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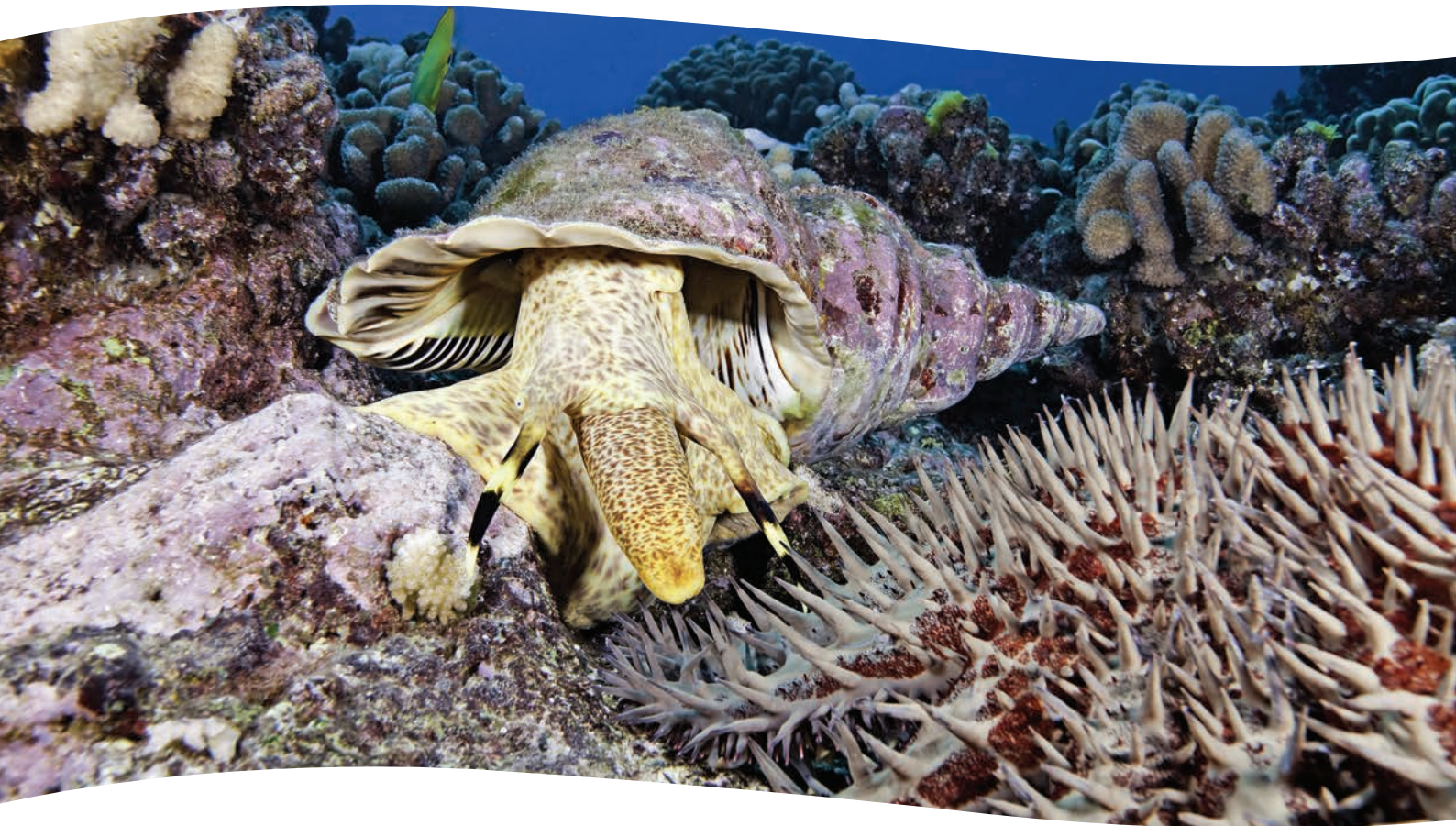
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The potential role of the giant triton snail, *Charonia tritonis* (Gastropoda: Ranellidae) in mitigating populations of the crown-of-thorns starfish

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Australian Government | AUSTRALIAN INSTITUTE OF MARINE SCIENCE

The potential role of the giant triton snail, *Charonia tritonis* (Gastropoda: Ranellidae) in mitigating populations of the crown-of-thorns starfish

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Cover photographs: Female *Charonia tritonis* laying (left) and protecting (right) clutches of eggs in the AIMS SeaSIM; Peter Thomas-Hall (AIMS, 2016).

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ACRONYMS

AIMS .... Australian Institute of Marine Science
CoTS............. Crown of Thorns Starfish
GBR .... Great Barrier Reef
NESP .... National Environmental Science Programme
TWQ.............. Tropical Water Quality

EXECUTIVE SUMMARY

This report reviews existing and historical literature on the biology and ecology of the giant triton, *Charonia tritonis*, in the context of their potential role in mitigating periodic outbreaks of the crown-of-thorns starfish (CoTS), *Acanthaster planci* species complex, and in particular *A. cf. solaris* on the Great Barrier Reef. Based on the available information, it is not possible to conclude whether giant tritons are rare due to natural causes or due to their historical exploitation. If the latter they may have been pushed to a tipping point and been unable to recolonise previous habitats. Prospects for captive rearing and release are examined with the intention to develop recommendations about future research and management directions with respect to their application in CoTS mitigation.

The various hypotheses to account for periodic outbreaks of CoTS, including the 'predator removal' and 'adult aggregation' hypotheses, are discussed in the context of integrated pest management of CoTS. To this end, the fundamental aspects of predator ecology in marine benthic ecosystems are outlined. Importantly, primary drivers are not necessarily just those associated with direct predation/consumption of prey but rather the very presence of predators. Predators can induce 'landscapes of fear' via trait-mediated indirect interactions, often regulated by chemoreception, and are being increasingly applied in biological control scenarios. The 'zone of impact' of these signals can extend some distance from the primary source; therefore the mere presence of the predator may be of critical importance when establishing biological control programs.

The predatory giant triton is an echinoderm specialist with a preference for asteroids including CoTS, as observed on the Great Barrier Reef and in controlled feeding studies. However, confident evaluation of their impact on the populations of CoTS and other echinoderms requires further research. In the laboratory, CoTS express a clear alarm response to *C. tritonis*, however, little is known of the specificity of this response and whether other putative prey species express similar behaviour.

Charonia tritonis have been bred in captivity. Although the planktonic larvae were held for ~300 days none completed the larval cycle to settlement and metamorphosis. A critical bottleneck to their successful aquaculture is the lack of understanding of the processes and chemical factors that induce and coordinate settlement. With recent advances in genomic techniques the sensory biology of *C. tritonis* larvae could be probed potentially revealing the chemoreceptors and chemical cues involved.

As large slow moving predators, giant tritons could be deployed at specific reefs on an *ad hoc* basis to predate and/or disperse CoTS. Alternatively, chemicals that comprise the giant triton's exosecretome could be released to create a landscape of fear. Reefs established as outbreak initiation zones could be preferentially targeted, potentially disrupting/interfering the formation of pre-spawning aggregations, which are crucial to fertilisation success of CoTS, ultimately reducing the severity of outbreaks.

1.0 INTRODUCTION

The crown-of-thorns starfish (CoTS), *Acanthaster planci* species complex ([Haszprunar *et al.* 2017](#)), is reported to be the primary cause of coral cover loss on many reefs in the Indo-Pacific and in particular *A. cf. solaris* on the Great Barrier Reef (GBR) ([Osborne *et al.* 2011](#)). Over recent decades CoTS account for 42% of the estimated losses in coral cover on the GBR, which has been experiencing an overall coral mortality rate of 3.4% y^{-1} ([De'ath *et al.* 2012](#)). Significant losses in coral cover occur primarily at times of CoTS population outbreaks during which they can increase in abundance by as much as 10-fold within a single year ([Kayal *et al.* 2012](#)). CoTS are extremely fecund, with an estimated spawn of 1.96×10^6 eggs for 157 mm diameter females, and therefore outbreaks could be expected purely based on random variation in reproductive success, larval survival and intensity of dispersal ([Caballes & Pratchett 2014](#); [Pratchett *et al.* 2017](#)). Outbreaks have been recorded over 328 times during the last 50 years throughout most of CoTS Indo-Pacific range ([Pratchett *et al.* 2014](#)). Recent studies clearly indicate that climate change, warming oceans and ocean acidification will improve the reproductive success and larval survival of CoTS, and will likely exacerbate frequency of outbreaks ([Pratchett *et al.* 2017](#)). Further, proposals to restock corals on reefs depleted due to mass coral bleaching will be undermined by the continued predation by CoTs, potentially negating any potential benefit ([Anthony *et al.* 2017](#)). Due to their propensity for population outbreaks and as obligate corallivores with high consumption rates, i.e. of up to 7 - $10m^2$ live coral per $year^{-1}$ $individual^{-1}$, CoTS have a disproportional large effect on the environment and as such hold keystone species status on coral reefs ([Mills *et al.* 1993](#); [Paine 1995](#); [Menge & Sanford 2013](#); [Grubbs *et al.* 2016](#)). As their impact is largely considered detrimental, management agencies require options for their mitigation, either preventing the initiation of outbreaks in the first place or culling the population when in excessive numbers ([GBRMPA 2014](#)).

The circumstances which lead to outbreaks of CoTS undoubtedly involve multiple factors and many hypotheses have been put forward over several decades to explain the phenomenon ([Birkeland & Lucas 1990](#); [Pratchett *et al.* 2014](#)). Single-factor hypotheses, however, are likely to oversimplify the unusual population dynamics of CoTS ([Bradbury & Antonelli 1990](#); [Babcock *et al.* 2014](#); [Morello *et al.* 2014](#)), and limited high-confidence unambiguous evidence exists to support one hypothesis over the other ([Pratchett *et al.* 2014](#)). The various hypotheses have been classified into two groups although they are not considered mutually exclusive and likely vary spatially and temporally ([Caballes & Pratchett 2014](#); [Pratchett *et al.* 2014](#)). One group places an emphasis on factors impacting recruitment rates and include the 'natural causes hypothesis' ([Vine 1973](#)), the 'larval recruitment/starvation hypothesis' ([Lucas 1973](#)) and the 'terrestrial run-off hypothesis' ([Birkeland 1982](#); [Wolfe *et al.* 2017](#)). The other group is based on changes in behaviour or survivorship of post-settlement CoTS with the primary hypotheses being the 'prey-threshold hypothesis' ([Antonelli & Kazarinoff 1984](#)), the 'predator removal hypothesis' ([Endean 1969](#)), which has been further modified to the 'recruitment initiated predation hypothesis' ([Ormond *et al.* 1990](#)), and the 'adult aggregation hypothesis' ([Dana *et al.* 1972](#)).

In this review, we focus on the potential role of the giant triton snail *Charonia tritonis* in influencing CoTS population biology in the context of the 'predator removal hypothesis', which proposes that populations of CoTS predators have been diminished over recent decades

thereby allowing CoTS populations to increase beyond natural levels (Hoey & Chin 2004), and the 'adult aggregation hypothesis', whereby without disruption of pre-spawning aggregations reproductive success in CoTS has been greatly enhanced (Dana *et al.* 1972).

To evaluate the potential role of the giant triton snail (*C. tritonis*) in mitigating population outbreaks of CoTS (*A. planci*) this report reviews existing and historical literature on the biology and ecology of the genus *Charonia*, with emphasis on *C. tritonis*. Based on the available information, potential of breeding and producing juvenile giant tritons through aquaculture are examined, in order to assist in the adequate management and protection of their populations and in the potential control of CoTS populations. Prospects for captive rearing and release are examined with the intention to develop recommendations about future research and management directions with respect to their application in CoTS mitigation.

2.0 PREDATORS OF COTS

As all coral reef organisms are exposed to predation the question is: what, in essence, is unique about CoTS which would account for the massive population cycling due to changes in predation and in particular a reduction in standing stock of predators? CoTS are exposed to predation throughout their life beginning with their planktonic larval phase (12 – 40 days duration), metamorphosis from a planktonic to benthic form (~2 days), a coralline algae feeding stage (up to approximately 6 months duration), a transition to coral feeding (typically occurring over 6 months), and onto adulthood and sexual maturity at +2 years onwards (Yamaguchi 1973; Zann et al. 1987). Zann reported that mortality of CoTS between the ages of 8 to 23 months was very high and estimated that 99% was attributed to a combination of disease, storms and predation. Although this claim, based on *in situ* observations, is speculative, if true it represents a primary bottleneck within the first 1-2 years of settlement and determines the survival rate to sexual maturity and subsequent production of the next generation. During these transition periods CoTS range in size from 0.5 mm diameter, as recently settled larvae, to approximately 200 mm diameter when feeding on coralline algae (Lucas 1984). If juveniles do not shift to a corallivore status they can remain in the 200-250 mm diameter range for at least 2 years (Lucas 1984). The risk of predation may be reflected in the observation that small 200 mm diameter CoTS exhibit distinct cryptic behaviour and usually remain well hidden within the reef matrix, particularly during daylight hours, with limited emergence at night, and has been attributed to avoidance of visual hunters (Lucas 1984; Yokochi & Ogura 1987; Zann et al. 1987). CoTS switch from nocturnal hiding to limited emergence during daylight hours at about 20 months of age at which time they express aggregation behaviour (Zann et al. 1987). This roughly coincides with the onset of sexual maturity at approximately 23 months of age (Lucas 1984).

The primary conundrum in the 'predator removal hypothesis' has been the lack of prevailing evidence necessary to quantify the level of predation on CoTS at any of its life stages. Very few predators have been observed feeding *in situ* on CoTS sperm (*Chaetodon auripes (Keesing & Halford 1992b)*) and eggs (*Abudefduf sexfasciatus* and *Amblyglyphidodon curacao (Endean 1969; Pearson & Endean 1969; Cowan et al. 2016)*) while reports of predation on CoTS larvae are based only on laboratory studies (Cowan *et al.* 2017). Despite various anti-predatory attributes approximately 17 species of invertebrates and vertebrates have been reported to occasionally attack or feed on healthy live juvenile and/or adults CoTS (Moran 1986; Birkeland & Lucas 1990; Pratchett *et al.* 2014; Cowan *et al.* 2017) (Table 1).

Table 1: Predators known to prey on healthy live juvenile and adult CoTS.

Taxa (Class)	Species	Reference
Anthozoa	*Stoichactis sp.* *Paracorynactis hoplites* *Pseudocorynactis sp.*	Chesher (1969); Moran (1986) Arthur R. Bos *et al.* (2008); Bos *et al.* (2011)
Polychaeta	*Pherecardia striata*	Glynn (1982, 1984)
Gastropoda	*Charonia tritonis,* *Cymatorium lotorium,* *Bursa rubeta*	Pearson and Endean (1969); Endean (1973); Ormond *et al.* (1973); Alcala (1974)
Malacostraca	*Hymenocera picta,* *Neaxius glyptocerus,* *Promidiopsis dormia*	Brown and Willey (1972); Alcala (1974); Glynn (1977, 1984)
Actinopterygii	*Epinephelus lanceolatus,* *Lethrinus* spp., *Cheilinus undulatus,* *Arothron hispidus, A. stellatus,* *A. nigropunctatus,* *Balistoides viridescens,* *Pseudobalistes flavimarginatus*	Chesher (1969); (Pearson & Endean 1969); Owens (1971); Ormond *et al.* (1973); Wilson and Marsh (1974); Endean (1976); Ormond *et al.* (1990); Keesing and Halford (1992a); Sweatman (1995); (Kroon pers. comms. 2017); Pratchett *et al.* (2014)

Most putative predators are generalised feeders and not obligate to CoTS, others have been reported to only prey upon injured or dead CoTS (Glynn 1984; Pratchett *et al.* 2014). Nevertheless, Glynn (1984) suggested that the lack of CoTS outbreaks on reefs of Pacific Panama was due to CoTS population regulation by the intensity of predation and scavenging by invertebrate predators including the amphinomid polychaete worm *Pherecardia striata*, and the harlequin shrimp *Hymenocera pieta*. Up to 70% of juvenile CoTS (110-200 mm diameter) throughout their Indo-Pacific range have been reported to have missing or regenerating arms (Pratchett *et al.* 2014; Rivera-Posada *et al.* 2014). Larger CoTS (>250 mm diameter; ~20 months old), which are not as cryptic, also suffer from apparent predation with missing or regenerating arms (McCallum *et al.* 1989). Such sub-lethal predator attacks potentially open up opportunities for scavenging predators (Glynn 1984; Rivera-Posada *et al.* 2014). To date research into the identification of the responsible predators has primarily focused on putative finfish predators, the majority of which are daylight visual hunters (Cronin 1997; Elvidge & Brown 2012; Pratchett *et al.* 2014). Gut content analysis of finfish, mainly lethrinids, have largely failed to detect any CoTS remains on the GBR or in the Indian Ocean (Sweatman 1997; Mendonça *et al.* 2010). Only rarely have remains of CoTS been found in the stomach of some generalist carnivorous finfish (Wilson & Marsh 1974; Endean 1976; Randall *et al.* 1978; Birdsey 1988). In manipulative experiments, predation rates by finfish on juvenile CoTS were estimated to be only 0.13% per day (Sweatman 1995). Nevertheless, Ormond and colleagues speculated that aggregations of CoTS in the Red Sea were dispersed as a result of predation by large triggerfish and pufferfish, including *Balistoides viridescens, Pseudobalistes flavimarginatus, Arothron hispidus, Arothron stellatus* as well as some Lethrinidae (Ormond & Campbell 1971; Ormond *et al.* 1973).

Giant tritons are known predators of juvenile and adult CoTS and likely prey on them through their juvenile and adult phases. Although there are few reports of *in situ* predation of CoTS by giant tritons (reviewed by Cowan *et al.* (2017)), divers have observed them chasing and

feeding on the starfish (Pearson & Endean 1969; Endean & Stablum 1973). Of 24 specimens encountered five of the giant tritons were feeding upon large juvenile *A. planci* and two on holothurians {Endean, 1973 #1570}. In a field study, an adult *A. planci* was caged with several carnivorous predators including numerous species of large fish (i.e. groper), turtles, crabs and carnivorous snails (*Melo* spp., *Cassis cornuta* and *C. tritonis*); only *C. tritonis* was observed attacking the starfish (Endean 1969). On the GBR, populations on Grubb Reef and John Brewer Reef were observed to actively hunt and eat CoTS suggesting that tritons seek *A. planci* in preference to other prey species (Paterson & Poulsen 1988). Four giant tritons on Grubb Reef were observed in the process of eating adult *A. planci* and one was found actively hunting an *A. planci*, and although *Linckia laevigata* was also abundant, tritons were not observed feeding on this species. Chesher (1969) noted that two specimens of *C. tritonis*, penned with COTS on a reef, actively sought out the starfish and could detect their presence from a distance of at least 1 m. Giant tritons have a narrow proboscis which is extendable up to 400 mm and capable of infiltrating narrow spaces in which juvenile COTS ($\leq$20 mm diameter) are primarily found. It is also capable of perforating the outer skin of adult COTS at which point it injects acidic venonmous saliva to immobilise the prey (Endean 1972; Percharde 1972). In addition, the radula is used to rasp the CoTS rendering the thorny outer skin ineffectual. Finally, the giant triton exosecretome elicits an escape response in individual adult CoTS thereby potentially flushing them out of hiding to be killed and consumed (Hall *et al.* 2016; Hall *et al.* 2017). Although a formidable predator, the slow and grasping attacks of the giant triton on CoTS are not always fatal. The starfish will autotomize the arm(s) not secured by the muscular foot and later regenerate them (Chesher 1969; Paterson 1990; Morton 2012), resulting in an incomplete attack.

CoTS are known to have significant chemical diversity in their saponin profile (Kitagawa & Kobayashi 1978; Lucas *et al.* 1979) that, at the very least, acts aposematically as a signal of unpalatability to potential predatory fish, and ultimately can be lethal (Montgomery *et al.* 2002; Prokof'eva *et al.* 2003; Podolak *et al.* 2010; Thakur *et al.* 2011; Van Dyck *et al.* 2011). The biological activities of marine-derived saponins are widely documented; they are particularly haemolytic through their interaction with cholesterol (a Δ^5-sterol) and are therefore damaging to cellular membranes (Mackie *et al.* 1975; Andersson *et al.* 1989; Francis *et al.* 2002). Dilute solutions of asterosaponins obtained from the tissue of many species of starfish are lethal to fish, annelids, molluscs, arthropods and vertebrates (Hashimoto & Yasumoto 1960; Mackie *et al.* 1975; Mackie *et al.* 1977; Komori 1997). Saponins in the eggs and larvae of CoTS deter feeding by the planktivorous fish *Acanthochromis polyacanthus* (Lucas *et al.* 1979). Similarly, Sweatman (1995) found that lethrinid fish presented with juvenile CoTS did not eat all the available starfish, and those that were eaten were often mouthed and rejected by several fish before eventually being swallowed, likely due to release of unpalatable factors such as saponins. Saponins have been detected in the seawater surrounding stressed individuals of the sea cucumber *Holothuria forskali* and Lucas *et al.* (1979) postulated that the release of saponins from stressed COTSinto the water column could, likewise, damage such soft tissues as respiratory epithelia of predatory fish, similar to the haemolytic activity induced by saponins isolated from CoTS tissues (Komori 1997). Giant tritons, however, appear immune to the toxic saponins extruded by alarmed CoTS. In fact they actively hunt, attack and consume live adult CoTS, therefore waterborne saponins are not acting as a deterrent as they can do for finfish (Lucas *et al.* 1979; Narita *et al.* 1984; Van Dyck *et al.* 2011). This immunity may arise from the fact that several glycosidases, which cleave the oligosaccharide chain of asterosaponins yielding the free sterol, have been isolated from the liver of *C. lampas*, including α-fucosidase,

β-xylosidase and β-glucosidase (Fukuda & Egami 1969; Butters *et al.* 1991). More recently, proteomics analysis detected arylsulfatase, a sulfur scavenging enzyme which may play a role in the breakdown of sulphated saponins, in the salivary glands of *C. tritonis* (Bose et al. 2017b). This is supported by a chemical investigation of *C. tritonis* tissue whereby the principal sterols of CoTS were isolated in significant amounts: Δ^7-sterols (34.4% of total sterols), 24-methylcholest-7-enol (15.5%), cholest-7-enol (5.4%), 24-methylcholest-7,22-dienol (6.7%) and acansterol (4.9%) (Teshima *et al.* 1979). Providing indirect evidence of a preference for asteroids and CoTS.

3.0 PREDATION ECOLOGY

Predators are pivotal as agents of natural selection which can drive rapid evolution of behaviour, defensive morphologies and chemical defences in prey (Tollrian & Harvell 1999; Khater *et al.* 2016). Defences may be constitutively expressed, phenotypically fixed, or induced when predators threaten, including in non-lethal contexts (Bouskila & Blumstein 1992; Agrawai *et al.* 1999; Werner & Peacor 2003; Hutson *et al.* 2005). The selective pressure can be profound incurring a transgenerational effect driven by a maternally-induced defence, whereby the attacked organisms offspring are better defended than offspring from unthreatened parents, in addition to the immediate defences invoked by the presence or attack of a predator (Bruno & Bertness 2001; Khater *et al.* 2014). Antipredatory behaviour in prey is typically exhibited as decreased feeding and activity levels as well as disruption to reproduction (Crowl & Covich 1990; Sih 1992; Houston *et al.* 1993; Sih 1994; Ruxton & Lima 1997; Wirsing *et al.* 2010; Trussell *et al.* 2011).

Changes in prey population density can be mediated by the predator and can, in turn, impact on other species/resources, termed *density-mediated indirect interactions* (Turner & Mittelbach 1990; Legault & Himmelman 1993; Soluk 1993; Dodson *et al.* 1994; Swisher *et al.* 1998; Bruno & Bertness 2001; Werner & Peacor 2003; Abrams 2007; Ferrer & Zimmer 2012; Ferrer & Zimmer 2013; Murray & Wyeth 2015). In Trinidad, pairs of *C. variegata* have been observed to methodically herd and attack congregations of spawning starfish, *Echinaster sentus*; rather than consuming entire individual starfish, the snails continue to chase and kill more starfish (Percharde 1972). The (deliberate) removal of marine benthic predators/grazers has been shown to not only influence the population of the primary prey but also to have knock-on effects through the benthic community (Fletcher 1987). For example, the widespread mortality of a single species of sea urchin (a herbivore consumer) on Caribbean reefs was directly followed by a several-fold increase in standing stock of benthic algae which in turn lead to second- and third-order effects through the ecosystem (Birkeland 1989a, b; Abjörbsson *et al.* 2004).

Predation on benthic communities has primarily focussed on density-mediated or lethal effects (Trussell *et al.* 2003). However, lethal effects, i.e. consumption rates, are not necessarily a good measure of a predator's impact on prey (Abrams 1993; Lima 1998; Lima & Bednekoff 1999; Yodzis 2000). The mere presence of predators in a community can force prey to modify their condition (alter a trait), including phenotypically (body shape, armour and size), as well as behaviourally (refuge seeking), and physiologically (chemical defences), which may influence other resource species, referred to as *trait-mediated indirect interactions* (Brown & Alexander 1994; Abrams 1995; Schmitz *et al.* 1997; Pinnegar *et al.* 2000; Bernot & Turner 2001; Dill *et al.* 2003; Witman *et al.* 2003; Bolnick & Preisser 2005; Toscano & Griffen 2014; Hall & Kingsford 2016; Morgan *et al.* 2016). Altering traits minimizes predation but may also lead to sub-optimal performance of the prey, i.e. slow growth and delayed maturity (Schmitz *et al.* 2004). Such trait-mediated interactions can reinforce or abate density-mediated effects (Werner & Peacor 2003; Preisser *et al.* 2008; Khater *et al.* 2016). As such the mere presence of predators can strongly influence prey density even if they consume few prey items (Luttbeg & Kerby 2005; Peckarsky *et al.* 2008a; Peckarsky *et al.* 2008b) (Orrock *et al.* 2010; Paterson *et al.* 2013). This phenomenon is a dominant facet of marine trophic interactions at both temporal and spatial scales (Dill 1987; Fletcher 1987; Shurin *et al.* 2002; Preisser *et al.* 2005; Schultz *et al.* 2016) and is likely driven by chemical reception of odours (Chivers & Smith 1998;

Kats & Dill 1998; Wisenden 2000; Briones-Fourzán 2009; Ferrari *et al.* 2010; Heethoff & Rall 2015). Such odours (chemical signals) can be transmitted over large distances, form gradients with differential intensities towards and away from the source and persist in time, from minutes, hours to days (Zimmer & Butman 2000; Buskirk *et al.* 2014). The scale and direction (i.e. currents) of the odour source determines the range of influence, which can vary from many kilometres (river plumes, reefs) to a few meters (lobster pheromones) to a few millimetres (copepods) (Gerlach *et al.* 2007; Atema *et al.* 2012). Furthermore, the sensitivity and specificity of a chemoreceptor is critical for an organism to be able to discriminate signals (Wicher 2012). For example, the foraging behaviour of the detritivore marine mud snail (*Illyanassa obsolete*), which siphons water allowing it to temporally and spatially integrate odour patches, modulates the spatial variation of detritus-feeding annelid species (Kelaher *et al.* 2003). Exposure to the chemical cues from green crabs (*Carcinus maenas*) caused herbivorous (*Littorina* spp.) snails to reduce their feeding with flow-on net community level effects (Turner 1997; Trussell *et al.* 2002). In laboratory experiments, the marine snail *Tegula funebralis* exposed to water conditioned by actively feeding predatory crabs previously maintained on a diet of *T. funebralis*, thus effectively chemically labelling them, exhibited predator avoidance behaviour (Jacobsen & Stabell 2004). Chemical cues derived from crabs actively feeding on another snail species, or from non-feeding *T. funebralis*-labelled crabs, did not induce a response. The snail's predator avoidance response is elicited by a mixture of the chemical cues leaking from the tissue of conspecifics when being eaten and the latent conspecific chemicals that are modified in crabs and which are subsequently released by feeding crabs.

The influence of a predator on prey behaviour is a product of both predator and prey density and movement rates, the persistence of predator avoidance by prey following an encounter and the spatial range over which their interactions occur (Turner & Montgomery 2003). The predation risk allocation hypothesis indicates that the greatest antipredator behaviour exhibited by prey is in high-risk situations that are brief and infrequent (Lima & Bednekoff 1999; Lima 2002; Fryxell *et al.* 2007; Ferrari *et al.* 2009; Khater *et al.* 2014). Risk perception by prey is mediated via a variety of cues, for example the scent of predators provides crucial information on immediate risk, especially in aquatic environments where it can be modulated depending on whether organisms are singular or in aggregations (Kats & Dill 1998; Mirza & Chiver 2001; McCarthy & Dickey 2002; Gras *et al.* 2009). Furthermore, behavioural responses of prey to a predator, such as a reduction in activity or an increase in refuge use, can cause trophic cascades and indeed quantitative support for behavioural effects dominating ecosystem community structure has been presented (Werner & Peacor 2003; Schmitz *et al.* 2004; Khater *et al.* 2016). For example, intertidal adults (up to 25 cm diameter) of the sunflower starfish (*Pycnopodia helianthoides*) are primary predators of small (6-8 cm diameter) sea urchins, including juvenile *Strongylocentrotus franciscanus*, *S. droebachiensis* and *S. purpuratus* (Duggins 1983). The presence of a single adult sunflower starfish (physical contact from a single ray) can disperse a large multi-species urchin aggregation by inducing an alarm and escape response, and not through consumption *per se* (Duggins 1981). Experimental re-introduction of *P. helianthoides* on a subtidal kelp bed (approximately 400 m^2) in Torch Bay, Alaska, resulted in decreased numbers of *S. droehbachiensis* after only 24 h (Duggins 1983). Similarly, *S. purpuratus* could be eliminated entirely. The natural invasion of *P. helianthoides* on a second kelp bed resulted in decreased numbers of *S. droehbachiensis* and *S. purpuratus*; *S. franciscanus* of size refuge (>9 cm) did not show the same escape response. Conversely, when the population density of the sunflower starfish decreases, there is a concurrent increase in the sea urchin population. The intensity of these effects is both dynamic and transient as

both predator and prey immigrate and emigrate within a specific area. Interestingly, adult *S. franciscanus* exhibited a defense response when exposed to starfish-conditioned seawater. A subsequent study found that the grazing behaviour of small (5-8 cm) *S. franciscanus* in the presence of waterborne cues from *P. helianthoides* was significantly reduced (Freeman 2005); waterborne cues from the predator directly and adversely influenced the prey.

The marine snail *Concholepas concholepas* can discriminate between odours originating from several different sources up to ~100-200 body lengths away (Manríquez *et al.* 2013). It moves towards the source of prey (mussels and barnacles) odours, however, in the presence of predatory crabs (*Homalaspis plana*) and asteroids (*Acanthocyclus hassleri* and *Heliaster helianthus*) it changes its behaviour, reducing its rate of prey consumption. Furthermore, the growth and survival rates of juvenile specimens (~1.5 cm) of *C. concholepas* maintained in the direct presence of its predators were significantly lower, while shell thickening increased.

This chemically-mediated phenomenon has been referred to as 'landscapes of fear' (Luttbeg & Kerby 2005; Preisser *et al.* 2005; Preisser *et al.* 2008) which is increasingly being applied to cases of biological control (Schmitz *et al.* 2004; Deletre *et al.* 2016) with potential application in the marine environment (Atalah *et al.* 2015). In this context, the predator avoidance behaviour displayed by CoTS exposed to *C. tritonis*-conditioned water could be exploited in the development of novel CoTS population control technologies (Hall *et al.* 2017).

4.0 GENERAL BIOLOGY OF *CHARONIA*

4.1 Species taxonomy and nomenclature

Molluscs are one of the most diverse phyla in the marine environment with estimates of 51,500 to 164,000 species, and are thought to comprise 60% of all coral reef invertebrates (Bouchet 2006; Appletans *et al.* 2012). Within the Mollusca, over 60% of the species are within the class Gastropoda, comprised of 10 subclasses (Bouchet *et al.* 2005). The most diverse of the Gastropoda subclasses is the monophyletic clade Caenogastropoda (5 orders), which comprises about 136 families and thousands of genera arranged into 41 superfamilies (Colgan *et al.* 2007; Ponder *et al.* 2008). A primary clade within the Caenogastropoda includes the Hypsogastropoda, within which are the clades of Littorinimorpha (within the group Taenioglossa, radula typically with 7 teeth per row) and Neogastropoda (within the group Stenoglossa, radula with only 1-5 teeth per row) (Ponder *et al.* 2008). The majority of gastropod species are marine predators with many having a geographical range through the tropics (Taylor *et al.* 1980). With such extensive species diversity the Gastropoda snails, being an order of magnitude greater than that of coral diversity, likely plays an influential role, as a whole and at an individual species level, on the ecology and community structure of coral reefs (Sorokin 1995; Glynn & Enochs 2010).

The Hypsogastropoda are numerically important key predators in shallow water communities, and particularly in tropical environments (Ponder *et al.* 2008). These primary predators have undergone an extraordinary adaptive radiation resulting in significant morphological, physiological, behavioural and ecological diversity (Table 2), primarily driven through diet and competition (Vermeij & Cambridge 1978; Wagner 2001; Strong 2003). Several apomorphies are shared within the taxa predominantly related to the digestive system including: a rectal (anal) gland, salivary glands that do not pass through the nerve ring, tubular accessory salivary glands, possession of either a stenoglossan or a toxoglossan radula, the esophageal gland separated from the esophagus (poison gland), and the enlargement of the ventral tensor muscle of the radula to enable the sliding movement of the radula (Ponder & Lindberg 1997; Strong 2003; Ponder *et al.* 2008). Modifications to the physiology and sensory biology specific to Hypsogastropoda include: elaboration of the anterior digestive system and the radula, formation of eversible proboscides, a specialised and well developed siphon and repeated folding in the chemoreceptor osphradium to extend the surface area capable of particular acute chemical sensitivity (Ponder & Lindberg 1997; Bigatti *et al.* 2010). Complex behaviour adaptations, compared to herbivorous gastropods, include searching, capture, immobilization, penetration of prey and subsequent digestion (Taylor *et al.* 1980; Bigatti *et al.* 2010).

Table 2: Primary superfamilies and families of the Hypsogastropoda clade containing the Littorinimorpha and Neogastropoda. Common name, diversity of taxa and primary diet are shown.

Hypsogastropoda		Common name	Taxa	Diet
Superfamily	Family			
Clade Littorinimorpha				
Littorinoidea	Littorinidae	Perwinkles	65	Algal grazers
Cypraeoidea	Cypraeidae	Cowries	112	Sponges
Calyptraeoidea	Calyptraeidae	Slipper limpets	28	Filter feeders
Tonnoidea	Tonnidae	Tuns	12	Echinoderms, bivalves, crustaceans, fish
Tonnoidea	Cassidae	Helmet shells	31	Echinoderms (sea urchins)
Tonnoidea	Ranellidae	Tritons	73	Echinoderms, molluscs
Stromboidea	Strombidae	Strombs	47	Herbivores, detritivores
Naticoidea	Naticidae	Moon snails	86	Bivalves
Clade Neogastropoda				
Muricoidea	Muricidae	Rock shells, oyster drills	340	Gastropods, bivalves, barnacles
Muricoidea	Volutidae	Baler shells	133	Bivalves, Gastropods, polychaetes, bryozoans, sipunculids, barnacles, crustacea
Muricoidea	Mitridae	Miters	25	Sipunculans
Buccinoidea	Buccinidae	Whelks	235	Molluscs, polychaetes, echinoderms, scavengers
Conoidea	Terebridae	Augers	47	Polychaetes
Conoidea	Conidae	Cone shells	147	Polychaetes, fish

The largest and most spectacular of the Caenogastropoda are those within the superfamily Tonnoidea (7 families) and in particular the large clade Littorinimorpha which includes the family Ranellidae of which there are two sub-families; the Ranellinae, with 8 genera, and the Cymatiinae, with 14 genera (Table 3) (Bouchet *et al.* 2005; Colgan *et al.* 2007; Liggia 2015). Within the Cymatiinae, three genera are known to feed on echinoderms: *Cymatium* (5 species) are major predators of tropical tridacnid clams, as well as echinoderms, *Sassia* (17) feed on echinoderms and ascidians, and *Charonia* (3 species) are specialist predators of echinoderms, primarily feeding upon species within the Asteroidea but also the Holothuroidea and to a lesser extent on Echinoidea (Govan 1995; Colgan *et al.* 2007). The giant triton (*C. tritonis*) is known by several other names, primarily because it is highly prized and collected in many cultures; Triton's trumpet [derived from the Greek god Triton who is often portrayed blowing a large seashell horn], the horagai (jinkai) in Japan, nagak (godong) in Korea, the sangu (sankha) in Hinduism and Buddhism ceremonies and the pūtātara (primarily *C. lampas*) in Maori culture as well as by numerous other names in various Polynesian (pu) and Melanesian cultures (Kira 1972; Abbott 1973).

Table 3: Genera of the subfamily Cymatiinae within the family Ranellidae, with common name, number of species ([Liggia 2015](#)), and general diet ([Taylor 1998](#)). Number of species includes accepted species with presently unaccepted species shown in brackets.

Cymatiinae	Common name	Species	Diet
Cabestana	Shouldered triton	6 (21)	Predatory: ascidians, polychaetes
Charonia	Giant triton/Triton's trumpet	3 (4)	Predatory (generalist): echinoderms primarily, bivalves, gastropods, spiny lobster occasionally
Cymatiella	Little Southern triton	7 (12)	Predatory
Cymatium	Hairy triton	5	Predatory (generalist): Tridacnid clams, bivalves, gastropods, echinoderms, ascidians, polychaetes
Gelagna	Lesser girdled triton	2 (5)	Predatory
Gutturnium	Knobbly triton	1 (6)	Predatory: Tridacnid clams
Linatella	Girdled triton	2 (17)	Predatory: Pearl oysters, bivalves
Lotoria	Large spotted triton	3 (7)	Predatory
Monoplex	Giant triton	25 (43)	Predatory: ascidians, bivalves
Ranularia	Pear triton	23 (48)	Predatory: pearl oysters, bivalves
Reticutriton	Pfeiffer triton	2	Predatory
Sassia	Distorted rock whelk	17 (23)	Predatory: echinoderms, ascidians
Septa	Ruby triton	9 (49)	Predatory
Turritriton	Thin-lined triton	4 (11)	Predatory

4.2 Appearance and morphology

The cymatiid gastropods within the genus *Charonia* have a large shell (up to 500 mm in length) with a pointed spire. The general shell shape is tall and narrow with an outer lip that flares pronouncedly. Varices are well developed, spaced about every 270° around the shell merging abaperturally and bearing the remains of the flaring outer lip. The main shell is a large body whorl with broad cords within a single narrow thread filling each interspace; nodules are low or absent. The shell has nearly no periostracum and is extremely glossy. The colour pattern is of high contrast between red-brown crescentic splashes against a cream to pink background ([Beu 1970](#)). The operculum is bark brown, oval in shape and thick with complete concentric growth lines.

The most distinctive non-shell feature of the genus is its radula which, although typically taenioglossan, has a central tooth that is broad and low with a very narrow basal plate that is curved down at the extremities whereas all other teeth are narrow and elongated ([Beu 1970](#)). *Charonia* has more synonyms than almost any other molluscan genus ([Beu 1970](#)). The systematics of the genus *Charonia* has been revised several times over the last few decades, as have the Gastropoda in general, and will undoubtedly evolve further as molecular analysis continues to be brought to bear. Presently, there are three species with additional subspecies, based on historical argument ([Beu 1970](#); [Bouchet & Gofas 2016](#)).

Charonia lampas (Linnaeus, 1758; common names include the knobbed triton and red triton shell) is the most morphologically variable of the genus, driven by ecophenotrypic rather than genetic variation ([Dodge 1957](#); [Beu 1998](#)). Nevertheless the species has previously been classified into four subspecies, namely *C. lampas lampas, C. l. pustulata, C. l. capax, C. l.*

rubicunda and C. l. sauliae but is now classed solely as *C. lampas* ([Beu 1970](#)). The other two species are *Charonia tritonis* (Linnaeus, 1758), common name giant triton or Triton's trumpet shell, and *Charonia variegata* (Lamarck, 1816), common name Atlantic or Caribbean triton's trumpet shell. *Charonia seguenzae* has recently been classified as a potential separate species from *C. variegate*, having being isolated in the Eastern Mediterranean Sea ([Beu 2010](#)).

4.3 Distribution, habitat and abundance

Charonia lampas has an extensive geographical distribution ranging from the temperate to sub-tropical waters of the Atlantic, Indian and Pacific Oceans with the exception of the tropical Indo-West Pacific and Panamic western America ([Beu & Kay 1988](#); [Beu 1998](#)) (Fig. 1). Within the Atlanic Ocean it has mostly been reported from the Western Atlantic, but may have had a more extensive range ([Coelho *et al.* 1981](#)). It is most widely known in the western Mediterranean, but largely absent in the eastern Mediterranean, where it is replaced by *C. (seguenzae) variegata* ([Beu 1998](#), [2010](#)). The species is recorded from False Bay to the northern coast of Natal in South Africa and from Jurien Bay in southern Western Australia and all around the southern and eastern coasts to Swain Reefs of the Great Barrier Reef ([Wilson 1993](#)). In New South Wales, Australia, it is commonly known as the intertidal 'red whelk' feeding on the ascidian *Pyura* ([Fairweather 1988](#); [Wilson 1993](#)). The species has been recorded in New Zealand and the Chatham, Kermadec, Raoul, Norfolk and Lowe Howe Islands. In the north Pacific the species is found around the islands of Japan and Taiwan ([Lai 1989](#)).
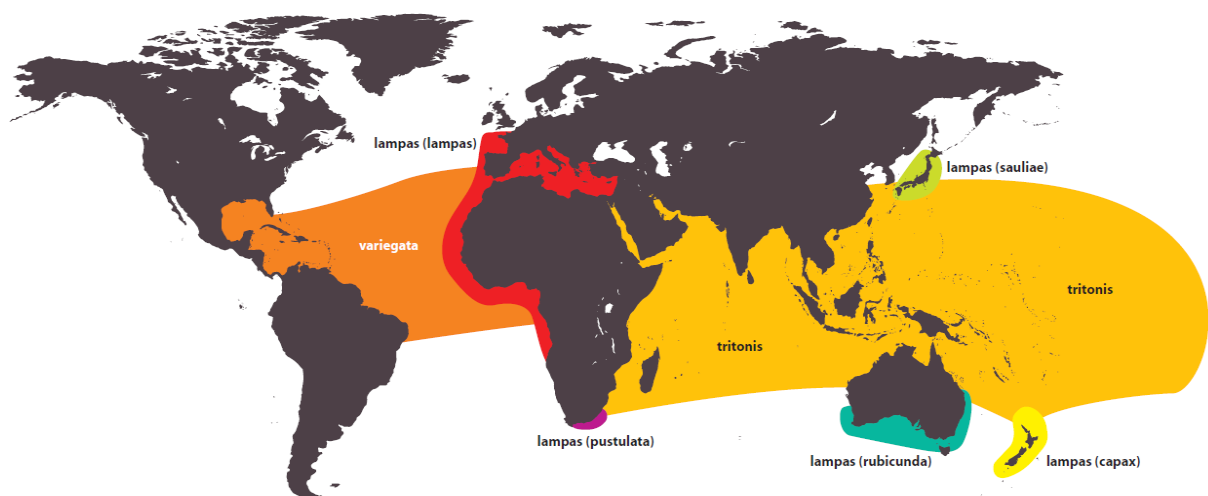
Figure 1: Distribution and range of the *Charonia* genus.

Charonia tritonis is distributed throughout the Indo-West Pacific region primarily in tropical waters ([Nateewathana & Aungtonya 1994](#); [Kay 1995b](#)) (Figure 1). It has been reported from the tropical east, north and west coasts of Australia (Fig. 2), and in the Pitcairn group of islands in the far southeast of Polynesia, Cocos, Galapagos, Easter and Hawaiian Islands through to New Zealand ([Montoya 1983](#); [Emerson 1989](#); [Beu 1998](#)). It has not been recorded from the coasts of the Americas in the tropical eastern Pacific. In the Indian Ocean it is found from the Red Sea to southern East Africa (to South Africa) across the islands of the Indian Ocean to north and central Western Australia ([Wilson 1993](#)).

Charonia variegata (Lamarck, 1816), common name Atlantic or Caribbean triton's trumpet shell, is distributed through the western tropical Atlantic, the Caribbean and subtropical regions of the Mediterranean ([Clench & Turner 1957](#); [Percharde 1972](#)) (Figure 1). *Charonia variegata* and *C. tritonis* have been geographically, and hence genetically, separated since the late Pliocene uplift of the Isthmus of Panama. This species differs from *C. tritonis* in having a shorter spire, more strongly shouldered whorls, a more constricted aperture with a smaller less flared lip, more prominent white ridges and large dark brown background areas inside the outer lip ([Beu 1998](#)). Documented knowledge of this species is scarce but it likely has co-occurrence with *C. lampas* in Malta ([Beu 2010](#)).

Figure 2: Sites of collection of *C. tritonis* from Australia. From ([Atlas of Living Australia](#) [http://biocache.ala.org.au/occurrences/search?q=charonia tritonis#tab_mapView accessed 15th June 2017](#)).

The primary habitat of *Charonia spp.* includes hard and sandy bottoms around shallow water reefs but specimens have also been found at depths of several hundred metres ([Beu 1998](#)). In addition, a few specimens have been collected in shallow water soft-bottom dredging programs ([Bouchet *et al.* 2008](#); [Tröndlé & Boutet 2009](#)). Tritons typically remain concealed during daylight hours in crevices and are primarily nocturnal, hence accurate sampling for population size is non-trivial ([Paterson 1990](#)).

4.4 Growth, development and morphological relationships

Some gastropod veligers hatch at an advanced stage (protoconch stage I) through an aperture in the capsule and complete their development in the water column (Figure 3 and Figure 4) ([Fioroni 1982](#)). Veliger spend an unknown length of time in the planktonic phase which may vary from weeks to over a year ([Scheltema 1966](#)). Growth of veligers is generally estimated in terms of shell length, *i.e. Crepidula fornicata* although this is not always the case, *i.e. Ilyanassa obsoleta* ([Pechenik 1980](#)).

The larvae of Ranellidae, including *C. tritonis*, are teleplanic, defined as larvae of benthic continental shelf organisms which can have an extensive and long larval development phase and hence are capable of dispersing across vast distances ([Scheltema 1971b](#)). The veliger of

the Ranellidae, and in particular tropical species within the genera *Lamellaria*, *Tonna*, *Cassis*, *Charonia*, *Cymatium* and *Bursa*, are often found mid-way across oceans during plankton sampling (Scheltema 1971b; Pechenik 1980). Many teleplanic veligers possess adaptations such as long periostracal spines, the reduction or complete lack of shell decalcification and an increase in length of the velar lobes used for swimming and feeding (Pechenik *et al.* 1984). A larval duration of over 4.5 years from hatching to metamorphosis has been reported in the Oregon hairy triton, *Fusitriton oregonensis* (Ranellidae), which is the longest larval period for any marine organism (Strathmann & Strathmann 2007). In *Cymatium parthenopeum* (Cymatiinae) larvae can develop up to the protoconch II stage in nearshore waters and then, in the teleplanic form, develop four large velar lobes extending 10 times the diameter of the larval shell length to aid trans-oceanic transport (Figure 5). Both growth and calcification are halted during oceanic transit (Lebour 1945; Scheltema 1971b, a, 1974; Pechenik *et al.* 1984; Richter 1984). Based on plankton tow collections it has been estimated that the larval period of species within the *Cymatium* genus is around 150 to 200 days with rough estimates of larval growth rate between 20 – 65 µm per day (Scheltema 1971b).

Episodic (or discontinuous) growth is characteristic of certain species of Ranellidae, Bursidae, Cassidae and Muricidae (Taylor 1977; Linsley & Javidpour 1980). In at least three species of New Zealand Randellidae (*Cabestana spengleri, Cymatium parthenopeum* and *Ranella Australasia*) the pattern is an initial rapid secretion and formation of shell via biomineralization (Marin *et al.* 2012). Up to half a whorl is formed in their first year along with the formation of a flared lip (varix) at the apertural margin, followed by a cessation of growth for an undefined period; eventually growth is resumed (Laxton 1970a, b). Shell formation can be independent of tissue growth. Tissue growth may proceed continuously and, at least in some species, sometimes greatly exceeds shell formation (Laxton 1970b). The mantle is responsible for production of the shell, with shell biomineralisation rate a function of mantle area. The rate of increase in shell thickness, on the other hand, is a function of the secretion of the largely proteinaceous, organic matrix by the mantle upon which calcium carbonate crystals are deposited. This process exhausts a significant proportion of the energy budget but nevertheless thickens the shell providing protection against the crushing power by the jaws of predators (Hughes 1986; Ruppert *et al.* 2003).
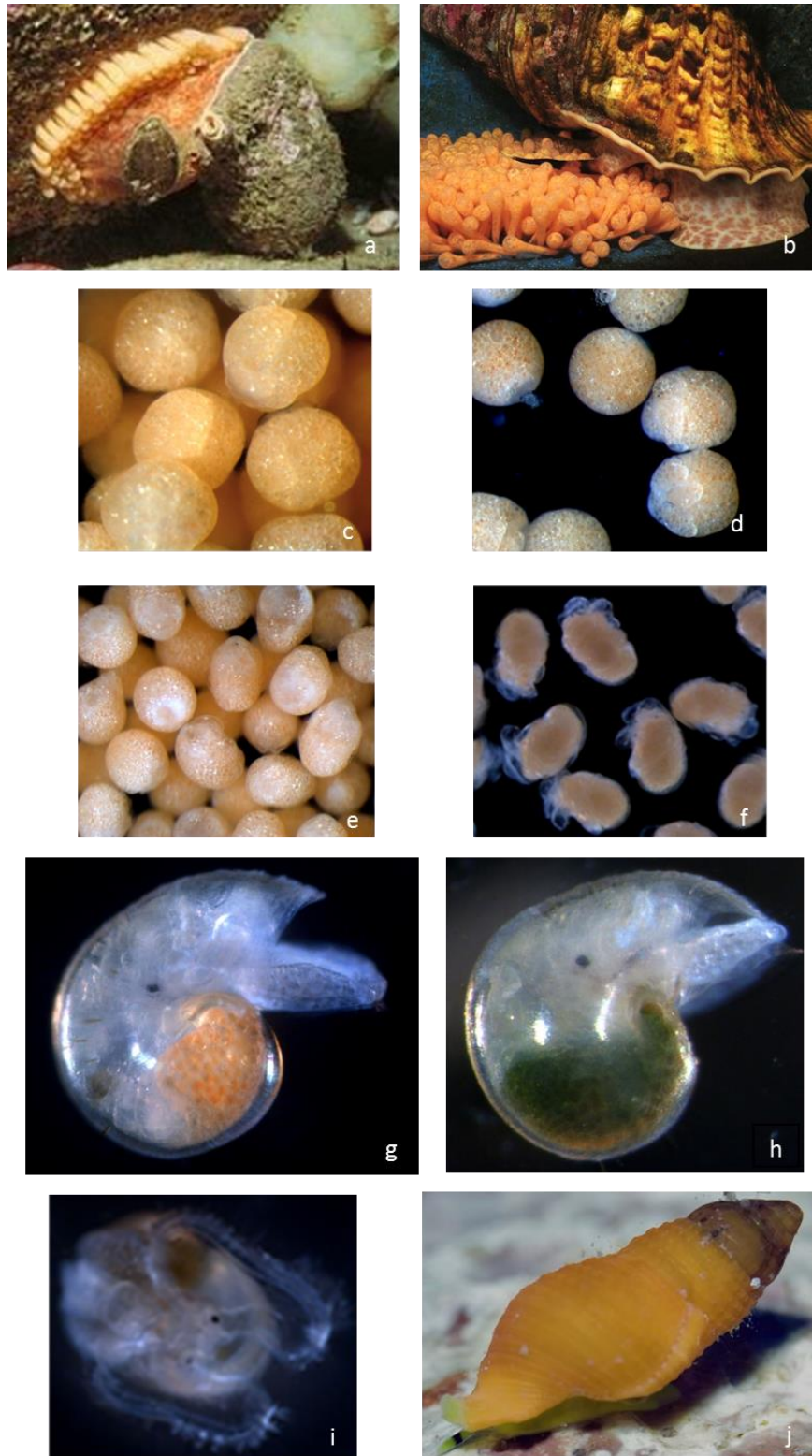
Figure 3: Growth and development of early life history stages of the giant triton, *Charonia tritonis.* Triton egg laying capsules *in situ* (a) and in the SeaSim laboratory at AIMS (b). Development of embryo within the egg capsule at day 3 (c), 8 (d), 12 (e) and 22 (f). Development of veligers post-hatching at day 56, showing empty guts with yolk reserves (g), gut filled with phytoplankton (h), and velum extended (i). Newly settled juvenile of *Charonis lampas* (j) (Photo: Everett Turner).
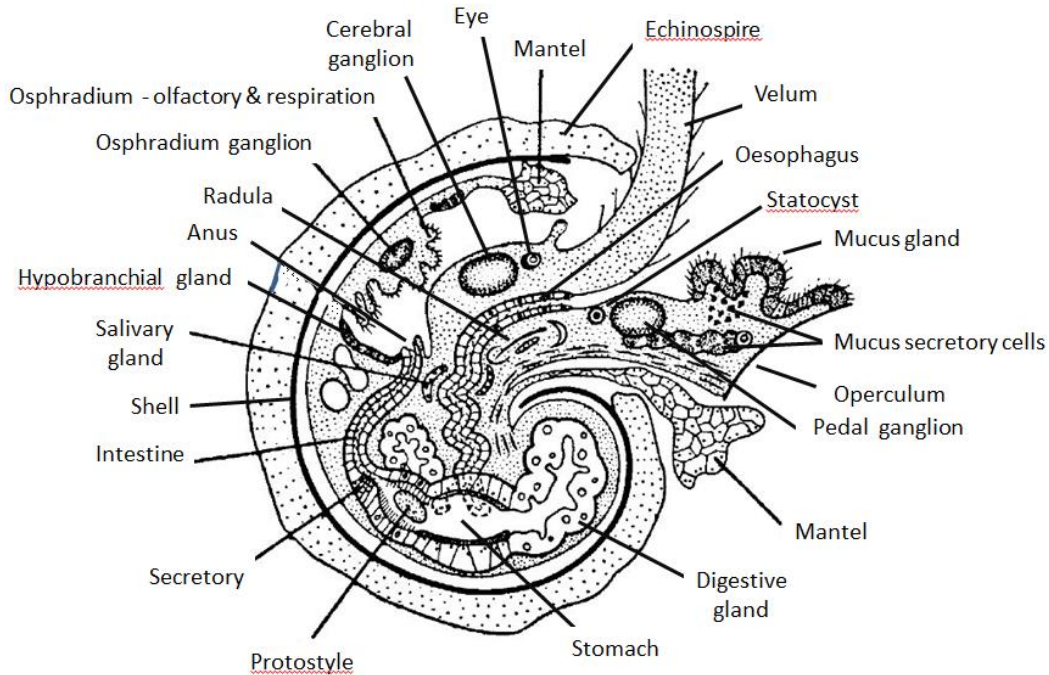
Figure 4: Schematic of primary anatomy of gastropod veliver. Adapted from Rodriguez-Babio and Thiriot-Quievreux (1974).

Shell biomineralization and growth in *Charonia* spp. larvae can be defined in terms of shell structure before and after metamorphosis. The protoconch, which consists of the first whorls of the apex of the shell, occurs in two stages: protoconch I which forms within the egg capsule before hatching, with typically less than two whorls, and protoconch II, which forms after hatching but before metamorphosis and typically consists of 2 to 3 whorls (Richter 1984; Waren & Bouchet 1990). After metamorphosis, the mantle edges of the growing snail form yet more whorls producing the teleconch (Lima & Lutz 1990; Ruppert *et al.* 2003). As there have been no reports of completing the larval cycle of *Charonia spp.* the only insights available are those from descriptions of veligers of the Ranellidae collected in plankton tows (Figure 6).

The shell length of newly hatched larvae of *C. lampas* measures 430 µm whereas those of *C. variegata* are between 770-930 µm (Berg 1971; Cazaux 1972). In the Atlantic, specimens of *C. variegata* from plankton tows have shells exceeding 5,000 µm in length when fully developed (Scheltema 1971b). In captivity, *C. tritonis* larval shell length progressively increases over time at least up to 2,000 µm but never metamorphosed or settled (Nugranad *et al.* 2001). Zhang *et al.* (2013) maintained veligers for over 140 days in larval rearing systems without metamorphosis; similarly, Nugranad *et al.* (2000) kept veliger for 300 days. To date there have been no reports of successfully advancing *C. tritonis* larvae through to settlement.
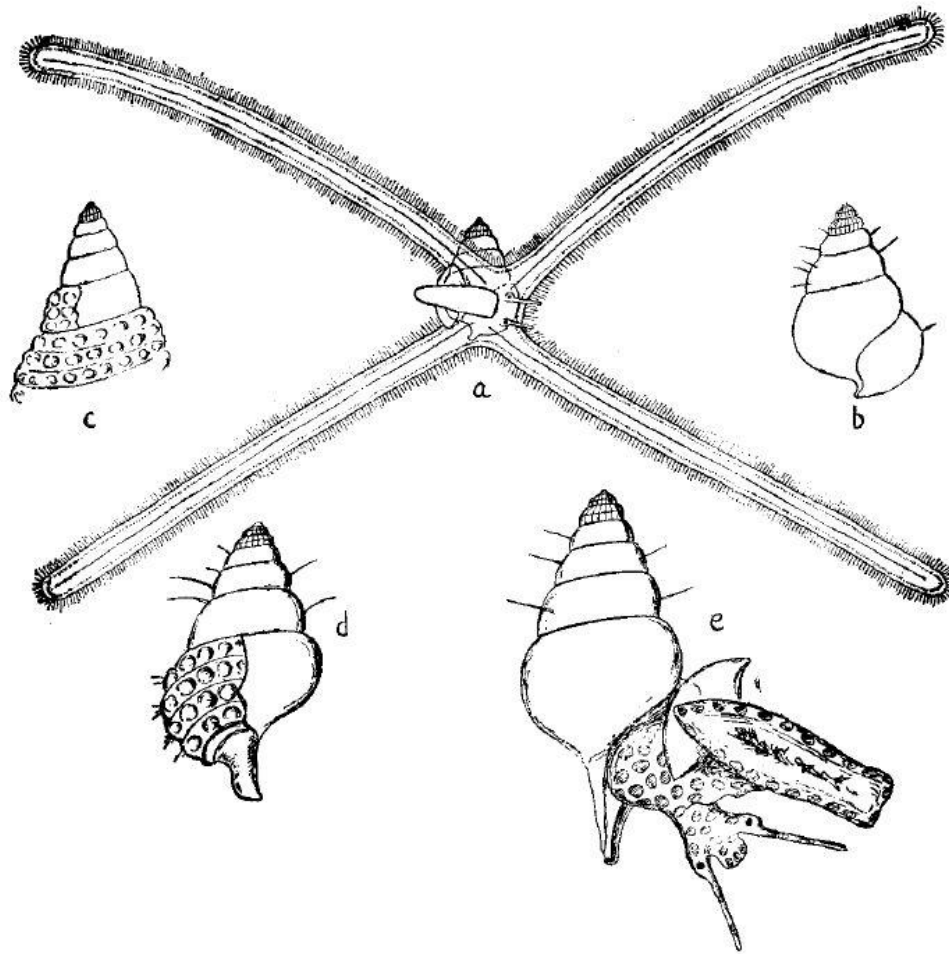
Figure 5: Veliger larvae of *Cymatium chlorostomum* from Bermuda showing the extreme extension of velum in teleplanic form. (a) Veliger, 3.5 mm long, (b) veliger shell, 4 mm long, (c,d,e) metamorphosed shell from veliger, 4.5 mm long ([Lebour 1945](#)).
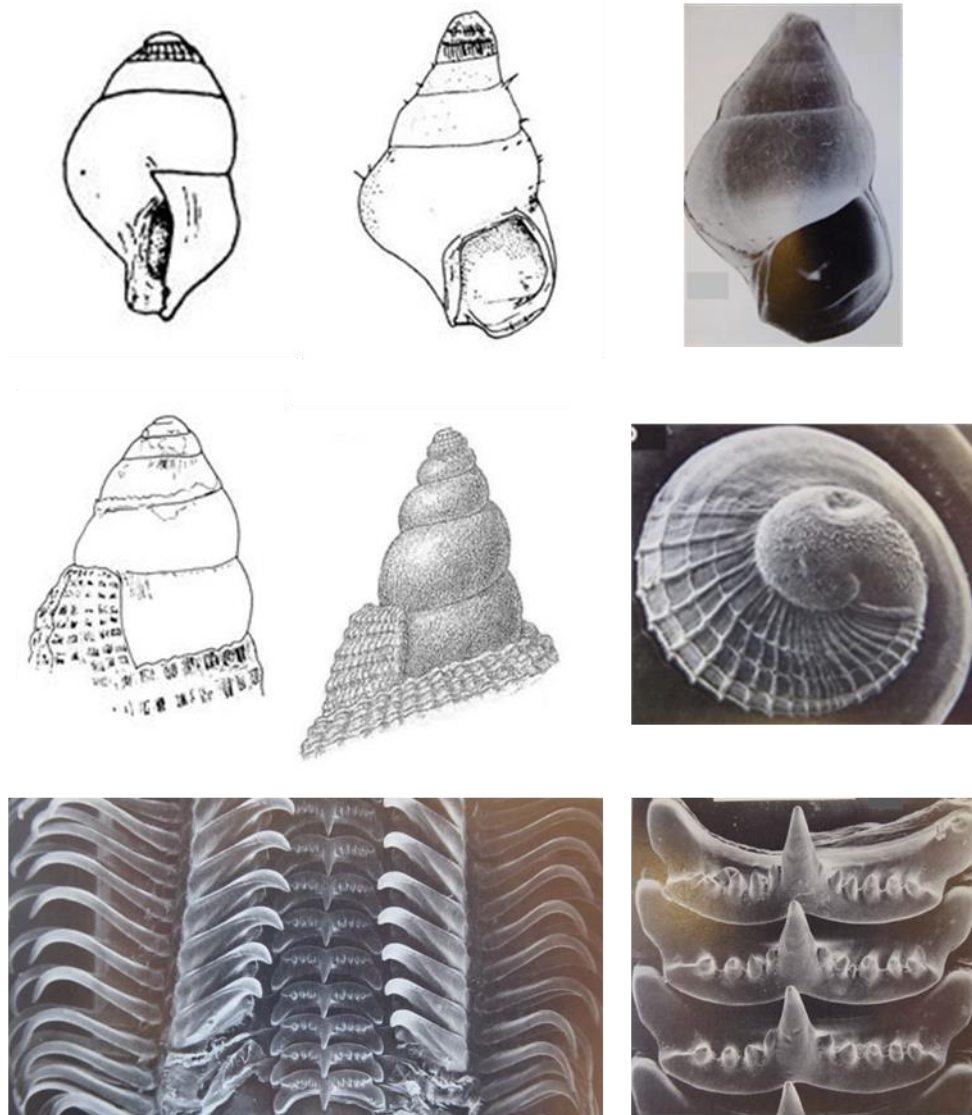
Figure 6: Growth and development of protoconchs and larval radula of the Ranellidae collected in plankton tows. Veliger larval shell of *Charonia variegata* (upper left), late veliger larvae of *Cymatium nicobaricum* (upper middle), late veliger larvae of *Charonia sp.* (upper right), protoconch of *C. variegata* (middle left), protoconch of *Cymatium intermedium* (middle middle) and dorsal view of protoconch as part of post-metamorphic *Cymatium sp.* larva. (middle right). Radula of larval *C. lampas* (bottom panels). From (Scheltema 1971a; Beu & Kay 1988; Waren & Bouchet 1990).

An obligatory larval developmental period is likely before veligers are competent and capable of metamorphosis and settlement, but even after this period they are capable of remaining in the plankton for months presumably until they encounter a suitable settlement cue (Scheltema 1986; Hadfield *et al.* 2001; Dalesman *et al.* 2006; Lesoway & Page 2008; Page 2009; Martel *et al.* 2014). It is generally considered that the larvae are not competent until the protoconch II phase with metamorphosis being defined as the loss of the veliger velum (Pechenik 1980; Riedel 1992). Factors which induce metamorphosis and settlement in larvae of the Ranellidae are largely unknown. It is likely that attainment of competency to achieve metamorphosis may involve factors such as minimum body size, sufficient energy reserves and the development of specific receptors or neural connections (Hadfield 1978; Hadfield & Strathmann 1996). Some teleplanic larvae, typically in late development stage, of *Cymatium* species captured in plankton tows have metamorphosed and settled in aquaria, perhaps in response to signals

emanating from biofilms within the high surface area-to-volume ratio of the tanks (Lebour 1945; Scheltema 1971a). High density mono-culture aquaculture of various molluscan bivalves, i.e. oysters, clams, scallops, etc., experience high larval settlement when presented with various substrates and chemical cues (Table 4). There is indirect evidence that veligers of carnivorous Ranellidae gastropods will settle in the presence of their adult prey, for example in *Cymatium* larvae will settle out of the plankton if they detect tridacnid clams on which adults feed (Govan 1995). Some gastropods are ecto-parasites and it has been reported that unidentified newly settled gastropods, speculated to be those of *C. tritonis*, might first settle and parasitize starfish, especially Echinasteridae, i.e. *Echinaster lozonicus* and Ophidiasteroidea, i.e. *Linckia multifora*, before preying on whole starfish (Paterson 1990). Overall indirect evidence suggests that the veligers of Ranellidae gastropods use the scent of their prey as a settlement cue (Heslinga *et al.* 1986).

Aspects of post-settlement, including growth rates, are known for some gastropods. In recently settled juvenile *Hemifusus tuba* (Buccinoidea:Melongenidae) growth rates have been estimated at 0.33 mm (shell length) day^{-1}, for *Cabestana spengleri* (Tonnoidea: Ranellidae) at 0.3 mm day^{-1} and for *C. muricinum* at 0.3-0.4 mm day^{-1} (Laxton 1970b; Perron *et al.* 1985). However, growth rates of juveniles from species in the families Naticidae, Muricidae, Columbellida and Mitridae were found to be only 0.02-0.07 mm day^{-1}. In contrast, growth of recently settled juvenile *Cymatium muricinum, C. aquatile* and *C. pileare* (Ranellidae: Cymatiinae) have been reported to be exceptionally high averaging 0.6-0.7 mm day^{-1} over 3 to 6 weeks of growth with some individuals reaching rates of 08.-0.9 mm day^{-1} (Govan 1995). Such growth rates allow these tritons, with abundant food supply, to reach the size of first varix formation from settlement within 33 days for *C. muricinum* and between 50-57 days for *C. aquatile* and *C. pileare* (Govan 1995). The formation of the varix and calcification increases the snail's size and strength such that vulnerability to predators is reduced (Vermeij & Signor 1992).

Table 4: Inducers of metamorphosis and settlement for gastropod veliger larvae.

Species	Compound	Solution/Dose/Time/ % metamorphosis	Reference
Concholepas concholepas	Adult conspecific shells covered in barnacles	Up to 4 to 5 days, 100%	Manríquez *et al.* (2004)
Crepidula fornicata	20 mM KCl	50% settlement after 30-50 mins	Cahill and Koury (2016)
	Adult conspecific conditioned water	40% settlement after 50 mins	Cahill and Koury (2016)
	Conspecific pedal mucus	25% settlement after 50 mins	Cahill and Koury (2016)
	Raise KCl to 20mM	55%, Highest settlement in those fed Isochrysis (400,000 cells/larva/day)	Padilla *et al.* (2014)
	Elevated KCl above background by 15-20 mM	50% within 4 hours	Pechenik and Heyman (1987)
	Tested serotonin, dopamine and FMRFamide (10^{-5}M/L)	Measured whether larvae go up (serotonin) or down (dopamine, FMRFamide) in the water column	Penniman *et al.* (2013)

	Dibromomethane (DBM)	90 – 100% metamorphosis at 5000 ppm, combined DBM and KCl	Taris *et al.* (2010)
	Red algae extract, ☐-aminobutyric acid (GABA), Hydrogen peroxide	70-95% metamorphosis	Boettcher *et al.* (1997); Boettcher and Targett (1998)
Strombus gigas	Nursery habitat sediment, KCl		Davis *et al.* (1990); Cob *et al.* (2010)
	Hydrogen peroxide (H_2O_2)	100% at 10 hrs in 50µM H_2O_2	Boettcher *et al.* (1997)
	Extract of *Laurencia poitei;* Phycoerythrins and related protein conjugants	88% metamorphosis	Siddall (1983); Davis *et al.* (1990); Davis and Stoner (1994)
	Bromomethane	90% at 600 ppm	Kang and Kim (2004)
Haliotis discus hannai, Haliotis rufescens Haliotis diversicolor, Haliotis asinine	conc KCl in normal seawater 9 mM	40% at 19 mM KCl	Kang and Kim (2004)
	1 x 10^{-6} M (final) GABA	37% - 99%	Searcy-Bernal and Anguiano-Beltrán (1998)
	Whole *Ulva australis* and *U. compressa* and *Amphiroa anceps* and *Corallina officinalis*	0.05 - 0.1 g wet wt algae or 1 cm^2 of 95% cover rock (CCA) added to 5 mL wells in 4 mL of seawater. CCA best (80%)	Huggett *et al.* (2005)
	Supplemented KCl	50% in 5 – 10 mM KCl (supplemented)	Li *et al.* (2006)
	GABA	40% 10^{-6} M GABA	Li *et al.* (2006)
	KCl, GABA	>40% 20mM KCl , >75% 10^{-6} M GABA	Bryan and Qian (1998)
	Biogenic amines	% metamorphosis at 10^{-6}M of GABA (98%), L-glutamate (80%), L-glutamine (0%), ☐-alanine (16-68%)	Morse (1990)
	10^{-3}, 10^{-4}, 10^{-5}, 10^{-6} M GABA	10^{-6} M GABA at 2 days, 73%	Sawatpeera *et al.* (2004)
	5 spp. Benthic diatoms (*Navicula* spp and *Nitzschia* spp.)	If fed 5 spp, at 2 days 90 – 94%	Sawatpeera *et al.* (2004)
Phestilla sibogae	Catecholamine precursor L-3,4-dihydroxyphenylalanine (L-DOPA)	20-50-fold increase in dopamine and 2-fold increase in norepinephrine production in 6-9-day larvae, treated with L-DOPA (0.01 mM for 0.5 h) potentiated the frequency of metamorphosis	Pires *et al.* (2000)

4.5 Courtship and Mating

Pairing and copulation have been described in several species of Ranellidae including *C. variegata* (Percharde 1972). Aspects of reproduction in *C. tritonis,* including copulation, spawning, embryogenesis and hatching, have also been described (Berg 1971; Nugranad *et al.* 2001; Cañete *et al.* 2012). Recently a detailed description of reproduction, embryogenesis and early larval development was presented based on a study at the South China Sea Institute of Oceanology, Yongxing Island, China (Zhang *et al.* 2013). From a stock population of eight *C. tritonis* adults, two of which were female, copulation occurred in August through to September with egg laying some 130 days later between December and January. Although this delay is similar to other northern Pacific species within the Ranellidae (Strathmann 1987), it is in sharp contrast to the 30-60 and 90 days reported in studies by reported by Nugranad *et al.* (2001) and Berg (1971), respectively. Whereas females mated with several males during the spawning season there was no evidence of flock (or group) mating, as has been reported in the predatory rock snails, *Thais chocolata* (Muricoidea) (Romero *et al.* 2004). Pairing is typically with the male mounted on the shell of a female with the apertures of the shells adjacent for copulation. There can be rivalry between males during mating. A single female can pair with a single male or with multiple males during copulation. Pairing can last up to a few hours (Zhang *et al.* 2013). No seasonality in reproduction in *C. tritonis* held in captivity over two years was reported in studies at the Phuket Marine Biological Station, Thailand (Nugranad *et al.* 2000; Nugranad *et al.* 2001). The spawning season may not be related to photoperiod as several species of Cymatiinae held in captivity, without controlled lighting, spawned precisely at the same time over a three year period (Laxton 1969). It has been suggested that water temperature is a primary determinate in spawning (Thorson 1950).

4.6 Reproduction

Although little is understood about the reproduction processes specific to *Charonia tritonis*, insights into this aspect of their biology can be garnered from other species within the genus. One of the major innovations in the Caenogastropoda was internal fertilization enabling the production of encapsulated eggs providing a protected environment during the early development phase of larvae (veliger). Sexes within the Ranellidae are always separate; the sperm is transferred through copulation with fertilization taking place internally in the female (Webber 1977; Kilburn & Rippey 1982). The male reproductive system has been described by Laxton (1969). In the male, the testis of mature animals occupies the upper side of the visceral whorls. The vas deferens is extensively coiled and is separated from the glandular pallial genital duct by a sphincter and from there the vas deferens passes beneath the pericardium and along the columella side of the mantle cavity to the prostate. The prostate is a closed ciliated tube with subepithelial glands opening into a lumen. The lumen in turn leads to an open ciliated groove that extends out of the mantle cavity to the head of the penis located just behind the right tentacle. The testis, as well as the ovary, may degenerate in *Charonia* after the breeding season (Laxton 1969).

The female reproductive system is divided functionally into two parts. The first part is the sperm storage system comprised of the bursa copulatrix and the receptaculum seminis which lie at opposite ends of the pallial section (Laxton 1969). The bursa is a muscular compartment lined with several layers of epithelium cells which can dilate to accept the penis of a male into which sperm and prostatic fluid is discharged. The sperm in the bursa is transferred for permanent

storage to the receptaculum seminis via a central non-ciliated channel which runs between the two tissues. The receptaculum seminis is a tubular organ connected to the proximal end of the pallial oviduct through a narrow duct. The duct is a single layer of cubical ciliated and non-ciliated cells with the heads of the stored sperm cells embedded in the surface of the non-ciliated cells from which they likely obtain nutrients (Laxton 1969). The second part of the female reproductive system is responsible for the formation and protection of the eggs. Mature eggs are discharged into the lumen of ovarian follicles within a thin renal oviduct and then flows to the pallial oviduct. The pallial oviduct secretes an albuminous fluid embedding the eggs which are then deposited into capsules. The oblong tear-dropped shaped capsules (oothecae) themselves are clear thin-walled gelatinous vessels. Eventually each individual capsule passes from the oviduct to the posterior pedal gland with one end cemented to a rocky surface. Exposure to seawater hardens the outside layer of the capsule protecting the eggs from pathogens and predation.

Egg laying usually occurs at night with egg capsules normally clustered together, typically cemented to vertical surfaces, i.e. underneath overhangs and in crevasses (Percharde 1972; Nugranad *et al.* 2000; Nugranad *et al.* 2001). Copulation in New Zealand *C. lampas* is first observed in July with eggs being laid in August to September (Laxton 1969). The egg mass of over 100 oothecae, which contains a total of 200,000 to 250,000 eggs, may take a female over a week to deposit (Laxton 1969; Cazaux 1972). The eggs incubate within the capsule for two months before emerging as planktrophic larvae through a terminal pore of the capsule (Laxton 1969). In the Caribbean, nocturnal egg laying in *C. variegata* is first observed in May approaching the summer solstice photoperiod and coinciding with the wet season (Percharde 1972). Conversely, captive *C. tritonis* females from the GBR have been observed laying between 2-50 egg capsules per day and up to 1,000 capsules between April and June, leading up to the winter solstice photoperid and coinciding with the dry season (Hall 2017 pers. Comm.). *C. tritonis* egg capsules are clear and approximately 34-60 mm long and 9-10 mm in diameter, with each containing between 2,000 – 2,750 orange-coloured eggs (Hall pers. comms. 2017) (Table 5).

Table 5: Reproductive statistics for *C. tritonis* reported in published studies from captivity breeding programs.

	Berg (1971)	Nugranad *et al.* (2001)	Zhang *et al.* (2013)
Location	Oahu, Hawaii, USA	Phuket,Thailand	Yongxing Island, China
Number of females	1	5	2
Date of reproductive behaviour	Oct	Year round	Aug – Sept
Copulation until laying (days)	120 - 150	30-60	133
Duration of spawning (days)	-	60	21 - 35
Total capsules spawned/female	88	500 - 1,000	549 - 602
Egg diameter (µm)	450 - 600	360 – 440	428
Capsule dimensions, HxL, (mm)	25 x 9	17 - 39 x 9 - 10	34 x 9
Number of eggs per capsule	-	2,000 – 4,400	2,740 – 3,000

Total number of eggs produced	-	$1.6 \times 10^6 – 3.2 \times 10^6$	$1.5 \times 10^6 – 1.6 \times 10^6$
Incubation period (days)	49-56	35 - 60	55 - 63
Hatching success of capsules	-	43 – 96%	86 – 96%
Veligers per capsule	1,140 – 1,447	973 – 1,459	2,046 – 2,110
Total veligers produced/female	-	$0.26 \times 10^6 – 1.47 \times 10^6$	$1.12 \times 10^6 – 1.27 \times 10^6$
Shell length at hatching (µm)	768 - 934	720 – 925	664 - 700
Settlement	None at 30 days	None at 300 days	None at 140 days

Fertilized *C. tritonis* eggs are either round or elliptical in shape, ranging from 360 - 600 µm in diameter (Table 5), and heavily yolked with yellow to red pigmentation (Figure 3). All eggs have an equal chance to undergo embryogenesis but there are no nurse cells as seen in some other molluscs (Laxton 1969). Embryogenesis up to a late larval (veliger stage) occurs within the egg capsule before hatching. Incubation of embryos within the oothecae varies but has been reported to be in the order of 35 to over 60 days (Berg 1971; Nugranad *et al.* 2001; Zhang *et al.* 2013). *C. tritonis* embryos gastrulate at approximately 7 days at 24°C with trochophore development occurring between day 9 – 12 followed by protoconch (or embryonic shell) formation between day 15-18 (Zhang *et al.* 2013). During the first stage of protoconch development, typified by the first whorls of the apex of the shell, the capsules become white and granular. Eyespots develop at day 25; operculum and foot formation starts at day 29 and larval heart beating can be detected at day 40. Larval development is temperature dependent; after up to 63 days of incubation at 24°C veligers emerge from the capsules having a shell length of between 664-934 µm. Even though veliger maintained for up to 300 days in aquaria shed their vela cilia, development did not proceed, with the left tentacle still absent (Nugranad *et al.* 2001).

Within a single spawning season females of *C. tritonis* may produce a total of 0.26 - 1.47 x 10^6 veligers from all the capsules (Table 5). With such fecundity, assuming this holds for females breeding in the wild, it begs the question why *C. tritonis* should be so rare on reefs. Potentially, larvae and juvenile survival is extremely low and/or their dispersal is so great that settlement on any one reef is rare (Shuto 1974). Some families of gastropods have full development of larvae within an egg capsule with no free-living larval stage, i.e. Buccinioidea and Volutidae. The relative population densities of species of adult gastropods on coral reefs which have planktonic larval development, *i.e.* Cypraeidae (pelagic phase 10 – 50 days), compared to those with direct development within an egg capsule (pelagic phase 0 days), i.e. Volutidae, has been reported to be in the region of 1:10 (Bouchet et al. 2002).

Rearing of *C. tritonis* has so far been unsuccessful due in part to a lack of understanding in the basic rearing requirements of the larvae, and to the limited information regarding the biochemical and physiological processes that regulate reproduction, larval development and growth. *De novo* transcriptome sequencing of a cerebral ganglion of *C. tritonis* identified a repertoire of 38 neuropeptide precursor genes that encode for conserved molluscan neuropeptides, including several associated with mollusc reproduction: APGWamide,

buccalin, conopressin, gonadotropin-releasing hormone, neuropeptide KY and egg-laying hormone ([Bose *et al.* 2017a](#)). Other neuropeptide genes annotated include achatin, allototropin, conopressin, FMRFamide, LFRFamide, LRFNVamide, myomodulin, PKYMDT, sCAPamide and insulin-like peptides. Further transcriptomic and genomic studies targeting the functional characterisation of these neuropeptides to elucidate the reproductive neuroendocrine pathway in *C. tritonis*, as well as those involved in larval development and growth, could lead to the development of reliable aquaculture methods ([Mazurais *et al.* 2011](#); [Li *et al.* 2016](#); [Song *et al.* 2016](#)).

4.7 Parental Care

Throughout the incubation period of the egg capsules the female exhibits maternal care protecting them from predation ([Laxton 1969](#); [D'Asaro 1970](#); [Latigan 1976](#); [Riedel 1992](#)) and cleaning them every 3-5 days with their large foot to prevent biofouling ([Zhang *et al.* 2013](#); [Motti pers. comms. 2017](#)). Females do not feed during egg laying or whilst exhibiting maternal care. Other females in the vicinity may also protect the clutch of egg capsules and display maternal care ([Laxton 1969](#)).

4.8 Foraging, diet and nutrition

The Ranellidae are carnivorous mesogastropods with various species specialist predators on polychaetes, ascidians, bivalves, gastropods, crustaceans and echinoderms ([Houbrick & Fretter 1969](#); [Morton 1990](#)). Ranellidae primarily feed at night but starved individuals will feed at any time of the day including on carrion ([Houbrick & Fretter 1969](#); [Govan 1995](#)). These gastropods differ from grazers in the development of a siphonal canal in the anterior lip of the shell which receives a fold of the pallial mantle margin that directs inhalant water current to a highly developed ospharium used in chemoreception of prey odours ([Hughes 1986](#)). There are also modifications of the long pleurembolic proboscis, for insertion into prey, and associated glands which discharge toxins and acidic pH 2.0 saliva ([Morton 1990](#); [Littlewood 1991](#)). Attacks on prey can range from almost instant immobilisation and death to parasitism, especially if the prey is much larger than the snail itself, such as *Cymatium* spp. preying on tridacnid clams ([Govan 1995](#)).

When hunting, giant tritons initially move randomly with tentacles being swept from side to side then upon detection of prey odour sweeping of tentacles intensifies, their velocity increases and movement becomes directional ([Percharde 1972](#)). In close proximity the large proboscis is extended to make contact with the prey and then injects either a toxin or acid saliva which rapidly causes paralysis ([Percharde 1972](#)). The giant triton is then able to hold its prey firmly by its large foot and completely envelopes the prey in thick mucus. In case of predation on CoTS, this mucus may prevent toxic saponins, present on the surface of CoTS and released into the water column, from entering the hypobranchial chamber where they would damage the delicate filaments of the monopectinate ctenidium ([Bose *et al.* 2017b](#)).

In general, prey preference is explained in terms of random encounter rates and capture success, with derivations from this indicative of selective predation. In New Zealand *Charonia rubinrnda* preys upon the most abundant echinoderm within the habitat but if offered a choice prefers the asteroids *Patiriella regularis* and *Coscinasterias calamaria* ([Laxton 1971](#)). For several species of *Cymatium* the preferred prey includes tridacnid clams and in particular

Tridacna gigas (Govan 1995). Based on available evidence many gastropods do make behavioural diet selections as simple encounter rates fail to account for prey selection (Broom 1983; Reichelt & Kohn 1985; Hughes 1986). Part of this may be explained by the well-developed chemosensory abilities of the Ranellidae snails which may direct tracking of specific prey. For example, when the echinoderm predatory snail *Cassis tuberosa* was presented with equal numbers of similar size *Echinometra lucunter* and *Tripneustes ventricosus* (both seastars), significantly more *E. lucunter* were eaten and when presented with four other species of urchins (*Diadema antillarum*, *Eucidaris tribuloides*, *Meoma ventricosus* and *Mellita quinquiesperforata*) none were eaten (Hughes & Hughes 1971). Under controlled experimental conditions, *Charonia rubicunda* responds to prey items placed in an upstream current but not to those in static conditions (Laxton 1971). More recently, Y-maze aquarium experiments have shown that water-borne factors released by CoTS attract the giant triton (Hall *et al.* 2016). It should be noted that in the wild predators have access to a vast diversity of potential prey items, while in controlled feeding preference experiments predators are presented with a limited selection and may well be impacted by 'ingestive conditioning'. Even though extrapolation of such results to the natural environment is fraught with ambiguity (Jory *et al.* 1984; Hughes 1986; Gutiérrez & Gallardo 1999) switching in predators can occur, whereby the number of attacks upon and the percentage prey mortality of a species is disproportionately large when the species is abundant relative to other prey and disproportionately small when the species is relatively rare (Murdoch 1969). It is not known whether this phenomenon influences feeding preferences of *C. tritonis in situ*.

For the genus *Charonia* the natural diet is reported to be primarily starfish, then sea cucumbers and, to a lesser extent, sea urchins (Laxton 1971; Percharde 1972; Russo *et al.* 1990; Doxa *et al.* 2006). *Charonia lampas* has been observed feeding on the holothurian *Holothuria forshali* and the echinoid *Paracentrotus lividus* in shallow rocky environments at depths of 0 to 27 metres in the Mediterranean (Kisch 1952). Kisch (1949) suggested that the distribution of *C. lampas* is at least partially controlled by the distribution of its prey and is often found in high numbers in areas where its prey aggregates. In New Zealand, *C. lampas* preys upon the most common large echinoderm in the area with a preference for the cushion star (*Patiriella regularis*) compared to *Coscinasterias clamaria* (Laxton 1971). Under controlled aquarium conditions *C. lampas* was presented with 15 different species including starfish (*Astropecten aranciacus, Marthasterias glacialis* and *Luidia sarsi*), sea urchins (*Arbacia lixula* and *Paracentrotus lividus*), sea cucumber (*Holothuria forskali*), finfish (*Boops boops, Merluccius merluccius* and *Sardina pilchardus*), molluscs (*Sepia officinalis, Octopus vulgaris, Notodarus sloanii* and *Mytilus chilensis*) and crustaceans (*Parapenaeus longirostris* and *Nephrops norvegicus*) (Doxa *et al.* 2012). Preferential predation was in the order of starfish > sea cucumber > fish > crustacea and then the various other species. In Korea, *C. lampas* (Noseworthy *et al.* 2007) held in aquaria and presented with a range of potential prey, including starfish (*Asterina pectinifera* and *Asterias amurensis*), molluscs (*Haliotis discus hannai, Anadara broughtonii* and *Tapes phillipairum*) and sea urchins (*Hemicentrotus pulcherrimus* and *Anthocidaris crassispina*) exhibited preferential predation on starfish > sea cucumber > sea urchin (Kang & Kim 2004). These authors concluded that *C. lampas* could be a means of biological control of predators of economically important shellfish. In the Mediterranean a group of 32 *C. sequenzae* (*C. lampas sequenzae*) was presented with starfish (*Astropecten aranciacus* and *Luidia sarcii*), mollusc (*Nototodarus sloanii*), crustacea (*Parapenaeus longirostris*) and finfish (*Boops boops*) (Doxa *et al.* 2013). Consumption rate (in wet weight per day) was: starfish 24.0 g (range 19.5-53.7 g), fish 11.4 g, crustacea 9.5 g and mollusc 7.4 g.In

the Caribbean *C. variegata* is considered one of the most active and voracious gastropod predators ([Percharde 1972](#)). Although the primary dietary items of *C. variegata* are echinoderms, including asteroids (*Echinaster sentus*), sea cucumbers (*Synapta sp., Cucumaria sp.*) and sea urchins (*Eucidaris tribuloides, Tripneustes sp.*), they will also consume various molluscs (*Laevicardium laevigatum, Chione cancellata, Fasciolaria tulipa and Cypraea zebra*) as well as crustaceans (*Panulirus argus* and *Panulirus guttatus*) ([Percharde 1972](#)). In the Caribbean it is purported to play an important role in the ecological balance of the extensive areas of its habitat ([Percharde 1972](#)).

The feeding preferences of *C. tritonis* have been investigated in the laboratory, but the preferred prey species appears to vary. In a 2 year feeding study of a single captive adult *C. tritonis* the animal was presented with starfish (*A. planci*, *Culcita novaeguineae* and *Echinaster*), sea urchin (*Diadema setosum*) and sea cucumbers (*Holothuria atra* and *Stichopus chloronotus*) ([Nugranad *et al.* 2000](#)). *A. planci* were the most preferred prey item whereas *C. novaeguineae* were only partially consumed, and although *H. atra* and *S. choloronotus* were readily consumed it was reported that these were unfavourable to the giant triton, the snail showing symptoms of anesthesia post feeding ([Nugranad *et al.* 2000](#)). When equal numbers of CoTS and *Linckia* were added to a tank containing C. tritonis, each CoTS was attacked and comsumed entirely within 12 hours of being introduced while some *Linckia* were always present, suggesting a preference for CoTS ([Paterson & Poulsen 1988](#)). An entire hunt, attack and consumption of an adult COTS by *C. tritonis*, fed solely on *A. planci*, could be completed within 4 h ([Bose *et al.* 2017b](#)). In a research project to breed *C. tritonis* in captivity, eight broodstock snails were fed solely on *A. planci* or *Stichopus horrens* ([Zhang *et al.* 2013](#)). In another reproductive study, the single giant triton broodstock was maintained on a diet of individual species of starfish (*A. planci* or *C. novaeguineae*) and sea cucumbers (*H. atra* and *S. chloronotus*) ([Nugranad *et al.* 2001](#)). Giant triton hunting behaviour and consumption, which occurred primarily at night, was initiated 83% of the time for *A. planci* (CoTS), 57% of the time for *C. novaeguineae* and 24% of the time for *H. atra* and *S. chloronotus.* Only *A. planci* (CoTS) were fully consumed whereas the other species were only partially or very slowly consumed ([Nugranad *et al.* 2001](#)).

COTS exhibit a strong predator avoidance reaction when one of its sensory tentacles comes into direct physical contact with the body of *C. tritonis* ([Paterson & Poulsen 1988](#)). In aquaria and y-maze assays naïve COTS display a rapid and adverse reaction to seawater conditioned with *C. tritonis*; COTS will actively move away from *C. tritonis* odour ([Hall *et al.* 2017](#)). This well developed chemosensory-driven escape response suggests that the starfish is the prey preference of *C. tritonis*, at least on the Great Barrier Reef. These results also support earlier observations that on infested/outbreak reefs, COTS are the predominant prey of *C. tritonis* ([Endean 1969](#)).

Consumption rate for giant tritons is largely unknown but in one *in situ* experiment on the GBR [Endean (1969)](#) found that over a period of three months (time of year not specified) in a 9 x 12 x 1 m fenced enclosure on a sandy/gravel bottom containing 15 adult giant tritons and 100 adult CoTS the giant tritons consumed 1.5 CoTS per week ([Endean 1969](#)). He surmised that a single giant triton would be capable of consuming more smaller-sized immature specimens of CoTS. In another study, two giant tritons (25 and 31 cm shell length) were observed to consume ten small and three large CoTS per month ([Birkeland 1989a](#), [b](#)) while [Kang and Kim (2004)](#) found that *Charonia sp.* (mean wet weight 751 g) consumed 319 g of the starfish

Asterina pectinifera and 334 g of *Asterina amurensis* over a 30 day period. Of 28 *C. tritonis* collected from the northern and central sections of the GBR between 1966-1968, seven had recently fed on CoTS, twelve on other species of starfish – only one of these was taken from a reef infested with CoTS - and nine were starved (Endean 1969). In a separate study, five *C. tritonis* specimens of 24 encountered during visits to 81 GBR reefs in the early 1970's were observed feeding on large juvenile CoTS (18-30 cm) (Endean & Stablum 1973). Endean (1969) reported that starfish of the genus *Nardoa* were preferred over CoTS but as infested reefs had more CoTS then giant tritons would presumably consume whichever starfish were first encountered although, caged *C. tritonis* were observed to preferentially feed on other starfish if given a choice (Pearson & Endean 1969). *C. tritonis* has also been observed to prey on the starfish *Linckia laevigata* and the sea cucumber *Stichopus sp.* (Laxton 1971). For juvenile *Cymatium* under 10 mm shell length, the relative rate of prey consumption is extremely high, being estimated at 100-250% of their body weight per day, whereas *C. muricinum* individuals of 18 mm consume approximately 30-40% of their total weight per day while *C. pileare* and *C. aquatile* average 60-90% and 50% of their total weight per day, respectively (Govan 1995). In contrast, adults of these same species have daily rates of consumption of 2-7% (mean 4-5%) of total wet weight (Govan 1995). These estimates are within the range observed by Morton (1990) for gastropod predators of bivalves, being 1-6% of their body weight per day under optimal feeding conditions. Consumption rates of several species of juvenile *Cymatium* have been determined in captivity, and although they fluctuate widely from week to week, they average between 16% and 47% of total gastropod weight (Govan 1995). In contrast, little is known about the dietary requirements of *C. tritonis* veliger or juveniles. However, preliminary aquaria-based feeding experiments indicate that veliger will consume mixed microalgae, copepod nauplii and adults, artemia nauplii and adult rotifers (Motti pers. comms. 2017).

4.9 Predators, parasites and threats

Little is known of the predators of *Charonia* from newly settled miniscule juveniles through to large adults. Groups of moribund and dead *C. variegata* have been observed in the Caribbean which had their opercula next to their shells but no indication of what was the cause of death although it was suggested the predator may have been *Octopus sp.* (Percharde 1972). In the Caribbean crushed triton shells have been found indicative of predation by rays (*Aetobatus* sp.) as well as Loggerhead (*Caretta caretta*) and Hawksbill (*Eretmochelys imbricate*) turtles (Percharde 1972). Although giant tritons are the largest of the marine snails they all exhibit sheltering during daylight hours under ledges or in caves and only venture out during nocturnal feeding events which likely indicates anti-predation behaviour.

Species within the genus *Charonia* have been, and in some instances are still being, harvested throughout their range. While they are collected for food consumption and for traditional and cultural uses in some communities it is their shells that are particularly sought after as a decorative object by collectors (Poulsen 1995). Historically, the giant triton shell has traditional and cultural significance to many cultures where it is used as a signalling trumpet-like instrument in religious and military situations.

The shell is a popular item in the international shell trade and over the past few decades the greatest pressure on giant triton populations has been due to collection for their highly attractive and large shell described 'as the most beautiful among large shells' (Abbott 1973;

Wells & Barzdo 1991; CITES 1994). Throughout their range giant tritons are listed as uncommon, rare or with seriously depleted populations approaching local extinction (Salm 1978; Nateewathana & Aungtonya 1994; Nijman *et al.* 2015). Although limited data exists, harvesting has occurred in many parts of the Indo-Pacific on a large scale over the last few decades (Wells 1981; McClanahan 1989). Two species found within the Mediterranean Sea (*C. lampas* and *C. variegata*) have also been heavily harvested with both species there being protected according to Annex II of the Bern convention and the Protocol of the Barcelona convention (Council of Europe 1979; European Community 1999). *Charonia lampas* and *C. variegata* were also regularly observed in the 1950s in their Atlantic and Caribbean habitats but are now uncommon to rare throughout (Percharde 1972; Marler & Marler 1982).

The perceived depletion of triton populations on the GBR, and elsewhere, was the basis for the 'predator removal hypothesis', originally proposed by Endean (1969) and Chesher (1969), as a causal factor increasing the propensity for outbreaks of CoTS. Endean (1969) presented anecdotal evidence that giant tritons were abundant before collection began in the 1930s but now rare to uncommon (Endean & Stablum 1973). Due to insufficient scientific data and limited to no documented harvesting or trade figures, it is not possible to accurately determine if giant tritons are rare due to exploitation alone. Giant tritons, like other Cymatiinae, may never have been common on reefs. While there are eye-witness accounts of exploitation of giant triton shells throughout much of their geographic range, including the GBR (Endean 1969), the vast majority of it is anecdotal; there being a dearth of documented records of the intensity, in either numbers or volume, of harvesting giant triton shells. Between 1947 and 1960, crews operating out of Thursday Island, Australia, from luggers harvesting Beche-de-mer and Trochus (*Trochus spp.*) for commercial purposes, collected giant tritons to supplement their incomes (James 1976). Further south along the east coast, one boat skipper reported seeing over 800 giant triton shells on the wharfs at Cooktown and Palm Island and from these accounts it was estimated that some 10,000 *C. tritonis* were collected annually (James 1976). However, there is some confusion as to the exact species that were collected as it has been suggested that the giant tritons referred to were in fact the false (or Australian) trumpet, *Syrinx aruanus*, which although also a carnivore, feeds on polychaetes, but others have dismissed such claims as having no foundation in fact (James 1976). In general, an analysis of trade statistics of ornamental shells showed that there was a considerable increase in the volume of shells traded in the 1970s and the subsequent depletion of the giant tritons on reefs that were harvested (Wells *et al.* 1983). Surveys conducted on over 130 GBR reefs between 1966 and 1972 found only 78 tritons (Sapp 1999). In another study spanning two years (1966 – 1968) only 28 tritons were found on various reefs between Princess Charlotte Bay and the Palm Islands (Endean 1969). In more recent times, 30 divers, whose primary objectives were the location and destruction of starfish, making 90 dives on the GBR over a period of 2 weeks were only able to locate 12 giant tritons (Paterson & Poulsen 1988). Furthermore, a population density of only <1 triton per km^2 was established after a 12 month survey (430 hours diving time; July 1993 to August 1994) of 12 GBR reefs between Port Douglas (16°S) and Airlie Beach (21°S) (Poulsen 1995). Through 2015-2016 divers of the Targeted Crown-of-thorns Starfish Control Program only reported sighting 1 or less giant triton per 10 day culling trip (Moon, Pers. Comm.). At such low densities, and as a dioecious species, the probability of successful reproduction in *C. tritonis* on the GBR may be severely limited as it has been for the endangered Queen conch, *Strombus gigas* in the Carribbean (Stoner & Lally 1994; Stoner & Ray-Culp 2000). However, due to the cryptic and nocturnal nature of giant tritons visual counts during daylight hours likely underestimate populations.

Similar anectodal evidence extends to other countries. In Tonga in the 1960s local fisherman could collect up to seven giant tritons per day whereas in 1993, despite a $70 bounty per giant triton, none were found over a two month period (Poulsen 1995). During a 6-month study on reefs in Guam divers found only seven giant tritons (Chesher 1969). A Tropical Marine Mollusc Programme (1991 – 1995) in Thailand listed giant tritons as a target species, however, only three specimens in total were procured between 1997-1998 (Tropical Marine Mollusc Programme 1991). Such anecdotal evidence suggests extreme rarity.

As many CoTS outbreaks on Pacific Islands have begun near human populations it has been argued as a plausible model that lowering the standing stock of giant tritons due to collection might be sufficient to raise population levels of CoTS beyond a critical minimum leading to conditions conducive to outbreaks (Chesher 1969). However, on coral reef islands where giant tritons are reported not to be collected, such as Ponape, Tinian and Truk, outbreaks of CoTS have been reported; the standing stock density of giant tritons in these areas is not known (Chesher 1969). Nevertheless, modelling studies have suggested that predatory species, such as *C. tritonis*, have the potential to limit population outbreaks of CoTS (Antonelli & Kazarinoff 1984; Bradbury *et al.* 1985; McCallum 1987).

Collection of *C. tritonis* has been prohibited under the Qld Fisheries Act, 1994, Group 4 and the Great Barrier Reef Marine Park Regulations 1983 Appendix 2 and is currently listed as a regulated no take species under the Queensland Fisheries Regulation 2008. Nevertheless, illegal poaching is still reported on the GBR and, as a demonstration of latent demand, hundreds of *C. tritonis* shells are imported annually into Australia (David Savage, QNPWS pers. comm. in Poulsen (1995)). In 1993 Australia proposed that *C. tritonis* should be included on the CITES Appendix II list (a species not necessarily presently threatened with extinction but may become so unless trade is closely controlled) but due to the lack of evidence on biological and trade status for the species the Berne criteria for listing could not be met (Chesher 1993; CITES 1994; Rosser & Haywood 2002). Independent of international agreement many countries in the Indo-Pacific have banned the collection or exportation of *C. tritonis* including Australia (1969), India (1972), Seychelles (1969/1978), Fiji (1971), Indonesia (1987) and Philippines (2001). Other countries, including Guam, Vanuatu and Kenya have regulated collection (Salm 1978; Wells *et al.* 1983; Kay 1995a; Weis *et al.* 2004; Nijman *et al.* 2015). Although legally protected in several jurisdictions many marine molluscs, including tritons, continue to be traded in large volumes, i.e. tens of thousands (Nijman *et al.* 2015). In other countries, such as Thailand, where collection is not banned, tritons are locally extinct or extremely rare (Nateewathana & Aungtonya 1994).

5.0 MANAGEMENT POTENTIAL OF *CHARONIA TRITONIS*

5.1 Restocking Potential

The captive breeding of endangered vertebrates is an established technique of conservation and a fundamental goal of many zoos around the world (Snyder *et al.* 1996). Over 2,000 species of vertebrates have been used in breeding programs in order to prevent their extinction or for re-stocking, either regionally or biologically (Holt *et al.* 2002). In contrast there have been few comparable breeding programs for invertebrates even though with shorter generation times they are potentially more readily bred in captivity (Cooper 1986). Many terrestrial invertebrates have, however, been captive bred due to their commercial importance, i.e. silk moths (*Mombyx mori*), butterflies (numerous species), snails (*Helix aspersa*) and medicinal leeches (*Hirudo medicinalis*) (Wells & Coombes 1987). Similarly, there are also several marine invertebrate species bred for commercial purposes, i.e. molluscs (oysters, clams), crustaceans (prawns, crabs), annelids, echinoderms (sea cucumbers, sea urchins) and cnidarians (jellyfish, corals) as well as for research as experimental models (Heslinga *et al.* 1986; Dwiono *et al.* 1997; Guo *et al.* 1999; Davis 2000; Katsanevakis *et al.* 2008; Calado & Leal 2015).

Populations of the commercially threatened Queen conch (*Strombus gigas*) have been severely depleted through the Caribbean and several aquaculture programs have been established for restocking in the wild (Laughlin & Weil 1983; Stoner *et al.* 1994; Davis 2000; Glazer *et al.* 2003; Spring & Davis 2005; Delgado & Glazer 2007; McCarthy 2008; Stoner 2012). Programs for restocking topshell (*Trochus niloticus*) have also been established (Nash 1993; Dwiono *et al.* 1997). Other examples of gastropod re-stocking include the terrestrial Polynesian tree snails (*Partula spp.*) which are endemic to Moorea but are under distinct threat of extinction due to a series of snail introductions onto the islands due to a cascading biological control effort which resulted in other exotic snails being introduced. The exotic giant African snail (*Achatina fulica*) was introduced onto the islands in 1977 but rapidly became an agricultural pest. In turn, the exotic carnivorous snail (*Euglandina rosea*) was introduced to control the giant African snail. However, *E. rosea* is non-selective and also predated heavily upon the endemic *Partula* species, threatening it with extinction (Wells 1986). The only hope to save the endemic *Partula* species was considered to be via captive breeding programs. Seven species of *Partula* have been successfully captive bred in laboratories in the United Kingdom, USA and Australlia (Wells 1986). Likewise, several species of threaten New Zealand land snails (*Placostylus spp.*) have been successfully translocated to islands with other translocations recommended (Ogle 1979).

Endangered or diminished mollusc populations have proved to be relatively easy to re-establish as their low mobility facilitates monitoring of translocated populations, although this is somewhat counter-balanced by their cryptic nature (Wells 1986). It must be emphasised that in the case of *Partula* species, the decline in population was initially caused by the introduction of an exotic species followed by the introduction of yet another exotic species and bares no relation to re-stocking of depleted native species such as *C. tritonis*.

5.2 Aquaculture Potential

A wide variety of different species of molluscs are consumed as seafood worldwide ([FAO 2016](#)). The majority are bivalves but also includes over 36 species of gastropods, primarily whelks (Buccinoidea), rock snails (Muricoidea), winkles (Littorinoidea) and conchs (Stromboidea), as well as over 10 species of cephalopods ([Leiva & Castilla 2002](#)). Giant tritons are not primarily harvested as food as their consumption has been associated with tetrodotoxin poisoning ([Noguchi *et al.* 1982](#); [Narita *et al.* 1984](#); [Shiu *et al.* 2003](#)). Although the majority of molluscs are harvested from wild populations some species are also fully farmed by aquaculture. The majority of cultured molluscan species are bivalves although there are established culture methodologies for production for marine gastropods, from larvae to adults, including abalone (*Haliotis* spp.), queen conches (*Strombus gigas*), trochus (*Trochus niloticus*) and common whelk (*Buccinum undatum*), amongst others (Table 6). In 2007 over 374,000 tonnes of gastropods were produced through aquaculture ([Nasution & Roberts 2004](#); [Castell 2012](#)).

Table 6: Major groups and species of marine molluscs which are produced at commercial scale through aquaculture. From FAO (2016) and (Castell 2012). [c] carnivore, [h] herbivore, [d] detritivore, [f] filter feeder

Group	Species
Bivalvia (44)	
Oysters [d/f]	*Ostrea edulis, O. chilensis, O. conchaphila, Crassostrea gigas, C. virginica, Saccostrea commercialis*
Mussels [d/f]	*Mytilus edulis, M. galloprovincialis, M. chilensis, Perna canaliculus, Anodonta cygnea, Aulacomya ater, Choromytilus chorus, Modiolus* spp.
Scallops [d/f]	*Patinopecten yessoensis, Aequipecten opercularis, A. (Agropecten) irradians, Argopecten purpuratus, Chlamys varia, Pecten maximus*
Clams [d/f]	*Mercenaria mercenaria, Corbicula flunimea, Scapharca broughtonii, Cyclina sinensis, Venus verrucosa, Donax* spp., *Mya arenaria, Protothaca staminea, Saxidomus giganteus, Tresus nuttallii*
Carpet shells [d/f]	*Ruditapes decussatus, R. (Venerupis) philippinarum, V. pullastra, V. rhombiodes*
Razor clams [d/f]	*Sinomovacula* spp., *Ensis ensis, Panopea abrupta*
Cockles [d/f]	*Anadara granosa, Cerastoderma edule, Cardiidae*
Pen shell clams [d/f]	*Atrina* spp.
Gastropoda (+5)	
Snails	*Rapana* spp.[c], *Babylonia* spp.[d/c], *Buccinum undatum*[c], *Lobatus gigas* [h], *Strombus gigas* [d/h], *S. pugilis* [d/h], *Trochus niloticus*[h], *Stromboidea* [h/d]
Abalone [h]	*Haliotis rufescens, H. discus, H. tuberculata*
Cephalopoda (1)	
Octopus [c]	*Octopus* spp.

Aquaculture technologies are also being developed for other marine gastropod species including the green snail (*Turbo marmoratus*), silvermouth snail (*Turbo argyrostomus*), red conch (*Rapana venosa*), mud snail (*Bullacta exarata*), sea hare (*Notarchus leachii cirrosus*), spotted babylon (*Babylonia areolate*), the muricids *Chorus ramosus* and *C. giganteus* and *Cassis cornuta* ([Murakoshi *et al.* 1993](#); [Guo *et al.* 1999](#); [Dwiono *et al.* 2001](#); [Nair 2004](#); [Castell 2012](#)). Numerous other species have been successfully reared on small scales for experimental research ([Castell 2012](#)).

There are four critical biological stages which require optimization for successful production of organisms by aquaculture: 1) procurement of broodstock, 2) production of seed (egg and larvae), 3) juvenile nursery culture and 4) grow-out of sub-adults to required size. For example, the successful aquaculture of the herbivorous topshell *Trochus niloticus* is due to a number of factors: ready access to breeding stock collected from intertidal reefs (ranging from Western Australia to Torres Strait to GBR; although there has been a decline in annual harvests from 135 tonnes in 1980 to 15 tonnes currently), spawning occurs all year round (following the luna cycle) and can be anticipated from changes in behaviour (i.e. feeding ceased, spending more time at the waterline and right siphon extended), lecithotrophic larvae hatch and settle within 2-5 days and feed on filamentous microalgae, juveniles reach ~3 mm one month after hatching, larger juveniles (>40 mm) can be transferred to cages on reef flats for grow-out, the legal minimum size of 9 cm maximum shell diameter is reached after three years (Nash 1989; Clarke & Komatsu 2001; Amos & Purcell 2003).

The spotted babylon snail has similar attributes (i.e. spawns year-round, lecithotrophic larvae, larval settlement with 18 days of hatching, rapid growth over 8 months to market size of 40 mm) favourable for commercial aquaculture. Other aspects of *B. areolate* biology have been investigated and exploited to improve survivorship rates in aquaria, such as water quality (i.e. waterflow, temperature and salinity), substrate requirements, and food conversion rates (Chaitanawisuti & Kritsanapuntu 2000; Chaitanawisuti *et al.* 2001).

Although adult *C. tritonis* are rare in the wild, sufficient numbers can be collected (typically under permit) from the wild to establish a small broodstock population (Nugranad *et al.* 2001; Zhang *et al.* 2013; Hall *et al.* 2016). Adult *C. tritonis* do breed spontaneously in captivity on an annual basis even when entirely fed for many months to years solely on a diet of just *A. planci* or a few species of echinoderms. Eggs and hatching of larvae from clutches of egg capsules has also been successful (see Table 4). However, almost all of the successful attempts to culture gastropods have involved species with lecithotrophic larvae (Castell 2012). These larvae can complete their larval phase without feeding, as they hatch with an ample supply of yolk reserves, and hence have been readily reared from hatching to settlement. In contrast, species with planktotrophic larvae such as *Charonia* spp. require substantially more husbandry and the supply of a suitably nutritional diet which is typically a cocktail of several species of phytoplankton and possibly zooplankton (Franz 1971; Bertram & Strathmann 1998).

The larvae of *C. tritonis* have been maintained in larval culture for over 300 days but there have been no reports of success in larval rearing culminating in metamorphosis and settlement (Nugranad *et al.* 2001). This may be due to the larval diet being suboptimal where the mixture of phytoplankton species fed to the larvae is sufficient for survival but is not satisfactory for larval growth and development. In short, the larvae may be on a near starvation maintenance only diet. However, these species also recruit locally so their larval phase must be extremely plastic with a temporal range from short to extremely long (Hadfield & Strathmann 1996; Oyarzun & Strathmann 2011). It is likely that the key to inducing settlement of *C. tritonis* larvae will be exposure to chemical cues that induce metamorphosis and settlement (Cob *et al.* 2010). Larvae have been shown to use a hierarchy of sensory cues to eventually select suitable settlement sites (Kingsford *et al.* 2002; Yu *et al.* 2010). The critical challenge towards the production of large numbers of *C. tritonis* for restocking will be identifying the optimum larval nutrition and understanding the role of sensory receptors in order to trigger the cascade leading to metamorphosis and settlement.

Recent advances in genomic techniques, including the ability to sequence and study the whole genome of individuals, have created opportunities for both animal breeding and population management (Nuijten *et al.* 2016). Genomic techniques are now being applied to conservation management for critically endangered species, including marine organisms (Titilade & Olalekan 2015), for example, through the identification of genes that are essential for fitness (McMahon *et al.* 2014; Khan *et al.* 2016; Nuijten *et al.* 2016). Functional genomics have also been effectively applied to fish and bivalve molluscs and specifically to improving breeding programs through better assessment of commercial traits such as growth, body conformation and disease resistance(Gjoen & Bentsen 1997; Figueras *et al.* 2012). For example, as a result of establishing the variation within and between different populations of Norwegian salmon, individuals with specific genotypes were bred resulting in an estimated 10% gain in commercial quality per generation (Gjoen & Bentsen 1997). Potential biomarkers of oocyte quality in the European clam (Ruditapes decussatus) have been identified using microarray technology along with specific genes involved in stress response and which are associated with poor oocyte quality (De Sousa *et al.* 2015). Subsequent proteomics detected a higher expression of 10 proteins, including 5 vitellogenins proteins some of which were breakdown products; cleavage products are an indication of resorbtion and/or oocyte aging. Initial heat shock experiments on the heat susceptible Pacific oyster *Crassostrea gigas* found transcription of genes putatively encoding heat shock proteins and for proteins that synthesize lipids, protect against bacterial infection, and regulate spawning were increased, while those for proteins that mobilise lipids and detoxify reactive oxygen species decreased (Lang *et al.* 2009). These gene markers could help identify thermotolerant oysters and provide the basis for broodstock selection to reduce incidences of summer mortality syndrome.

To date work published in the area of marine gastropod genomics has focused on key commercial and experimental model species including those from *Aplysia*, *Biomphalaria, Haliotis*, *Helix*, *Lottia*, *Lymnaea* and *Strombus* (Knudsen *et al.* 2006; Spade *et al.* 2010; Márquez *et al.* 2013; Simakov *et al.* 2013). Gene expression studies on the queen conch (*Strombus gigas*) has provided better understanding of the reproductive mechanisms and the factors that influence successful spawning in wild populations (Spade *et al.* 2010). *S. gigas* veligers can remain in the plankton for two months suggesting possible extensive gene flow through larval dispersal, however, microsatellite analysis found that *S. gigas* populations (based on 490 individuals separated by 600 km) in the Caribbean were not panmictic. A global deficit of gene heterozygosity, indicating low genetic diversity, was found and four stock populations were identified highlighting the need to re-focus management and conservation efforts at both a local and regional level (Márquez *et al.* 2013). Sequencing the *C. tritonis* genome and establishing genetic connectivity and diversity will provide a valuable resource to elucidate the mechanisms driving population structure, reproduction competency and larval development, to assess effects of captivity on broodstock including disease resistance and response to environment stress parameters. For example, probing the genome/transcriptome of *C. tritonis* larvae could potentially reveal the chemoreceptors and chemical cues involved in detection of settlement cues. As described above, information relating to genetic connectivity and diversity could also be used to guide conservation efforts and the development of effective science-driven management plans to ensure long-term sustainability of this threatened species.

6.0 CONCLUSION

The continuing decline of coral cover on the GBR requires urgent attention, including through the mitigation of the impacts of CoTS population outbreaks. This report reviewed existing and historical literature on the biology and ecology of the giant triton, *Charonia tritonis*, in the context of their potential role in mitigating CoTS outbreaks. *Charonia tritonis* is a primary predator of echinoderms, with both field and laboratory-based evidence suggesting a proclivity for *Acanthaster planci*, but will also consume other starfish, sea cucumbers and to a lesser extent sea urchins. Based on estimates of consumption rates from aquaria-based observations, it is unlikely that *C. tritonis* can significantly reduce outbreak populations of CoTS. However, it is possible that, due to the flight response of CoTS in the presence of giant tritons, as observed in the laboratory, deployment of giant triton to outbreak initiation reefs i.e. during the early stages of CoTS outbreaks, could potentially delay and/or reduce the size of these outbreaks. The mere presence of giant tritons and associated release of their chemical signals may, based on evidence from aquarium exposures, influence the biology and behaviour of CoTS through the creation of a 'landscape of fear'. This concept is increasingly being applied to cases of biological control, with potential to mitigate pests in the marine environment, and could result in a proximity deterrence effect in CoTS. Such deterrence could be effective in dispersing or preventing aggregations of CoTS during the spawning season. In this context, this review also examines the potential for aquaculture and restocking of the giant triton on the GBR. *Charonis tritonis* have been spawned in captivity with the planktonic larval phase maintained for ~300 days although there are no reports of successful larval settlement. The critical bottleneck to their successful aquaculture is identifying the factors that induce metamorphosis and settlement of larvae.

7.0 RECOMMENDATIONS FOR FUTURE RESEARCH AND MANAGEMENT DIRECTIONS

Feeding preferences and foraging behaviours of *C. tritonis*:

- To elucidate predation by *C. tritonis* on CoTS in the field, an environmental DNA (eDNA) survey should be conducted on the gut content of freshly collected specimens for remains of CoTS.
- To establish the full feeding spectrum of *C. tritonis* through both physical presence and choice experiments for successful maintenance in captivity.
- To determine the 'attractiveness' of putative prey species as well as prey odour (water-borne factors) to *C. tritonis* for predicting the impacts of their presence the non-COTS echinoderm community.
- To develop a robust method for acoustically tagging and monitoring *C. tritonis* in controlled laboratory experiments, which will enable the o establishment of parameters that describe behaviour and range of movement in the field.

Aquaculture of *C. tritonis*:

- To establish robust methods (aquaculture husbandry, molecular, transcriptomic) for the rearing of *C. tritonis*, including the assessment of larval viability (i.e. hatching, competency, settlement and dietary requirements beneficial for growth).
- To determine physical and chemical factors which may drive the development and induce settlement of *C. tritonis* larvae in controlled laboratory experiments.
- To undertake de novo whole-genome sequencing of the giant triton genome. Knowledge of the *C. tritonis* genome sequence will enable us to understand how the genetic information determines the development, reproduction, structure and function of the giant triton, information that could for example help assess effects of captivity on broodstock.
- By studying the similarities and differences between *C. tritionis* genes and those of other organisms, discover the functions of particular genes and identify which genes are critical for larval development and settlement.
- To use genomics and transcriptomics to identify target traits and gain knowledge on the types of proteins encoded by these genes to exploit in the development of *C. tritonis*-derived CoTS control technologies.

Deployment of *C. tritonis* for CoTS control:

- To determine aggregation behaviour of different life history stages of CoTS, and in particular reproductively active CoTS, in the presence of *C. tritonis*, in controlled laboratory experiments.
- To determine whether the physical presence and/or odour of *C. tritonis* affects the behaviour and mortality of other known and potential prey species (.e. other species of starfish, sea cucumbers, etc.) in controlled laboratory experiments.
- To determine the stability of the chemical(s) that elicit the alarm response in CoTS in seawater, and evaluate the potential applicability in the field for influencing CoTS aggregations at scales relevant for management (i.e. tourist sites, whole reefs) in controlled laboratory experiments.
- The chemical nature of this signal should be identified and potentially produced as a dispersant.

- To examine the response of CoTS aggregation behaviour to the presence of *C. tritonis* in the field, by deploying a selected number of *C. tritonis* at known locations on a reef with a current CoTS outbreak.
- To examine the response of CoTS aggregation behaviour to *C. tritonis* chemicals in the field, by releasing isolated chemistry at known locations on a reef with a current CoTS outbreak.

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