p. 81-84. *In* E.C. De Guzman and D.L. Gonzales (eds.) Culture of giant clams (Bivalvia: Tridacnidae). Proceedings of the Symposium-Workshop on the Culture of Giant Clams (Bivalvia: Tridacnidae), Silliman University, Dumaguete City, Philippines. Philippine Council for Aquatic and Marine Research and Development, Los Baños, Laguna and Australian Centre for International Agricultural Research, Canberra.

Analytical Software. 1991. Statistix 3.5: An interactive statistical analysis program for the IBM PC. Analytical Software, St. Paul, Minnesota.

Anderson, D. T. 1959. The reproduction and early life history of the gastropod *Cymatilesta spengleri* (Perry) (Cymatiidae). Proc. Linn. Soc. NSW 84: 232-238.

Angell, C. L. 1986. The biology and culture of tropical oysters. ICLARM Stud. Rev. 13, 42 p.

Ansell, A. D. 1982. Experimental studies of a benthic-predator prey relationship: 1. Feeding, growth and egg collar production in long term cultures of the gastropod drill *Polinices alderi* (Forbes) feeding on the bivalve *Tellina tenuis* (da Costa). J. Exp. Mar. Biol. Ecol. 56: 235-255.

Arakawa, K.Y. 1960. Miscellaneous notes on Mollusca: mating and spawning habits of some marine molluscs. Venus 21: 72-78.

Asher, H. B. 1976. Causal modeling. Sage University Paper Series on Quantitative Applications in the Social Sciences. Series No. 07-003. Sage Publications, Beverly Hills and London.

Auster, P.J., R. Malatesta and B. Haskell. 1989. Bivalves as model organisms to elucidate patterns of predation. North Atlantic Fisheries Organization Serial No. N1565: 1-11.

Bailey, N.T.J. 1981. Statistical methods in biology. Hodder and Stoughton, London, Sydney and Toronto.

Bakun, A. 1985. Comparative studies and the recruitment problem: searching for generalizations. CalCOFI Rep. 25: 30-40.

Bakun, A. 1986. Definition of environmental variability affecting biological processes in large marine ecosystems, p. 88-109. *In* K. Sherman and L. M. Alexander (eds.) Variability and management of large marine ecosystems. American Association for the Advancement of Science (AAAS) Selected Symposium 99, Washington, DC, USA.

Bandel, K: 1975. Embryonalgehause karibischer Meso- und Neogastropoden (Mollusca). Akademie Der Wisenschaften und der literatur. Franz Steiner Verlag, Wiesbaden.

Barker, J.R., C.M. Crawford, C. Shelley, R.D. Braley, J.S. Lucas, W.J. Nash and S. Lindsay. 1988. Ocean-nursery technology and production data from lines and covers for the giant clam, *Tridacna gigas*, p. 225-228. *In* J.W. Copland and J.S. Lucas (eds.) Giant clams in Asia and the Pacific. ACIAR Monograph 9. Canberra.

Barnes, R. D. 1980. Invertebrate zoology. Holt-Saunders International Editions, Tokyo.

Bayne, B. L. and C. Scullard. 1978. Rates of feeding by *Thais (Nucella) lapillus* (L.). J. Exp. Mar. Biol. Ecol. 32: 113-129.

Beckvar, N. 1981. Cultivation, spawning and growth of the giant clams *Tridacna gigas, Tridacna derasa* and *Tridacna squamosa* in Palau, Caroline Islands. Aquaculture 24: 21-30.

Bell, L. 1992. Giant clam culture: project update. Center for Tropical and Subtropical Aquaculture, Report, July 1992: 1-4.

Bell, L.J. and J.C. Pernetta. 1988. Reproductive cycles and mariculture of giant clams in Papua New Guinea, p. 133-138. *In* J.W. Copland and J.S. Lucas (eds.) Giant clams in Asia and the Pacific. ACIAR Monograph 9. Canberra.

Berg, C. J. 1971. Egg capsule and early veliger of *Charonia tritonis*. Veliger 13: 298.

Bertalanffy, L. von. 1957. Quantitative laws in metabolism and growth. Q. Rev. Biol. 32: 217-231.

Beu, A.G. 1970. The Mollusca of the Subgenus *Monoplex* (Family Cymatiidae). Trans. R. Soc. NZ 11(17): 225-237.

Beu, A.G. 1980. Australian Gastropods of the family Bursidae. Part 1. The families of Tonnacea, the genera of Bursidae, and revision of species previously assigned to *Tutufa* Jousseaume, 1881. Rec. Aust. Mus. 33(5): 248-324.

Beu, A.G. 1985. A classification and catalogue of living world Ranellidae (=Cymatiidae) and Bursidae. Conchologists of America Bull. 13(4): 55-66.

Beu, A.G. 1988. Taxonomy of Gastropods of the families Ranellidae (=Cymatiidae) and Bursidae. Part 5. Early history of the families, with four new genera and recognition of the family Personidae. Saito Ho-on Kai Spec. Publ.: 69-96.

Beu, A.G. and W.O. Cernohorsky. 1986. Taxonomy of gastropods of the families Ranellidae (=Cymatiidae) and Bursidae. Part 1. Adoption of Ranellidae, and review of Linatella Gray 1857. NZ J. Zool. 13: 241-266.

Beu, A.G. and E.A. Kay. 1988. Taxonomy of gastropods of the families Ranellidae (=Cymatiidae) and Bursidae. Part IV. The *Cymatium pileare* complex. J. R. Soc. NZ 18(2): 185-223.

Beverton, R.J.H. and S.J. Holt. 1957. On the dynamics of exploited fish populations. U.K. Min. Agric. Fish. London, Fish. Inv. Ser. 2, Vol. 19.

Beyer, J.E. 1987. On length-weight relationships. Part 1: Computing the mean weight of the fish in a given length class. Fishbyte 5(1): 11-13.

Beyer, J.E. 1991. On length-weight relationships. Part 2: Computing mean weights from length statistics. Fishbyte 9(2): 50-54.

Bisker, R. and M. Castagna. 1989. Biological control of crab predation on hard clams *Mercenaria mercenaria* (Linnaeus, 1758) by the toadfish *Opsanus tau* (Linnaeus) in tray cultures. J. Shellfish Res. 8(1): 33-36.
Black, K.P. 1993. The relative importance of local retention and inter-reef dispersal of neutrally buoyant material on coral reefs. Coral Reefs 12: 43-53.
Black, K.P., S.L. Gay and J.C. Andrew. 1990. Residence times of neutrally-buoyant matter such as larvae, sewage or nutrients on coral reefs. Coral Reefs 9: 105-114.
Black, K.P., P.J. Moran and L.S. Hammond. 1991. Numerical models show coral reefs can be self-seeding. Mar. Ecol. (Prog. Ser.) 74: 1-11.
Boullaire, C. 1953. La ponte de *Cymatium tuberosum*. J. Conchyliol. 93: 73-76.
Box, G.E.P. and G.W. Jenkins. 1976. Time-series analysis: forecasting and control. Holden-Day, Oakland, California.
Braley, R.D. 1992. The giant clam: hatchery and nursery culture manual. ACIAR Monograph 15. Canberra.
Braley, R.D. 1993. Pros and cons of methodologies used in the hatchery and land-based nursery phase of giant clam culture, p. 87-93. *In* W. K. Fitt (ed.) The biology and mariculture of giant clams. ACIAR Proceedings 47. Canberra.
Braley, R.D., W.J. Nash, J.S. Lucas and C.M. Crawford. 1988. Comparison of different hatchery and nursery culture methods for the giant clam *Tridacna gigas*, p. 110-114. *In* J.W. Copland and J.S. Lucas (eds.) Giant clams in Asia and the Pacific. ACIAR Monograph 9. Canberra.
Brohmanonda, P., K. Mutarasint, T. Chongpeepien and S. Amornjaruchit. 1988. Oyster culture in Thailand, p. 31-39. *In* E.W. McCoy and T. Chongpeepien (eds.) Bivalve mollusc culture research in Thailand. ICLARM Tech. Rep. 19, 170 p.
Broom, M.J. 1982. Size selection, consumption rates and growth of the gastropods *Natica maculosa* (Lamarck) and *Thais carinifera* (Lamarck) preying on the bivalve *Anadara granosa* (L.). J. Exp. Mar. Biol. Ecol. 56: 213-233.
Broom, M.J. 1983. A preliminary investigation into prey species preference by the tropical gastropods *Natica maculosa* Lamarck and *Thais carinifera* (Lamarck). J. Moll. Stud. 49: 43-52.
Broom, M.J. 1985. The biology and culture of marine bivalve molluscs of the genus *Anadara*. ICLARM Stud. Rev. 12, 37 p.
Burrows, M.T. and R.N. Hughes. 1990. Variation in growth and consumption among individuals and populations of *Nucella lapillus*: a link between foraging behaviour and fitness. J. Anim. Ecol. 59: 723-742.
Butman, C.A. 1987. Larval settlement of soft-sediment invertebrates: the spatial scales of pattern explained by active habitat selection and the emerging role of hydrodynamical processes. Oceanogr. Mar. Biol. Ann. Rev. 25: 113-165.
Calumpong, H.P., Editor. 1992. The giant clam: an ocean culture manual. ACIAR Monograph 16. Canberra.
Cazaux, C. 1972. Ponte et larves du gastéropode prosobranche *Tritonalia nodifer* Lam. Bull. Soc. Lin. Bord. 11: 143-148.
Cernohorsky, W.O. 1967. Marine shells of the Pacific. Pacific Publications, Sydney.
Clench, W.J. and R.D. Turner. 1957. The family Cymatiidae in the Western Atlantic. Johnsonia 3(36): 189-244.
Colebrook, J.M. and A.H. Taylor. 1984. Significant time scales of long-term variability in the plankton and the environment. Rapp. P.-V. Réun. CIEM 183: 20-26.
Coleman, N. 1975. What shell is that? Lansdowne Press, NSW, Australia.
Copland, J.W. and J.S. Lucas, Editors. 1988. Giant clams in Asia and the Pacific. ACIAR Monograph 9. Canberra.
Coull, B.C. 1985. Long-term variability of estuarine meiobenthos: an 11 year study. Mar. Ecol. (Prog. Ser.) 24: 205-218.
Crawford, C.M., J.S. Lucas and J.L. Munro. 1987. The mariculture of giant clams. Interdiscip. Sci. Rev. 12(4): 333-340.
Crawford, C.M., J.S. Lucas and W.J. Nash. 1988. Growth and survival during the ocean-nursery rearing of giant clam, *Tridacna gigas*: 1. Assessment of four culture methods. Aquaculture 68: 103-113.
Crawford, C.M., W.J. Nash and J.S. Lucas. 1986. Spawning induction, and larval and juvenile rearing of the giant clam, *Tridacna gigas*. Aquaculture 58: 281-295.
Cumming, R.L. 1988. Pyramidellid parasites in giant clam mariculture systems, p. 231-236. *In* J.W. Copland and J.S. Lucas (eds.) Giant clams in Asia and the Pacific. ACIAR Monograph 9. Canberra.
Cury, P. and C. Roy. 1989. Optimal environmental window and pelagic fish recruitment success in upwelling areas. Can. J. Fish. Aquat. Sci. 46: 670-680.
Dalzell, P. 1990. Biology and population dynamics of tuna baitfish in Papua New Guinea, p. 100-113. *In* S.J.M. Blaber and J.W. Copland (eds.) Tuna baitfish in the Indo-Pacific region. ACIAR Proceedings 30. Canberra.
Dare, P.J., G. Davies and D.B. Edwards. 1983. Predation on juvenile Pacific oysters (*Crassostrea gigas* Thunberg) and mussels (*Mytilus edulis* L.) by shore crabs (*Carcinus maenas* (L.)). Fish. Res. Tech. Rep. 73. MAFF Direct Fish. Res., Lowestoft.
Dare, P.J. and D.B. Edwards. 1976. Experiments on the survival, growth and yield of relaid seed mussels (*Mytilus edulis* L.) in the Menai Strait, North Wales. J. Cons. CIEM 37: 16-28.
D'Asaro, C.N. 1970. Egg capsules of prosobranch mollusks from South Florida and the Bahamas and notes on spawning in the laboratory. Bull. Mar. Sci. 20: 414-440.
Davies, G., P.J. Dare and D.B. Edwards. 1980. Fenced enclosures for the protection of seed mussels (*Mytilus edulis* L.) from predation by shore crabs (*Carcinus maenas* (L.)). Fish. Res. Tech. Rep. 56. MAFF Direct Fish. Res., Lowestoft.
Davis, M., C.A. Bolton and A.W. Stoner. 1993. A comparison of larval development, growth and shell development in 3 Caribbean *Strombus* species. Veliger 36: 236-244.
Dawson, R. 1986. Report on a study of the market for giant clam products in Taiwan, Japan, Hong Kong and Singapore. South Pacific Forum Fisheries Agency Report 86/37.
Demond, J. 1957. Micronesian reef associated gastropods. Pacific Sci. 11: 275-342.
Dharmaraj, S., A. Chellam and T.S. Velayudhan. 1987. Biofouling, boring and predation of pearl oyster. CMFRI Bulletin 39: 92-97.
Diggle, P.J. 1990. Time-series: a biostatistical introduction. Oxford University Press, Oxford, UK.
Dobberteen, R.A. and J.A. Pechenik. 1987. Comparison of the larval bioenergetics of two marine gastropods with widely differing lengths of planktonic life, *Thais haemostoma* (Gray) and *Crepidula fornicata* (L.). J. Exp. Mar. Biol. Ecol. 111: 173-191.

Drinkwater, K.F. and R.A. Myers. 1987. Testing predictions of marine fish and shellfish landings from environmental variables. Can. J. Fish. Aquat. Sci. 44: 1568-1573.
Eckman, J.E. 1983. Hydrodynamic processes affecting benthic recruitment. Limnol. Oceanogr. 28: 241-257.
Edwards, D.C. and J.D. Huebner. 1977. Feeding and growth rates of *Polinices duplicatus* preying on *Mya arenaria* at Barnstable Harbor, Massachusetts. Ecology 58: 1218-1236.
Emerson, W.K. 1991. First records for *Cymatium mundum* (Gould) in the Eastern Pacific Ocean, with comments on the zoogeography of the tropical trans-Pacific tonnacean and non-tonnacean prosobranch gastropods with Indo-Pacific faunal affinities in West American waters. Nautilus 105: 62-80.
Estacion, J.S. 1988. Ocean-nursery phase for giant clams in the Central Visayas, Philippines, p. 115-119. *In* J.W. Copland and J.S. Lucas (eds.) Giant clams in Asia and the Pacific. ACIAR Monograph 9. Canberra.
Fabens, A.J. 1965. Properties and fitting of the von Bertalanffy growth curve. Growth 29: 265-289.
Fitt, W.K., Editor. 1993a. The biology and mariculture of giant clams. ACIAR Proceedings 47. Canberra.
Fitt, W.K. 1993b. Nutrition of giant clams, p. 31-40. *In* W. K. Fitt (ed.) The biology and mariculture of giant clams, ACIAR Proceedings 47. Canberra.
Fitt, W.K. and R.K. Trench. 1981. Spawning, development and acquisition of zooxanthellae by *Tridacna squamosa* (Mollusca, Bivalvia). Biol. Bull. 161: 213-235.
Fogarty, M.J. 1988. Time-series models of the Maine lobster fishery: the effect of temperature. Can. J. Fish. Aquat. Sci. 45: 1145-1153.
Fogarty, M.J. 1993. Recruitment in randomly varying environments. ICES J. Mar. Sci. 50: 247-260.
Fraenkel, P. 1986. Water pumping devices. Intermediate Technology Publications, London.
Franz, D.R. 1972. Opisthobranch culture, p. 245-256. *In* W. L. Smith and M. H. Chanley (eds.) Culture of marine invertebrates. Plenum Press, New York and London.
Gallagher, B.S., K.M. Shimada, F.I. Gonzalez and E.D. Stroup. 1970. Tides and currents in Fanning Atoll lagoon, p. 5-18. *In* Fanning Island Expedition, January 1970. University of Hawaii.
Galtsoff, P.S. 1964. The American oyster *Crassostrea virginica* Gmelin. Fish. Bull., Fish Wildl. Serv., U.S. Department of the Interior: 421-440.
Ganapati, P.N. and R.S. Sastry. 1973. The spawn of a cymatiid gastropod *Cymatium pileare* (L.). Curr. Sci. 42: 25-25.
Gaschütz, G., D. Pauly and N. David. 1980. A versatile BASIC program for fitting weight and seasonally oscillating length growth data. ICES CM 1980/D:6, Statistics Cttee. 1-23.
Gayanilo, F.C., Jr., M. Soriano and D. Pauly. 1988. A draft guide to the Compleat ELEFAN. ICLARM Software 2, 65 p.
Gervis, M.H. and N.A. Sims. 1992. The biology and culture of pearl oysters (Bivalvia: Pteriidae). ICLARM Stud. Rev. 21, 49 p.
Gibbons, M.C. and W.C. Blogoslawski. 1989. Predators, pests, parasites and diseases, p. 167-200. *In* J.J. Manzi and M. Castagna (eds.) Clam mariculture in North America. Elsevier, Amsterdam.
Gibbons, M.C. and M. Castagna. 1985. Biological control of predation by crabs in bottom culture of hard clams using a combination of crushed stone aggregate, toadfish and cages. Aquaculture 47: 101-104.
Giese, A.C. and H. Kanatani. 1987. Maturation and spawning, p. 252-331. *In* A.C. Giese, J.S. Pearse and V.B. Pearse (eds.) Reproduction of marine invertebrates. Vol. 9: General aspects: seeking unity in diversity. Blackwell Scientific Publications, California.
Gomez, E.D. and C.A. Belda. 1988. Growth of giant clams in Bolinao, Philippines, p. 178-182. *In* J.W. Copland and J.S. Lucas (eds.) Giant clams in Asia and the Pacific. ACIAR Monograph 9. Canberra.
Gottman, J.M. 1981. Time-series analysis: a comprehensive introduction for social scientists. Cambridge University Press, Cambridge, UK.
Govan, H. 1992a. Predators and predator control, p. 41-50. *In* H. P. Calumpong (ed.) The giant clam: an ocean culture manual. ACIAR Monograph 16, Canberra.
Govan, H. 1992b. A low-cost ocean-nursery cage for juvenile tridacnid clams. Clamlines. Newsletter of the Giant Clam Research Group 10: 2-13.
Govan, H. 1992c. Cerithiids clean up killer clams. Clamlines. Newsletter of the Giant Clam Research Group 10: 21-22.
Govan, H. 1993. Participatory research in giant clam farming. Naga, ICLARM Q. 16(1): 8-10.
Govan, H. 1994. Predators of maricultured tridacnid clams. Proc. 7th Int. Coral Reef Symp. 2: 749-753.
Govan, H., L.Y. Fabro and E. Ropeti. 1993. Controlling predators of cultured tridacnid clams, p. 111-118. *In* W.K. Fitt (ed.) The biology and mariculture of giant clams. ACIAR Proceedings 47. Canberra.
Govan, H., P.V. Nichols and H. Tafea. 1988. Giant clam resource investigations in Solomon Islands, p. 54-57. *In* J.W. Copland and J.S. Lucas (eds.) Giant clams in Asia and the Pacific. ACIAR Monograph 9. Canberra.
Grizel, H. 1993. World bivalve culture. World Aquaculture 24(2): 18-23.
Gwyther, J. and J.L. Munro. 1981. Spawning induction and rearing of larvae of tridacnid clams (Bivalvia: Tridacnidae). Aquaculture 24: 197-217.
Halberg, F., K. Shankaraiah, A.C. Giese and F. Halberg. 1987. The chronobiology of marine invertebrates: methods of analysis, p. 332-384. *In* A.C. Giese, J.S. Pearse and V.B. Pearse (eds.) Reproduction of marine invertebrates. Vol. 9: General aspects: Seeking unity in diversity. Blackwell Scientific Publications, California.
Hambrey, J. and M. Gervis. 1993. The economic potential of village based farming of giant clams (*Tridacna gigas*) in Solomon Islands, p. 138-146. *In* W. K. Fitt (ed.) The biology and mariculture of giant clams. ACIAR Proceedings 47. Canberra.
Hancock, D.A. 1974. Oyster pests and their control. MAFF Laboratory Leaflet (New Series) 19.
Harrold, C., S. Lisin, K.H. Light and S. Tudor. 1991. Isolating settlement from recruitment of sea urchins. J. Exp. Mar. Biol. Ecol. 147: 81-94.
Henning, T. and J. Hemmen. 1993. Ranellidae and Personidae of the world. Verlag Christa Hemmen, Wiesbaden, Germany.

Hernandez, A., Editor. 1990. Cultivo de moluscos en America Latina. CIID - Canada/Editora Guadalupe, Bogotá, Colombia.
Heslinga, G.A. 1989. Biology and culture of the giant clam, p. 293-322. *In* J.J. Manzi and M. Castagna (eds.) Clam mariculture in North America. Elsevier, Amsterdam.
Heslinga, G.A., F.E. Perron and O. Orak. 1984. Mass culture of giant clams (Fam. Tridacnidae) in Palau. Aquaculture 39: 197-215.
Heslinga, G.A., T.C. Watson and T. Isamu. 1986. Cultivation of giant clams: beyond the hatchery, p. 53-58. *In* J.L. Maclean, L.B. Dizon and L.V. Hosillos (eds.) The First Asian Fisheries Forum. Asian Fisheries Society, Manila.
Heslinga, G.A., T.C. Watson and T. Isamu. 1990. Giant clam farming. Pacific Fisheries Development Foundation, Honolulu, Hawaii.
Hidu, H., C. Conary and S.R. Chapman. 1981. Suspended culture of oysters: biological fouling control. Aquaculture 22: 189-192.
Hilborn, R. and C.J. Walters. 1992. Quantitative fisheries stock assessment: choice, dynamics and uncertainty. Chapman and Hall, New York.
Hinton, A. 1975. Guide to the shells of Papua New Guinea. Robert Brown and Associates, Port Moresby, Papua New Guinea.
Hopkins, K.D. 1992. Reporting fish growth: a review of the basics. J. World Aquacult. Soc. 23: 173-179.
Houbrick, J.R. and V. Fretter. 1969. Some aspects of the functional anatomy and biology of *Cymatium* and *Bursa*. Proc. Malacol. Soc. Lond. 38: 415-429.
Hughes, R.N. 1986. A functional biology of marine gastropods. Croom Helm, London.
Hughes-Games, W.L. 1977. Growing the the Japanese oyster (*Crassostrea gigas*) in subtropical seawater fish ponds. I. Growth rate, survival and quality index. Aquaculture 11: 217-229.
Hviding, E. 1993. The rural context of giant clam mariculture in Solomon Islands: an anthropological study. ICLARM Tech. Rep. 39, 93 p.
Inaba, A. 1967. Growth of *Chicoreus asianus*. Venus 26: 5-7.
Jameson, S.C. 1976. Early life history of the giant clams *Tridacna crocea, T. maxima* and *Hippopus hippopus*. Pacific Sci. 30: 219-233.
Janacek, G. and L. Swift. 1993. Time-series: Forecasting, simulation and applications. Ellis Horwood, Hemel Hampstead, England.
Jeffers, J.N.R. 1978. An introduction to systems analysis: with ecological implications. Edward Arnold, London.
Johannes, R.E. 1978. Reproductive strategies of coastal marine fishes in the tropics. Env. Biol. Fish. 3: 65-84.
Johnson, D.R. and B.S. Hester. 1989. Larval transport and its association with recruitment of blue crabs to Chesapeake Bay. Estuarine Coastal Shelf Sci. 28: 459-472.
Johnson, R.A. and D.W. Wichern. 1988. Applied multivariate statistical analysis. Prentice Hall International, Englewood Cliffs, New Jersey.
Jory, D.E., M.R. Carriker and E.S. Iversen. 1984. Preventing predation in molluscan mariculture: an overview. J. World Maricult. Soc. 15: 421-432.
Kay, E.A. 1971. The littoral marine molluscs of Fanning Island. Pacific Sci. 25: 260-281.
Kendall, M. and J.D. Gibbons. 1990. Rank correlation methods. Edward Arnold, London and Melbourne.
Kilburn, R. and E. Rippey. 1982. Seashells of Southern Africa. Macmillan, Johannesburg.
Kohn, A.J. and P.J. Leviten. 1976. Effect of habitat complexity on population density and species richness in tropical intertidal predatory gastropod assemblages. Oecologia (Berl.) 25: 199-210.
La Barbera, M. 1975. Larval and post-larval development of the giant clams, *Tridacna maxima* and *Tridacna squamosa* (Bivalvia: Tridacnidae). Malacologia 15: 69-79.
Lasi, F. 1993. Modifications to long-line system at the CAC. Clamlines. Newsletter of the Giant Clam Research Group 12: 17.
Laursen, D. 1981. Taxonomy and distribution of teleplanic prosobranch larvae in the North Atlantic. Dana Report 89: 1-43.
Laws, E.A. and J.W. Archie. 1981. Appropriate use of regression analysis in marine biology. Mar. Biol. 65: 13-16.
Laxton, J.H. 1969. Reproduction in some New Zealand Cymatiidae (Gastropoda: Prosobranchia). Zool. J. Linn. Soc. 48: 237-253.
Laxton, J.H. 1970a. Shell growth in some New Zealand Cymatiidae. J. Exp. Mar. Biol. Ecol. 4: 250-260.
Laxton, J.H. 1970b. The relationship between the number of varices and total shell length in some New Zealand Cymatiidae (Gastropoda: Prosobranchia) and its ecological significance. Veliger 13: 127-134.
Laxton, J.H. 1971. Feeding in some Australasian Cymatiidae (Gastropoda: Prosobranchia). Zool. J. Linn. Soc. 50: 1-9.
Lebour, M.V. 1945. The eggs and larvae of some prosobranchs from Bermuda. Proc. Zool. Soc. Lond. 114: 462-489.
Lewis, J.B. and J.J. Boers. 1991. Patchiness and composition of coral reef demersal zooplankton. J. Plank. Res. 13: 1273-1289.
Lima, G.M. and R.A. Lutz. 1990. The relationship of larval shell morphology to mode of development in marine prosobranch gastropods. J. Mar. Biol. Assoc. (U.K.) 70: 611-637.
Linsley, R.M. and M. Javidpour. 1980. Episodic growth in gastropoda. Malacologia 20: 153-160.
Littlewood, D.T.J. 1988. *Cymatium muricinum* predates cultivated *Crassostrea rhizophorae*. J. Conchol. 33: 107.
Littlewood, D.T.J. 1989. Predation on cultivated *Crassostrea rhizophorae* (Guilding) by the gastropod *Cymatium pileare* (Linnaeus). J. Moll. Stud. 55: 125-127.
Littlewood, D.T.J. 1991. Pests and predators of cultivated mangrove oysters, p. 109-146. *In* G.F. Newkirk and B.A. Field (eds.) Oyster culture in the Caribbean. Mollusc Culture Network, International Development Research Centre, Halifax, Canada.
Lobel, P.S. and A.R. Robinson. 1986. Transport and entrapment of fish larvae by ocean mesoscale eddies and currents in Hawaiian waters. Deep Sea Res. 33: 483-500.
Longhurst, A.R. and D. Pauly. 1987. Ecology of tropical oceans. Academic Press, London.
Lucas, J.S. 1988a. Giant clams: description, distribution and life history, p. 21-33. *In* J.W. Copland and J.S. Lucas (eds.) Giant clams in Asia and the Pacific. ACIAR Monograph 9, 274 p. Canberra.
Lucas, J.S. 1988b. Testing an anti-fouling treatment for ocean-nursery meshes, p. 170-172. *In* J.W. Copland and J.S. Lucas (eds.) Giant clams in Asia and the Pacific. ACIAR Monograph 9. Canberra.
Lucas, J.S., R.D. Braley, C.M. Crawford and W.J. Nash. 1988. Selecting optimum conditions for ocean-nursery culture for *Tridacna gigas*, p. 129-132. *In* J.W. Copland and J.S. Lucas (eds.) Giant clams in Asia and the Pacific. ACIAR Monograph 9. Canberra.

Lucas, J.S., E. Ledua and R.D. Braley. 1990. A new species of giant clam (Tridacnidae) from Fiji and Tonga. ACIAR Working Paper 33. Canberra.

McCoy, E.W. and T. Chongpeepien, Editors. 1988. Bivalve mollusc culture research in Thailand. ICLARM Tech. Rep. 19, 190 p.

McShane, P.E., K.P. Black and M.G. Smith. 1988. Recruitment processes in *Haliotis rubra* (Mollusca: Gastropoda) and regional hydrodynamics in southeastern Australia imply localized dispersal of larvae. J. Exp. Mar. Biol. Ecol. 124: 175-203.

Meekan, M.G., M.J. Milicich and P.J. Doherty. 1993. Larval production drives temporal pattern of larval supply and recruitment of a coral reef damselfish. Mar. Ecol. (Prog. Ser.) 93: 217-225.

Moran, M.J., P.G. Fairweather and A.J. Underwood. 1984. Growth and mortality of the predatory intertidal whelk *Morula marginalba* Blainville (Muricidae): the effects of different species of prey. J. Exp. Mar. Biol. Ecol. 75: 1-17.

Morton, B. 1986. Reproduction, juvenile growth, consumption and the effects of starvation upon the South China Sea whelk *Hemifusus tuba* (Gmelin) (Prosobranchia: Melongenidae). J. Exp. Mar. Biol. Ecol. 102: 257-280.

Morton, B. 1990a. The physiology and feeding behaviour of two marine scavenging gastropods in Hong Kong: the subtidal *Babylonia lutosa* (Lamarck) and the intertidal *Nassarius festivus* (Powys). J. Moll. Stud. 56: 275-288.

Morton, B. 1990b. Prey capture, preference and consumption by *Linatella caudata* (Gastropoda: Tonnoidea: Ranellidae) in Hong Kong. J. Moll. Stud. 56: 477-486.

Munro, J.L. 1989. Fisheries for giant clams (Tridacnidae: Bivalvia) and prospects for stock enhancement, p. 541-558. *In* J.F. Caddy (ed.) Marine invertebrate fisheries: their assessment and management. John Wiley & Sons Inc., New York.

Munro, J.L., L.A. Gilkes, M.H. Gervis and J.B. Hambrey. 1993. Growth and survival of giant clam spat in floating ocean nurseries, p. 61-68. *In* W.K. Fitt (ed.) The biology and mariculture of giant clams. ACIAR Proceedings 47. Canberra.

Munro, J.L. and G.A. Heslinga. 1983. Prospects for the commercial cultivation of giant clams (Bivalvia: Tridacnidae). Proc. Gulf Caribb. Fish. Inst. 35: 122-134.

Munro, J.L. and W.J. Nash. 1985. A bibliography of the giant clams (Bivalvia:Tridacnidae). ICLARM Bibliogr. 3, 26 p.

Munro, P.E., J.H. Beard and E. Lacanienta. 1982. Investigations of the substance which causes sperm release in tridacnid clams. Comp. Biochem. Physiol. C 74: 219-223.

Murdoch, W.W. 1969. Switching in general predators: experiments on predator specificity and stability of prey populations. Ecol. Monogr. 39: 335-354.

Muthiah, P.D., D. Sundararajan, G. Srinivasan and N. Vaithinathan. 1985. Pests and predators of oysters. CMFRI Bulletin 38: 71-74.

Nelson, J.R. 1931. Trapping the oyster drill. N.J. Agric. Exp. Stn. Bull. 523.

Nielsen, C. 1975. Observations on *Buccinum undatum* L. attacking bivalves and on prey responses, with a short review on attack methods of other prosobranchs. Ophelia 13: 87-108.

Norton, J.H. and G.W. Jones. 1992. The giant clam: an anatomical and histological atlas. ACIAR Monograph 17. Canberra.

Norton, J.H., M.A. Shepherd and H.M. Long. 1993. The zooxanthellal tube system in the giant clam, p. 14-17. *In* W. K. Fitt (ed.) The biology and mariculture of giant clams. ACIAR Proceedings 47. Canberra.

Paine, R.T. 1963. Trophic relationships of eight sympatric predatory gastropods. Ecology 44: 63-73.

Palmer, A.R. 1981. Do carbonate skeletons limit the rate of body growth? Nature 292: 150-152.

Palmer, A.R. 1983. Relative cost of producing skeletal organic matrix versus calcification: evidence from marine gastropods. Mar. Biol. 75: 287-292.

Pauly, D. 1986. A simple method for estimating the food consumption of fish populations from growth data and food conversion experiments. Fish. Bull. 84: 827-840.

Pauly, D. 1991. Growth performance in fishes: rigorous description of patterns as a basis for understanding causal mechanisms. Aquabyte 4(3): 3-6.

Pauly, D. and M.L. Palomares. 1987. Shrimp consumption by fish in Kuwaiti waters: a methodology, preliminary results and their implications for management and research. Kuwait Bull. Mar. Sci. 9: 101-125.

Pechenik, J.A. 1987. Environmental influences on larval survival and development, p. 551-608. *In* A.C. Giese, J.S. Pearse and V.B. Pearse (eds.) Reproduction of marine invertebrates. Vol. 9: General aspects: Seeking unity in diversity. Blackwell Scientific Publications, California.

Pechenik, J.A. and W.D. Heyman. 1987. Using KCl to determine size at competence for larvae of the marine gastropod *Crepidula fornicata*. J. Exp. Mar. Biol. Ecol. 112: 27-38.

Pechenik, J.A., R.S. Scheltema and L.S. Eyster. 1984. Growth stasis and limited shell calcification in larvae of *Cymatium parthenopeum* during trans-Atlantic transport. Science 224: 1097-1099.

Pennings, S.C. 1990. Predator-prey interactions in opisthobranch gastropods: effects of prey body size and habitat complexity. Mar. Ecol. (Prog. Ser.) 62: 95-101.

Pepin, P. 1990. Biological correlates of recruitment variability in North Sea fish stocks. J. Cons. CIEM 47: 89-98.

Percharde, P.L. 1972. Observations on the gastropod *Charonia variegata*, in Trinidad and Tobago. Nautilus 85: 84-92.

Perio, N.S. and C. A. Belda. 1988. Predators and parasites of giant clams (Bivalvia: Tridacnidae), p. 81-83. *In* E.C. De Guzman and D.L. Gonzales (eds.) Culture of giant clams (Bivalvia: Tridacnidae). Proceedings of the Symposium-Workshop on the Culture of Giant Clams (Bivalvia: Tridacnidae), Silliman University, Dumaguete City, Philippines. Philippine Council for Aquatic and Marine Research and Development, Los Baños, Laguna and Australian Centre for International Agricultural Research, Canberra.

Perron, F.E. 1980. Laboratory culture of the larvae of *Conus textile* Linné (Gastropoda: Toxoglossa). J. Exp. Mar. Biol. Ecol. 42: 27-38.

Perron, F.E. 1981. Larval biology of six species of the genus *Conus* (Gastropoda: Toxoglossa) in Hawaii, USA. Mar. Biol. 61: 215-220.

Perron, F.E., G.A. Heslinga and J.O. Fagolimul. 1985. The gastropod *Cymatium muricinum*, a predator on juvenile tridacnid clams. Aquaculture 48: 211-221.

Platt, T. and K.L. Denman. 1975. Spectral analysis in ecology. Annu. Rev. Ecol. Syst. 6: 189-210.

Ponwith, B.J. 1990. Giant clam (*T. derasa*) growth and survival in American Samoa. Report to Department of Marine and Wildlife Resources, Pago Pago, American Samoa.

Prein, M. 1990. Multivariate analysis of tilapia growth experiments in ponds: case studies from the Philippines, Israel, Zambia and Peru. Christian-Albrechts-Universität, Kiel, Doctoral dissertation.

Price, C.M. and J.O. Fagolimul. 1988. Reintroduction of giant clams to Yap State, Federated States of Micronesia, p. 41-43. *In* J.W. Copland and J.S. Lucas (eds.) Giant clams in Asia and the Pacific. ACIAR Monograph 9. Canberra.

Purtymun, R. 1974. *Cymatium* egg-laying in a home aquarium. Hawaiian Shell News 22: 1.

Ramón, M. 1991. Spawning and development characteristics of *Cymatium cutaceum* and *C. corrugatum* (Gastropoda: Prosobranchia) in the laboratory. Ophelia 33: 31-43.

Reichelt, R.E. and A.J. Kohn. 1985. Feeding and distribution of predatory gastropods on some Great Barrier Reef platforms. Proc. 5th Int. Coral Reef Congress. Tahiti 5: 191-196.

Richter, G. 1984. Die Gehauseentwicklung bei den Larven der Cymatiiden (Prosobranchia: Tonnacea). Arch. Moll. 115: 125-141.

Ricker, W.E. 1954. Stock and recruitment. J. Fish. Res. Board Can. 11(5): 559-623.

Ricker, W.E. 1973. Linear regressions in fishery research. J. Fish. Res. Board Can. 30: 409-434.

Ricker, W.E. 1979. Growth rates and models, p. 677-742. *In* W.S. Hoar, D.J. Randall and J.R. Barett (eds.) Fish physiology. Vol. 8. Academic Press, New York.

Riedel, F. 1992. A re-evaluation of the ontogeny of *Cabestana spengleri* (Perry, 1811) (Gastropoda: Tonnoidea: Ranellidae). Veliger 35: 117-121.

Robertson, D.R. 1990. Differences in the seasonalities of spawning and recruitment of some small neotropical reef fishes. J. Exp. Mar. Biol. Ecol. 144: 49-62.

Robertson, R. 1983. Extraordinarily rapid post-larval growth of a tropical wentletrap (*Epitonium albidum*). Nautilus 97: 60-66.

Rosewater, J. 1965. The family Tridacnidae in the Indo-Pacific. Indo-Pacific Mollusca 1: 347-396.

Rosewater, J. 1982. A new species of *Hippopus* (Bivalvia: Tridacnidae). Nautilus 96: 3-6.

Rumrill, S.S. 1990. Natural mortality of marine invertebrate larvae. Ophelia 32: 163-198.

Scheltema, R.S. 1962. Pelagic larvae of New England gastropods. I. *Nassarius obsoletus* Say and *N. vibex* Say. Trans. Am. Microsc. Soc. 81: 1-11.

Scheltema, R.S. 1966. Evidence for trans-Atlantic transport of gastropod larvae belonging to the genus *Cymatium*. Deep Sea Res. 13: 83-95.

Scheltema, R.S. 1967. The relationship of temperature to the larval development of *Nassarius obsoletus* (Gastropoda). Biol. Bull. 132: 253-265.

Scheltema, R.S. 1971a. The dispersal of the larvae of shoal-water benthic invertebrate species over long distances by ocean currents. Fourth European Marine Biology Symposium: 7-28.

Scheltema, R.S. 1971b. Larval dispersal as a means of genetic exchange between geographically separated populations of shallow water benthic marine gastropods. Biol. Bull. 140: 284-322.

Scheltema, R.S. 1974. Biological interactions determining larval settlement of marine invertebrates. Thalassia Jugosl. 10: 263-296.

Scheltema, R.S. 1977. Dispersal of marine invertebrate organisms: Paleobiogeographic and biostratigraphic implications. *In* E.G. Kauffman and J.E. Hazel (eds.) Concepts and methods of biostratigraphy. Hutchinson and Ross Inc., Pennsylvania.

Scheltema, R.S. 1986. Long distance dispersal by planktonic larvae of shoal-water benthic invertebrates among Pacific Islands. Bull. Mar. Sci. 39: 241-256.

Shelley, C.C. and R.G.B. Reid. 1988. An improved gonad biopsy technique for *Hippopus hippopus*, p. 95-97. *In* J.W. Copland and J.S. Lucas (eds.) Giant clams in Asia and the Pacific. ACIAR Monograph 9, Canberra.

Shepherd, J.G., J.G. Pope and R.D. Cousens. 1984. Variations in fish stocks and hypotheses concerning their links with climate. Rapp. P.-V. Réun. CIEM 185: 255-267.

Shulman, M.J. 1985. Variability in recruitment of coral reef fishes. J. Exp. Mar. Biol. Ecol. 89: 205-219.

Silvert, W. and D. Pauly. 1987. On the compatibility of a new expression for gross conversion efficiency with the von Bertalanffy growth equation. Fish. Bull. 85: 139-140.

Sims, N.A. and N.T. Howard. 1988. Indigenous tridacnid clam populations and the introduction of *Tridacna derasa* in the Cook Islands, p. 34-40. *In* J.W. Copland and J.S. Lucas (eds.) Giant clams in Asia and the Pacific. ACIAR Monograph 9. Canberra.

Sirenko, B.I. and O.A. Scarlato. 1991. *Tridacna rosewateri* sp. n. A new species of giant clam from the Indian Ocean. Conchiglia 22(261): 4-9.

Sokal, R.R. and F.J. Rohlf. 1981. Biometry. W.H. Freeman and Co., New York.

Soriano, M., J. Moreau, J.M. Hoenig and D. Pauly. 1990. New functions for the analysis of two-phase growth of juvenile an adult fishes, with application to Nile perch. ICES C.M. 1990/D:16 Statistics Cttee.

Sparre, P., E. Ursin and S.C. Venema. 1989. Introduction to tropical fish stock assessment. Part 1 - Manual. FAO Fish. Tech. Pap. 306/1.

Sprent, P. 1993. Applied nonparametric statistical methods. Chapman and Hall, London.

Springsteen, F.J. and F.M. Leobrera. 1986. Shells of the Philippines. Carfel Seashell Museum, Manila.

Sprugel, D.G. 1983. Correcting for bias in log-transformed allometric equations. Ecology 64: 209-210.

Staples, D.J., W. Dall and D.J. Vance. 1984. Catch predictions of the banana prawn, *Penaeus merguiensis* in the South-eastern Gulf of Carpentaria, p. 259-267. *In* J.A. Gulland and B.S. Rothschild (eds.) Penaeid shrimps: their biology and management. Fishing News Books, Farnham, UK.

Stasek, C.R. 1965. Behavioural adaptation of the giant clam *Tridacna maxima* in the presence of grazing fishes. Veliger 8: 29-35.
STSC. 1985. Statgraphics: statistical graphics system. STSC Inc., Plusware Products, Rockville, Massachusetts.
Tafea, H. 1993. Cage and trestle construction. Clamlines. Newsletter of the Giant Clam Research Group 12: 13-15.
Taylor, J.B. 1977. Growth rates in juvenile carnivorous prosobranchs (Mollusca: Gastropoda) of Kaneohe Bay, Oahu (Hawaii). Proc. 3rd Int. Coral Reef Symp.: 253-259.
Taylor, J.D. 1976. Habitats, abundance and diets of Muricacean gastropods at Aldabra Atoll. Zool. J. Linn. Soc. 59: 155-193.
Taylor, J.D. 1978. Habitats and diet of predatory gastropods at Addu Atoll, Maldives. J. Exp. Mar. Biol. Ecol. 31: 83-103.
Taylor, J.D. 1984. A partial food web involving predatory gastropods on a Pacific fringing reef. J. Exp. Mar. Biol. Ecol. 74: 273-290.
Taylor, J.D. 1986. Diets of sand-living predatory gastropods at Piti Bay, Guam. Asian Mar. Biol. 3: 47-58.
Taylor, J.D. 1993. Dietary and anatomical specialization of mitrid gastropods (Mitridae) at Rottnest Island, Western Australia, p. 583-599. *In* F.E. Wells, D.I. Walker, H. Kirkman and R. Lethbridge (eds.) Proceedings of the Fifth International Marine Biological Workshop: The marine flora and fauna of Rottnest Island, Western Australia. Western Australian Museum, Perth.
Thamasavate, T., K. Silapajarn, J. Nugranad, W. Pattharapinyo, C. Sangrungruang, S. Limsurat and S. Yangponlakan. 1988. Growth, mortality and transportation studies on transplanted cockles (Fam. Arcidae) in Nakhon Bay, Thailand, p. 109-112. *In* E.W. McCoy and T. Chongpeeplen (eds.) Bivalve mollusc culture research in Thailand. ICLARM [illegible], 190 p.
Thangavelu, R. and P. Muthiah. 1983. Predation of oyster *Crassostrea madrasensis* by gastropod *Cymatium cingulatum* (Lamarck) in the oyster farm at Tuticorin. Proc. Symp. Coastal Aquaculture 2: 488-494.
Thompson, K.R. and F.H. Page. 1989. Detecting synchrony of recruitment using short, autocorrelated time-series. Can. J. Fish. Aquat. Sci. 46: 1831-1838.
Thorson, G. 1946. Reproduction and larval development of Danish marine bottom invertebrates. Medd. Dan. Fisk. Havunders, Plankton 4: 1-523.
Thorson, G. 1950. Reproductive and larval ecology of marine bottom invertebrates. Biol. Rev. 25: 1-45.
Thorson, G. 1966. Some factors influencing the recruitment and establishment of marine benthic communities. Neth. J. Sea Res. 3: 267-293.
Thouzeau, G. 1991. Experimental collection of postlarvae of *Pecten maximus* (L.) and other benthic macrofaunal species in the Bay of Saint-Brieuc, France. I. Settlement patterns and biotic interactions among the species collected. J. Exp. Mar. Biol. Ecol. 148: 159-179.
Tisdell, C.A. and L. Tacconi. 1993. Economics of giant clam production in Australia and Fiji and sensitivity factors, p. 133-137. *In* W. K. Fitt (ed.) The biology and mariculture of giant clams. ACIAR Proceedings 47. Canberra.
Tisdell, C.A., W.R. Thomas, L. Tacconi and J.S. Lucas. 1993. The cost of production of giant clam seed *Tridacna gigas*. J. World Aquacult. Soc. 24: 352-360.
UNEP/IUCN. 1988. Coral reefs of the world. Volume 3: Central and Western Pacific. UNEP Regional Seas Directories and Bibliographies, Switzerland and Cambridge.
Urosa, L.J. 1972. Algunos depredadores del mejillon comestible *Perna perna* (L.). Bol. Inst. Oceanogr. Univ. Oriente 11: 3-18.
Usher, G.F. 1990. The Coastal Aquaculture Centre's larval rearing protocol for *Tridacna gigas*. Clamlines. Newsletter of the Giant Clam Research Group 9: 4-8.
Usher, G.F. and J.E. Munro. 1988. ICLARM Coastal Aquaculture Centre: current facilities and progress, p. 106-109. *In* J.W. Copland and J.S. Lucas (eds.) Giant clams in Asia and the Pacific. ACIAR Monograph 9. Canberra.
Yakily, J.M. 1989. The biology and culture of mussels of the genus *Perna*. ICLARM Stud. Rev. 17, 63 p..
Yakily, J.M. 1992. Determination and comparison of bivalve growth, with emphasis on Thailand and other tropical areas. ICLARM Tech. Rep. 36, 125 p.
Vance, D.J., D.J. Staples and J.D. Kerr. 1985. Factors affecting year-to-year variation in the catch of banana prawns (*Penaeus merguiensis*) in the Gulf of Carpentaria. J. Cons. CIEM 42: 83-97.
Velez, A. 1975. Algunas observaciones sobre la ostricultura en el oriente de Venezuela. Lagena 35-36: 9-19.
Vermeij, G.J. 1978. Biogeography and adaptation: patterns of marine life. Harvard University Press, Cambridge, Massachusetts.
Vermeij, G.J. and P.W. Signor. 1992. The geographic, taxonomic and temporal distribution of determinate growth in marine gastropods. Biol. J. Linn. Soc. 47: 233-247.
Villalobos, C.R. and A.L. Baez. 1983. Tasa de crecimiento y mortalidad en *Anadara tuberculosa* (Bivalvia: Arcidae) bajo dos sistemas de cúltivo en el Pacífico de Costa Rica. Rev. Lat. Acui Lima-Peru 17-1-54: 9-18.
Wada, S.K. 1954. Spawning in the tridacnid clams. Jap. J. Zool. 11: 273-285.
Walters, C.J. and J.S. Collie. 1988. Is research on environmental factors useful to fisheries management? Can. J. Fish. Aquat. Sci. 45: 1848-1854.
Waren, A. and P. Bouchet. 1990. Laubierinidae and Pisanianurinae (Ranellidae), two new deep-sea taxa of the Tonnoidea (Gastropoda: Prosobranchia). Veliger 33: 56-102.
Webber, H.H. 1977. Gastropoda: Prosobranchia. *In* A.C. Giese and J.S. Pearse (eds.) Reproduction of marine invertebrates. Vol. 4. Molluscs: gastropods and cephalopods. Academic Press, London and New York.
Wilbur, K. M. 1964. Shell formation and regeneration, p. 243-282. *In* K.M. Wilbur and C.M. Yonge (eds.) Physiology of Mollusca. Vol. 1. Academic Press, London and New York.
Wilbur, K.M. and G.O. Owen. 1964. Growth, p. 211-242. *In* K. M. Wilbur and C.M. Yonge (eds.) Physiology of Mollusca. Vol. 1. Academic Press, London and New York.
Wootton, R.J. 1990. Ecology of teleost fishes. Chapman and Hall, London.
Yonge, C.M. 1975. Giant clams. Sci. Am. 232: 96-105.
Yonge, C.M. 1980. Functional morphology and evolution in the Tridacnidae (Mollusca: Bivalvia: Cardiacea). Rec. Aust. Mus. 33(17): 735-777.

Young, C.M. and F.S. Chia. 1987. Abundance and distribution of pelagic larvae as influenced by predation, behaviour, and hydrographic factors, p. 385-464. *In* A.C. Giese, J.S. Pearse and V.B. Pearse (eds.) Reproduction of marine invertebrates. Vol. 9: General aspects: seeking unity in diversity. Blackwell Scientific Publications, California.

Zimmerman, K.M. and J.A. Pechenik. 1991. How do temperature and salinity affect relative rates of growth, morphological differentiation and time to metamorphic competence in larvae of the marine gastropod *Crepidula plana*?. Biol. Bull. 180: 372-386.

Appendix 1

A List of Species Mentioned in the Text in Alphabetical Order and Including Taxonomic Authorities

Anadara granosa (Linné, 1758)
Anadara tuberculosa (Sowerby, 1837)
Babylonia lutosa (Lamarck, 1822)
Barbatia virescens (Reeve, 1844)
Buccinum undatum Linné, 1758
Bursa cruentata (Sowerby, 1841)
Cymatium aquatile (Reeve, 1844)
C. comptum (A. Adams, 1854)
C. corrugatum amictum (Reeve, 1844)
C. corrugatum corrugatum (Lamarck, 1816)
C. cynocephalum (Lamarck, 1816)
C. gemmatum (Reeve, 1844)
C. intermedium (Pease, 1869)
C. labiosum (Wood, 1828)
C. martinianum (d'Orbigny, 1846)
C. mundum (Gould, 1849)
C. muricinum (Röding, 1798)
C. nicobaricum (Röding, 1798)
C. parthenopeum echo Kuroda & Habe in Kira, 1961
C. parthenopeum keenae (Beu, 1970)
C. parthenopeum parthenopeum (von Salis, 1793)
C. pileare (Linné, 1758)
C. vespaceum (Lamarck, 1822)
Cabestana cutacea cutacea (Linné, 1767)
Ca. spengleri (Perry, 1811)
Callinectes sapidus Rathbun, 1896
Cerithium tesselatus Sowerby, 1855
Charonia lampas lampas (Linné, 1758)
Ch. lampas rubicunda (Perry, 1811)
Ch. tritonis variegata (Lamarck, 1816)
Conus ebraeus Linné, 1758
Co. imperialis Linné, 1758
Co. lividus Hwass in Bruguière, 1792
Co. marmoreus Linné, 1758
Co. rattus Hwass in Bruguière, 1792
Co. textile Linné, 1758
Crassostrea gigas (Thunberg, 1793)
Cra. rhizophorae (Guilding, 1828)
Crepidula fornicata (Linné, 1758)
Cre. plana (Say, 1822)
Cronia margariticola (Broderip, 1833)
Cr. ochrostoma (Blainville, 1832)
Dardanus guttatus (Olivier, 1812)
D. lagopodes (Forskål, 1775)
D. megistos (Herbst, 1804)
Epitonium ulu Pilsbry, 1921
Fusitriton magellanicus laudandus Finlay, 1927
Gonodactylus chiragra (Fabricius, 1775)
Haliotis rubra Leach, 1814
Hemifusus ternatanus (Röding, 1798)
He. tuba (Gmelin, 1791)
Hippopus hippopus (Linné, 1758)
H. porcellanus Rosewater, 1982
Latirolagena smaragdula (Linné, 1758)
Latirus gibbulus (Gmelin, 1791)
L. lanceolatus (Reeve, 1847)
Linatella caudata (Gmelin, 1791)
Mercenaria mercenaria (Linné, 1758)
Mitrella albina (Kiener, 1841)
Morula marginalba (Blainville, 1832)
Muricodrupa fiscella (Gmelin, 1791)
Mya arenaria Linné, 1758
Mytilus edulis Linné, 1758
Nassarius albescens (Dunker, 1846)
N. echinatus (Adams, 1852)
N. festivus (Powys, 1835)
N. obsoletus (Say, 1822) = *Ilyanassa obsoleta*
Natica maculosa Lamarck, 1812 = *N. tigrina* (Röding, 1798)
Opsanus tau (Linné, 1766)
Pecten maximus (Linné, 1758)
Peristernia nassatula (Lamarck, 1822)
P. ustulata (Reeve, 1847)
Perna perna (Linné, 1758)
Pinctada fucata (Gould, 1850)
P. maculata (Gould, 1850)
P. margaritifera (Linné, 1758)
P. maxima (Jameson, 1901)
Pleuroploca filamentosa (Röding, 1798)
P. trapezium (Linné, 1758)
Polinices alderi = *Euspira poliana* (Chiaje, 1826)
P. duplicatus (Say, 1822)
Pteria penguin (Röding, 1798)
Pyrene scripta (Lamarck, 1822)
Pyrene turturina (Lamarck, 1822)
Ranella australasia australasia (Perry, 1811)
Strombus costatus Gmelin, 1791
S. gigas Linné, 1758
Symbiodinium microadriaticum Freudenthal, 1962
Tellina tenuis da Costa, 1778
Th. carinifera (Lamarck, 1822)
Th. haemastoma (Linné, 1767)
Th. lapillus = *Nucella lapillus* (Linné, 1758)
Tridacna crocea Lamarck, 1819
T. derasa (Röding, 1798)
T. gigas (Linné, 1758)
T. maxima (Röding, 1798)
T. rosewateri Sirenko & Scarlato, 1991
T. squamosa Lamarck, 1819
T. tevoroa Lucas, Ledua & Braley, 1990
Vexillum exasperatum (Gmelin, 1791)

Appendix 2

Tridacna gigas Measurements and Biomass Estimations

Data pertaining to the length:weight ratio and general morphometrics of juvenile *T. gigas* have been collected at the ICLARM Coastal Aquaculture Centre in recent years by Dr. P. Munro, T. Shearer, H. Rota and H. Govan. These data were compiled by the present author in order to calculate various allometric relationships. Raw data are presented in Table A.

Table A. Size and weight measurements of juvenile *T. gigas* of 9.6-116.2 mm in shell length. Total volume was calculated based on the formula for two paraboloids as discussed in the text.

Length (mm)	Height (mm)	Depth (mm)	Volume (mm^3)	Shell dry (g)	Flesh wet (g)	Flesh dry (g)
9.6	7.3	4.0	111.0	N/A	0.018	0.0035
10.5	8.3	4.3	146.3	N/A	0.023	0.0044
11.3	8.5	4.3	161.7	N/A	0.024	0.0047
12.6	8.5	4.8	203.4	N/A	0.033	0.0053
13.9	9.8	5.5	292.2	N/A	0.054	0.0092
14.7	10.3	5.7	336.2	N/A	0.049	0.0074
15.5	11.0	6.4	431.3	N/A	0.075	0.0123
15.8	11.3	6.0	421.1	N/A	0.074	0.0154
17.1	12.0	6.4	518.9	N/A	0.101	0.0182
18.6	13.5	7.3	713.7	N/A	0.145	0.0250
19.3	12.0	6.8	619.4	N/A	0.097	0.0151
20.0	12.8	7.7	778.3	0.684	0.158	0.0245
20.4	14.0	7.0	782.6	0.718	0.171	0.0292
20.6	15.2	8.4	1,033.9	N/A	0.211	0.0365
21.5	15.6	8.3	1,095.2	N/A	0.211	0.0368
22.4	16.4	9.1	1,319.5	N/A	0.240	0.0417
23.3	17.6	9.2	1,491.8	N/A	0.386	0.0540
24.5	14.8	8.1	1,147.0	N/A	0.196	0.0338
25.4	16.7	9.1	1,514.4	N/A	0.295	0.0465
26.6	17.3	9.6	1,741.7	1.337	0.426	0.0576
27.7	17.2	9.5	1,759.7	1.130	1.156	0.0430
27.8	15.9	9.1	1,570.0	1.179	1.110	0.0370
28.4	19.0	9.6	2,039.2	1.420	0.618	0.0679
28.5	16.8	8.8	1,654.7	1.241	1.201	0.0484
29.0	15.8	8.2	1,478.7	1.139	1.220	0.0468
29.0	18.4	9.4	1,967.3	1.451	1.213	0.0552
29.5	17.2	9.4	1,871.2	1.377	1.405	0.0463
29.6	19.0	11.0	2,425.7	1.693	1.819	0.0660
29.7	19.3	9.4	2,118.8	1.541	0.590	0.0779
29.9	17.0	9.6	1,910.6	1.656	1.478	0.0488
30.9	20.8	10.1	2,543.8	1.793	0.388	0.0806
31.3	18.5	9.3	2,116.1	1.412	N/A	0.0462
31.8	22.6	11.6	3,273.5	2.186	0.687	0.0920
31.8	23.4	12.5	3,634.2	2.584	0.789	0.0987
32.5	22.3	11.2	3,175.7	2.308	0.706	0.0898
33.9	20.3	10.7	2,885.9	1.849	0.467	0.0606
35.6	23.8	13.1	4,340.5	N/A	0.715	0.1047
37.5	23.4	12.7	4,381.0	N/A	0.740	0.1036

Continued

Table A. Continuation.

Length (mm)	Height (mm)	Depth (mm)	Volume (mm^3)	Shell dry (g)	Flesh wet (g)	Flesh dry (g)
38.8	25.4	12.8	4,958.2	2.752	N/A	0.1157
39.3	25.1	13.3	5,170.7	3.248	0.782	0.1179
39.5	26.0	13.9	5,604.6	3.606	0.709	0.1305
40.7	28.3	13.4	6,045.6	3.686	N/A	0.1523
40.9	26.7	13.3	5,690.8	3.661	N/A	0.1458
42.2	27.5	14.4	6,566.9	3.900	N/A	0.1529
42.2	25.7	13.5	5,763.4	3.647	N/A	0.1467
42.6	28.9	13.3	6,431.9	4.327	1.631	0.1932
42.9	27.7	16.1	7,500.7	3.858	N/A	0.1553
43.2	29.3	14.2	7,042.9	4.229	N/A	0.1878
43.8	29.4	16.3	8,244.1	5.105	N/A	0.1863
44.1	26.6	14.6	6,721.7	4.078	1.495	0.1663
45.4	30.3	18.3	9,903.1	N/A	1.869	0.2533
45.6	27.9	14.7	7,331.3	4.426	N/A	0.1963
45.9	28.7	15.8	8,175.1	4.881	N/A	0.2108
47.6	30.8	16.0	9,225.5	N/A	1.502	0.2156
48.4	33.4	17.0	10,777.8	N/A	1.801	0.2617
50.5	33.8	18.3	12,287.1	N/A	2.022	0.2906
51.5	32.6	18.3	12,079.9	N/A	1.986	0.2711
51.6	35.2	22.1	15,792.3	10.820	3.633	0.3253
52.3	34.2	21.1	14,782.5	10.123	2.817	0.3047
54.6	34.9	18.3	13,678.6	9.217	2.555	0.3106
54.8	34.4	20.8	15,423.3	9.114	2.127	0.2911
55.2	37.0	22.6	18,065.0	10.862	2.093	0.3610
55.2	34.0	19.8	14,546.8	10.360	2.308	0.3110
55.9	35.6	20.2	15,763.0	9.561	2.812	0.3460
57.6	37.3	19.9	16,765.5	10.826	3.714	0.3631
58.9	35.8	18.4	15,208.8	10.632	2.228	0.2876
59.9	39.0	23.6	21,634.1	14.334	3.120	0.4029
60.2	37.1	23.6	20,673.6	12.480	4.466	0.4410
60.6	41.4	24.1	23,763.9	15.282	4.230	0.4436
61.3	40.1	21.2	20,448.1	13.907	3.723	0.4692
61.4	37.9	19.7	17,968.9	12.768	3.623	0.4256
61.8	43.9	23.4	24,977.7	16.504	5.009	0.5562
63.3	40.0	21.9	21,716.5	15.642	2.952	0.4355
63.8	42.6	20.4	21,807.2	13.798	4.110	0.4345
65.2	44.5	25.9	29,477.7	20.146	7.174	0.7399
71.9	52.5	30.1	44,638.9	27.447	6.189	0.7596
73.9	47.3	27.3	37,572.8	23.517	6.031	0.6393
74.0	51.2	30.9	45,989.7	31.207	6.970	0.8382
74.6	44.2	27.1	35,074.7	21.272	4.334	0.5637
75.3	49.1	31.9	46,264.8	32.217	5.990	0.6834
77.3	54.3	31.0	51,136.2	30.201	9.805	1.0803
77.9	50.9	24.5	38,184.6	19.540	4.992	0.5789
78.5	51.5	28.6	45,408.4	34.447	8.490	0.8954
79.0	52.3	28.6	46,467.4	27.585	7.713	0.9356
79.6	53.7	30.2	50,686.1	35.714	10.479	1.1934
80.2	53.8	31.7	53,639.1	35.358	9.580	1.0964
80.9	52.9	29.9	50,260.1	26.753	8.023	0.8222
83.6	56.3	34.6	63,873.3	36.404	12.375	1.3076
83.9	55.4	28.4	51,887.0	28.975	10.606	1.1275
84.5	55.6	33.2	61,201.2	38.335	10.936	1.1332
85.9	59.7	31.6	63,666.3	33.286	16.499	1.3700
85.9	56.8	30.6	58,720.2	34.106	14.310	1.3256
86.5	59.4	34.6	69,905.1	48.671	12.714	1.1752
87.7	59.4	35.8	73,302.2	38.288	11.211	1.2509
90.5	60.7	35.9	77,483.6	45.597	16.861	1.5928
91.8	60.7	36.0	78,758.1	47.515	13.111	1.4271
92.2	65.3	39.0	92,296.6	53.557	15.727	1.7048
92.4	63.7	39.2	90,681.6	N/A	N/A	1.8200
[illegible]	57.3	38.8	83,020.6	N/A	N/A	1.4100
	71.6	46.0	137,318.5	N/A	N/A	1.9900
	79.7	51.5	187,128.2	N/A	N/A	2.3300

Length (L), shell height (H) and shell depth (D) of the juvenile *T. gigas* were measured to the nearest 0.1 mm using Vernier calipers. Wet tissue weights were obtained after standard blotting techniques on an electronic balance to the nearest 0.0001 g. Dry tissue weights were measured after samples were dried using a microwave oven set at low power until a constant weight was attained, usually around four hours. This drying technique was observed to provide similar results to those obtained using conventional drying ovens (pers. observ. and P. Munro, pers. comm.). Electric power was only available 16 hours per day which, combined with the high ambient humidity, precluded the use of the slower electric ovens.

The ratio of shell measurements for the size range of clams measured were calculated to be: L:H:D = 1:0.66:0.38. The equations relating volume and length of juvenile *T. gigas* with wet and dry tissue weights are shown in Table B and were derived using GM regression as described in Chapter 2. Various formulae for estimating the volume of juvenile *T. gigas* based on geometric shapes were tested empirically. The best approximation was provided by the formula for two paraboloids facing each other (equation A.1).

$$V = \pi \cdot \frac{L}{2} \cdot \frac{H}{2} \cdot \frac{D}{2} \qquad \text{...A.1)}$$

Table B. Relationship of shell length (L) in mm and volume (V) in mm^3 of juvenile *T. gigas* between 9.6 and 95.2 mm in shell length with dry (DW) and wet (WW) tissue weights (mg).

$DW = 0.00689 \times L^{2.7036}$	$n = 99$	$r^2 = 0.985$
$DW = 22.2640 + 0.0189 \times V$	$n = 99$	$r^2 = 0.979$
$WW = 0.02817 \times L^{2.9021}$	$n = 86$	$r^2 = 0.951$
$WW = -10.1327 + 0.1864 \times V$	$n = 86$	$r^2 = 0.943$

Appendix 3

Publications (by H. Govan) Related to the Subject of This Work

Govan, H. 1992. Predators and predator control, p. 41-50. *In* H. P. Calumpong (ed.) The giant clam: an ocean culture manual. ACIAR Monograph 16. Canberra.

Govan, H. 1993. Participatory research in giant clam farming. Naga, ICLARM Q. 16(1): 8-10.

Govan, H. 1994. Predators of maricultured tridacnid clams. Proc. 7th Int. Coral Reef Symp. 2: 749-753.

Govan, H., L.Y. Fabro and E. Ropeti. 1993. Controlling predators of cultured tridacnid clams, p. 111-118. *In* W.K. Fitt (ed.) The biology and mariculture of giant clams. ACIAR Proc. 47. Canberra.

Govan, H., P.V. Nichols and H. Tafea. 1988. Giant clam resource investigations in Solomon Islands, p. 54-57. *In* J. W. Copland and J.S. Lucas (eds.) Giant clams in Asia and the Pacific. ACIAR Monograph 9. Canberra.

***Cymatium muricinum* and other ranellid gastropods: major predators of cultured tridacnid clams.** H. Govan. 1995. ICLARM Tech. Rep. 49. 136 p. US$9 surface, $12 airmail, P200.

Titles of Related Interest

- **Genetic aspects of conservation and cultivation of giant clams.** P. Munro, editor. 1993. ICLARM Conf. Proc. 39. 47 p. US$3 surface, $5 airmail, P90.
- **The rural context of giant clam mariculture in Solomon Islands: an anthropological study.** E. Hviding. 1993. ICLARM Tech. Rep. 39. 93 p. US$5 surface, $8 airmail, P100.
- **A bibliography of giant clams (Bivalvia: Tridacnidae).** J.L. Munro and W.J. Nash. 1985. ICLARM Bibliogr. 5. 26 p. US$2.50 surface, $4.50 airmail, P40.
- **Giant clams and the animals that kill them.** H. Govan, compiler. 1992. ICLARM Poster 3. 28 X 43 cm. Free upon request. US$5 by airmail.

HOW TO ORDER

Enquirers from the USA, Canada and Central and South America should order directly from our exclusive distributor, the **International Specialized Book Services**, 5804 N.E. Hassalo St., Portland, Oregon 97213-3644, to whom payment should be directed using the ***airmail*** price.

Enquirers from the Philippines may use the peso price and order directly from ICLARM. Enquirers elsewhere should address orders and payment (payable to ICLARM) in US$ by international money order, bankdraft or UNESCO coupons to: The Editor, ICLARM, MCPO Box 2631, 0718 Makati City, Philippines. We can accept US$ checks only if from a US-based bank due to high clearance fees of other banks.

Airmail is strongly recommended.