



*diversity*

IMPACT  
FACTOR  
**2.1**

CITESCORE  
**3.4**

Review

---

# A Review of the Giant Triton (*Charonia tritonis*), from Exploitation to Coral Reef Protector?

---

Cherie A. Motti, Scott F. Cummins and Michael R. Hall



<https://doi.org/10.3390/d14110961>

## Review

# A Review of the Giant Triton (*Charonia tritonis*), from Exploitation to Coral Reef Protector?

Cherie A. Motti <sup>1,\*</sup>, Scott F. Cummins <sup>2,3</sup>  and Michael R. Hall <sup>1</sup><sup>1</sup> Australian Institute of Marine Science (AIMS), Townsville, QLD 4810, Australia<sup>2</sup> Centre for Bioinnovation, University of the Sunshine Coast, Maroochydore, QLD 4558, Australia<sup>3</sup> School of Science, Technology and Engineering, University of the Sunshine Coast, Maroochydore, QLD 4558, Australia

\* Correspondence: c.motti@aims.gov.au; Tel.: +61-7475-34143

**Abstract:** *Charonia tritonis* (Charoniidae), one of the largest marine gastropods and an echinoderm specialist, preys on Crown-of-Thorns starfish (CoTS), a recurring pest that continues to be a leading cause of coral mortality on Indo-Pacific reefs. Widespread historical exploitation has impacted their numbers, with standing populations considered rare throughout their habitat. Their life-stage attributes, i.e., teleplanic larvae, planktrophic phase spanning years permitting transoceanic dispersal, and recruitment to coral reefs through oceanic influx with intense larval mortality, have likely hindered their recovery. Decline in numbers is hypothesised to account partially for periodic CoTS outbreaks, yet predator-prey dynamics between these two species that might influence this are poorly understood. The *C. tritonis* excretory secretome elicits a proximity deterrence effect on CoTS, the nature of which is under investigation as a possible tool in CoTS biocontrol scenarios. However, specificity and zone of impact in situ are unknown, and whether the mere presence of *C. tritonis* and/or predation pressure has any regulatory influence over CoTS populations remains to be established. The fundamental taxonomy and distinctive characteristics, biology and ecology of *C. tritonis* is summarized, and knowledge gaps relevant to understanding their role within coral reefs identified. Information is provided regarding exploitation of *C. tritonis* across its habitat, and prospects for conservation interventions, including captive rearing and stock enhancement to repopulate local regions, are discussed. Its predator-prey ecology is also examined and potential to mitigate CoTS considered. Recommendations to direct future research into this predator and for its inclusion in a CoTS integrated pest management strategy to improve coral reef health are offered.

**Keywords:** aquaculture; biocontrol; Crown-of-Thorns starfish; indigenous predator; integrated pest management; marine gastropod; trophodynamics; predation efficiency



**Citation:** Motti, C.A.; Cummins, S.F.; Hall, M.R. A Review of the Giant Triton (*Charonia tritonis*), from Exploitation to Coral Reef Protector? *Diversity* **2022**, *14*, 961. <https://doi.org/10.3390/d14110961>

Academic Editor: Bert W. Hoeksema

Received: 8 September 2022

Accepted: 7 October 2022

Published: 9 November 2022

**Publisher's Note:** MDPI stays neutral with regard to jurisdictional claims in published maps and institutional affiliations.



**Copyright:** © 2022 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (<https://creativecommons.org/licenses/by/4.0/>).

## 1. Introduction

*Charonia tritonis*, commonly known as the giant triton, is one of the largest marine gastropod snails. The historical (and continuing) exploitation of the *C. tritonis* as a curio throughout its full habitat range has led to a significant decline in its numbers, to the point of it becoming rare and endangered, and localised protection has not alleviated the problem [1,2]. As an echinoderm specialist and the primary predator of adult Crown-of-Thorns starfish (CoTS; *Acanthaster* cf. *solaris* species complex [3,4]), its deliberate removal may have also altered trophic interactions, triggering cascading effects on coral reef ecosystem processes [5]. Endean's [6] 'predator removal hypothesis' proposed the decline in the *C. tritonis* population as a possible driver for the alarming increase in CoTS numbers (referred to as outbreaks), a concept that is still being debated several decades later [4,6–9]. The increase in CoTS outbreak frequency and severity continues to have a devastating impact on coral reef ecosystems, prompting a resurgence in research and management efforts to control CoTS numbers [10–12]. A compounding factor is the elevated reproductive success

of CoTS and high larval survival rates, the latter augmented by the same stressors that adversely impact coral reefs, further fueling the need to develop novel CoTS management adaptive tools and methods [13–15]. In contrast, *C. tritonis* is relatively understudied, and its role in coral reef trophodynamics is poorly understood [12].

In recent years, biocontrol methods as a strategy to mitigate CoTS outbreaks (i.e., ecological goal to reduce CoTS populations to levels below damaging thresholds) on a regional scale have gained traction [16,17]. The success of biocontrol programs relies on efficient selection of effective natural enemies [18–24], and to achieve this, it is critical to have full knowledge of the pest's biology, as well as that of their natural enemies. Additionally, in any biocontrol effort, conservation of natural enemies is a critical component and requires knowledge not only of the predator's effectiveness against the pest species, but also the factors which interfere with or threaten their natural populations. As a natural indigenous enemy, the potential restocking of *C. tritonis* as a conservation intervention may also present the opportunity to naturally control CoTS populations on selected 'at-risk' reefs. The inclusion of such a strategy within a considered and complementary multi-faceted CoTS integrated pest management (IPM) program is of interest to reef managers [17,25,26], however, there exists many clear and evident knowledge gaps, least of all in the breeding and rearing of juvenile *C. tritonis* [27] for stock enhancement.

Presented here is a comprehensive review of literature on the *C. tritonis* taxonomy and morphology, biogeographical distribution, movement ecology, reproduction and growth. The state of exploitation and the anthropogenic threats they face are evaluated, and prospects for their captive rearing and restocking on the Great Barrier Reef (GBR; Australia) is discussed, the intent being to assist in the effective management and protection of their populations. Attributes suited to their use as a biocontrol agent to mitigate CoTS population outbreaks naturally and sustainably in the long-term, are also examined in the context of predator-prey dynamics, and recommendations to guide future research and establish environmental management strategies, with respect to their application within an IPM approach, are offered.

## 2. Taxonomy and Distinctive Characteristics

Members of Hypsogastropoda (phylum: Mollusca, class: Gastropoda, subclass: Caenogastropoda) are numerically important key predators in shallow water tropical marine environments [28,29]. Within clade Caenogastropoda, the Hypsogastropoda comprises the Non-Latrogastropoda clade corresponding largely to the former Littorinimorpha, with radula typically having 7 teeth per row, and the Latrogastropoda clade, which includes the previously named Neogastropoda clade and the Calyptraeioidea, Cypraeoidea, Ficoidea, Stromboidea, Tonnoidea, and Xenophoroidea, with radula having only 1–5 teeth per row [30]. The largest shells are associated with the Latrogastropoda superfamilies Turbinellidae (*Syrinx aruanus*) and Tonnoidea, the latter having been recently updated, based on mitochondrial and nuclear gene analysis [31], to comprise nine families: Bursidae, Cassidae, Charoniidae, Cymatiidae, Laubierinidae, Personidae, Ranellidae, Thalassocyronidae and Tonnidae. Some species within the Tonnidae, Cassidae, Cymatiidae and Charoniidae families are known to prey on echinoderms, for example: *Tonna perdx*, *T. galea* [32] and *T. zonatum* [33]; *Cassis tuberosa* [34] and *Galeodea echinophora* [35]; and *Charonia* spp. [36–38], respectively [31]. *Charonia lampas* (Linnaeus, 1758) [30,39], previously classified into five subspecies (*C. lampas capax*, *C. lampas lampas*, *C. lampas pustulata*, *C. lampas rubicunda* and *C. lampas sauliae*), is the most morphologically variable of the *Charonia* genus, driven by ecophenotypic rather than genetic variation [40,41] (Table 1). *Charonia seguenzae*, having been geographically isolated in the Eastern Mediterranean Sea and therefore split from *C. variegata* (Lamarck, 1816) [42], has since been reclassified as *C. variegata*. *C. tritonis* (Linnaeus, 1758) is the largest species within the genus and the only *Charonia* known to predate on CoTS.

**Table 1.** Taxonomic status of the genus *Charonia*. Key taxonomic groups in bold, \* denotes initial subspecies. Adapted from [30,31,39].

Scheme	Author(s)	Status	Accepted Name
<b><i>Charonia lampas</i></b>	<b>Linnaeus, 1758</b>	<b>accepted name</b>	<b><i>Charonia lampas</i></b>
<i>Charonia lampas capax</i> *	Finlay, 1926	synonym	<i>Charonia lampas</i>
<i>Charonia capax euclioides</i>	Finlay, 1926	synonym	<i>Charonia lampas</i>
<i>Charonia crassa</i>	Grateloup, 1847	synonym	<i>Charonia lampas</i>
<i>Charonia euclia</i>	Hedley, 1914	synonym	<i>Charonia lampas</i>
<i>Charonia euclia instructa</i>	Iredale, 1929	synonym	<i>Charonia lampas</i>
<i>Charonia lampas lampas</i> *	Linnaeus, 1758	synonym	<i>Charonia lampas</i>
<i>Charonia lampas macilenta</i>	Kuroda & Habe, 1961	synonym	<i>Charonia lampas</i>
<i>Charonia (lampas) pustulata</i> *	Euthyme, 1889	synonym	<i>Charonia lampas</i>
<i>Charonia lampas sauliae</i> *	Reeve, 1844	synonym	<i>Charonia lampas</i>
<i>Charonia lampas weisbordi</i>	Gibson-Smith, 1976	synonym	<i>Charonia lampas</i>
<i>Charonia lampas ventricose</i>	Grateloup, 1833	Synonym	<i>Charonia lampas</i>
<i>Charonia mirabilis</i>	Parenzan, 1970	synonym	<i>Charonia lampas</i>
<i>Charonia nodifera</i>	Lamarck, 1822	synonym	<i>Charonia lampas</i>
<i>Charonia lampas rubicunda</i> *	Perry, 1811	synonym	<i>Charonia lampas</i>
<i>Charonia powelli</i>	Cotton, 1956	synonym	<i>Charonia lampas</i>
<b><i>Charonia tritonis</i></b>	<b>Linnaeus, 1758</b>	<b>accepted name</b>	<b><i>Charonia tritonis</i></b>
<b><i>Charonia variegata</i></b>	<b>Lamarck, 1816</b>	<b>accepted name</b>	<b><i>Charonia variegata</i></b>
<i>Charonia variegata seguenzae</i> *	Aradas & Benoit, 1870	accepted name	<i>Charonia variegata</i>
<i>Charonia tritonis variegata</i>	Lamarck, 1816	synonym	<i>Charonia variegata</i>

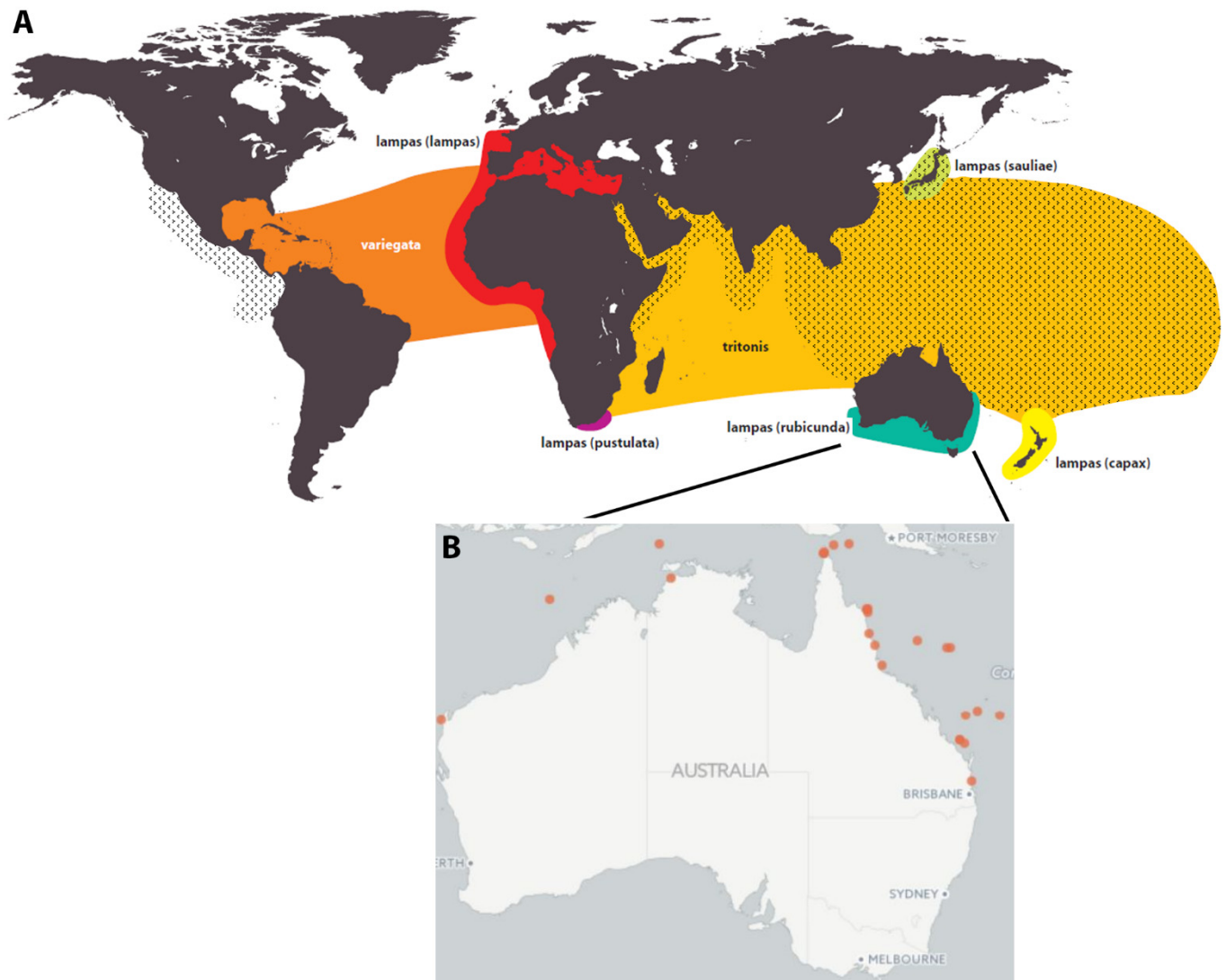
An extraordinary adaptive radiation driven through diet and competition has seen the morphological, physiological, behavioural and ecological diversity of the Hypsogastropoda expand [43–45]. Several apomorphic forms (or derived traits) within this clade of caenogastropods, and which are shared by *Charonia* spp., predominantly relate to the digestive system, specifically: a distinct rectal gland, salivary glands that do not pass through the nerve ring, tubular accessory salivary glands, possession of a 1–5 toothed radula, an esophageal gland detached from the esophagus, an enlarged radula ventral tensor muscle to aid sliding [28,45,46], formation of an eversible proboscis, a specialised siphon, and repeated folding in the chemoreceptor osphradium to increase the surface area capable of selective and acute chemical sensitivity [47]. Furthermore, they differ from herbivorous gastropods, having complex behaviour adaptations that include searching, capture, immobilization and penetration of prey, as well as an altered biochemical composition suited to the digestion of animal tissues [47,48].

*Charonia* spp. are readily distinctive, having a large, tall shell measuring up to 500 mm in length, with a pointed spire. The shell consists of a large body whorl with broad cords within a single narrow thread filling each interspace and a pronounced flaring outer lip. Well-developed varices are evenly spaced approximately every 270° around the shell, each merging abaperturally and bearing the remnants of older outer lips. The shell is high gloss with a contrasting colour pattern of red-brown crescentic splashes against a cream to pink background [39]. There is no periostracum. The brown oval shaped operculum is distinct in that it has concentric growth lines. The radula is the most distinctive non-shell feature, consisting of a central broad tooth with a very narrow basal plate that curves downward at the extremities and is surrounded by several narrow, elongated teeth [39]. Prominent features of the *C. tritonis* shell include the presence of smooth, broad, and flattened spiral ribs, the edge of which are wavy and puckered, and a broad, short siphonal canal with thin folds along the columellar wall.

### 3. Distribution, Habitat and Abundance

*Charonia* spp. have an extensive geographical distribution (Figure 1A). *C. lampas* ranges from the temperate waters of the Atlantic [49] to the sub-tropical waters of the Indian and Pacific Oceans [41,50] (Figure 1A). It is commonly found in the western Mediterranean, but

largely absent in the eastern Mediterranean [42,50]. The species has been documented in the northern coast of Natal in South Africa, southern and eastern Australia [51,52], New Zealand, the Chatham, Kermadec, Raoul, Norfolk and Lowe Howe Islands and around the islands of Japan and Taiwan [53]. *C. variegata* (Lamarck, 1816) is distributed through the western tropical Atlantic, the Caribbean and subtropical regions of the Mediterranean [42,50,54,55] (Figure 1A). As a result of the late Pliocene uplift of the Isthmus of Panama *C. variegata* has been geographically, and hence genetically, separated from *C. tritonis*.



**Figure 1.** Distribution and range of (A) the *Charonia* genus, coloured by species, and *Acanthaster* cf. *solaris* [10], shown by hashed overlay, and (B) locations of reported sightings and collections of *Charonia tritonis* in Australia, shown by orange dots. Adapted from [56–58].

Of all the *Charonia* spp., *C. tritonis* has the greatest distribution, extending throughout the tropical Indo-West Pacific region [57,58] (Figure 1A). It has been documented from central Japan [59], tropical Australia (Figure 1B), New Zealand and the Pitcairn, Cocos, Galapagos, Easter and Hawaiian Islands [50,60,61]. Its range also extends from the Red Sea to southern East Africa and across the islands of the Indian Ocean to western Australia [52].

*Charonia tritonis* inhabits hard and sandy bottoms in and around shallow water coral reefs [62,63], although some specimens have been observed at depths of several hundred meters [39]. They are generally considered nocturnal, and their cryptic nature (hiding in crevices during the day) makes accurate sampling to survey population size non-trivial [64].



With the full-length mitochondrial genome of *C. lampas* [65] and *C. tritonis* sequenced [66], the identification of candidate sequences suitable for use as species-specific barcodes in environmental DNA (eDNA) technology [67,68], in combination with impromptu citizen surveys, may assist in establishing their current spatial distribution and true numbers. Accurate mapping of their spatial co-occurrence with CoTS (Figure 1A) will also provide some insight into their potential role in CoTS outbreaks and biocontrol.

#### 4. Movement Ecology

Understanding movement ecology (e.g., foraging, dispersal and seasonal migration) has proven critical to the management and conservation of several marine species [69]. Importantly, such information underpins a species' population distribution, which is also influenced by seasonal phenology and predator-prey interactions [70,71]. Yet, information is scarce regarding the habitat and home range of the *C. tritonis*, their fine-scale movements as they move through their habitat, their normal (non-stressed) behaviours and how they interact with prey species (including CoTS) in situ. Recently, modelling of acoustic array data found *C. tritonis* have the capacity to move across an entire local reef [72] and are likely to be able to move between adjacent reef systems, having been found at depth on sandy bottoms [39]. Conversely, acoustic tagging of CoTS revealed they did not move beyond a single receiver within a linear array over a four month deployment, moving less than 100 m [73]. If these results prove robust, the home range of *C. tritonis* is well beyond that of their CoTS prey, at least on reefs in non-outbreak status. The small home range of CoTS is likely linked to food availability, sedentary coral prey and limited predation pressure, whereas the larger home range of *C. tritonis* is more likely a consequence of their low population, mobile and cryptic prey (not just CoTS), and the need to locate a mate. Preliminary findings [16,74] have shown the CoTS excretory secretome acts as an attractant to *C. tritonis* and that CoTS exhibit a flight response to *C. tritonis* predator odor. Yet, revealing the nature and role of specific excretory semiochemicals (e.g., kairomones and pheromones) in motivating both predator and prey behaviors [75] is required to establish the parameters that describe the full range of each animal's behaviour and movements, as well as their predator-prey dynamics, in the field.

The movement rates of *C. tritonis* and CoTS need to be considered in tandem to establish the extent to which the predator alters the behaviour of CoTS and exerts downward pressure on the population. Based on modelling of acoustic tagging data, release of *C. tritonis* on a local reef has the potential to alter CoTS behaviour in the short-term [72], possibly forcing them to become more cryptic and forcing them take greater risk. However, it remains to be seen whether increasing *C. tritonis* populations (via conservation or restocking) over the longer-term will impact local or regional CoTS populations.

#### 5. Reproduction

Members of the Tonnoidea are always gonochoric. Female *C. tritonis* can pair with multiple males during a single copulation event, the pairing lasting for several hours [76]. Copulation in captivity has been observed from August to September (Yongxing Island, China) with egg laying approximately 130 days after [76] (Table 2). A similar gestation period has been observed in other northern Pacific *Charonia* species [77], although much shorter time periods of 30–60 and 90 days have been reported [78,79]. No seasonality was observed in the reproduction of captive *C. tritonis* held for over two years at the Phuket Marine Biological Station, Thailand [78,80], indicating the photoperiod is not necessarily the cue for spawning. Furthermore, several species of Cymatiidae, held in captivity under ambient conditions (i.e., without controlled lighting), were observed spawning at precisely the same time over three consecutive years [81], giving credence to the suggestion that water temperature is a primary determinate [82]. This has since been confirmed for *C. tritonis* [25].

Detailed observations of *C. tritonis* reproduction, including copulation, spawning, embryogenesis and hatching, have been described in detail [25,78,79,83]. Internal fertilization represents a major innovation in the Caenogastropoda, along with encapsulation of the

eggs, both of which provide a protected environment during early trochophore development [28]. Briefly, the male sperm and prostatic fluid is transferred during copulation via the penis located behind the right tentacle [81]. Fertilization takes place internally in the female [55,84,85], the inseminated sperm embedding in the non-ciliated nutrient-rich surface cells of the pallial oviduct [81]. Under the right conditions (~26 °C water temperature; April to June coinciding with the austral winter solstice photoperiod and the dry season [25]) mature eggs are discharged into the pallial oviduct where they are fertilized, producing between 2000–2750 heavily yolked orange-coloured embryos ~360–600 µm in diameter (Figure 2A) (Table 2). Batches of embryos are deposited into ootheca (oblong tear-dropped shaped gelatinous capsules ~34–60 mm long and ~10 mm diameter), each containing a clear albuminous fluid. As each individual ootheca passes from the oviduct it is cemented via one end to a vertical (often cryptic) rocky surface [55,78,80]. The outer layer hardens upon exposure to the seawater offering protection against biofouling, pathogens and predation. The egg mass of 50–1000 oothecae, containing up to  $1.47 \times 10^6$  eggs (Table 2) [78,80] may take up to a week to deposit [81,86]. At the end of the breeding season both the testis and ovary degenerate [81].

**Table 2.** Reproductive statistics for *Charonia tritonis* reported from ex situ breeding programs. CoTS = Crown-of-Thorns starfish; PSU = practical salinity unit.

	Berg (1971) [79]	Nugranad et al. (2000) [80]	Nugranad et al. (2001) [78]	Zhang et al. (2013) [76]	Motti et al. (2019) [25]
Location	Oahu, USA	Phuket, Thailand	Phuket, Thailand	Yongxing Island, China	Townsville, Australia
Number of females	1	1	5	2	4
Number of males	At least 1	-	At least 1	At least 1	At least 2
Broodstock diet	Natural diet	CoTS, Culcita novaeguineae, Holothuria atra and Stichopus chloronotus	CoTS, C. novaeguineae, H. atra and S. chloronotus	CoTS and Stichopus horrens	CoTS, Linckia sp. and S. chloronotus
Date of reproductive behaviour	Oct	-	Year round	August–September	March–June
Temperature of broodstock tank	-	25.5–33.0 °C	-	-	23 °C (winter)–30 °C (summer)
Copulation until laying (days)	120–150	-	30–60	133	-
Duration of spawning (days)	42–56	19	60	21–35	-
Temperature of egg hatchery	-	-	-	24 °C	24.5 °C
Total capsules spawned female <sup>-1</sup>	88+	50	500–1000	549–602	~400
Egg diameter (µm)	450–600	400–430	360–440	428	-
Capsule dimensions, H × L (mm)	25 H × 9 L	17–39 H × 9–10 L	17–39 H × 9–10 L	34 H × 9 L	-
Number of eggs per capsule	-	2000–3400	2000–4400	2740–3000	~2500
Total number of eggs produced	-	~ $1.5 \times 10^5$	$1.6 \times 10^6$ – $3.2 \times 10^6$	$1.5 \times 10^6$ – $1.6 \times 10^6$	-

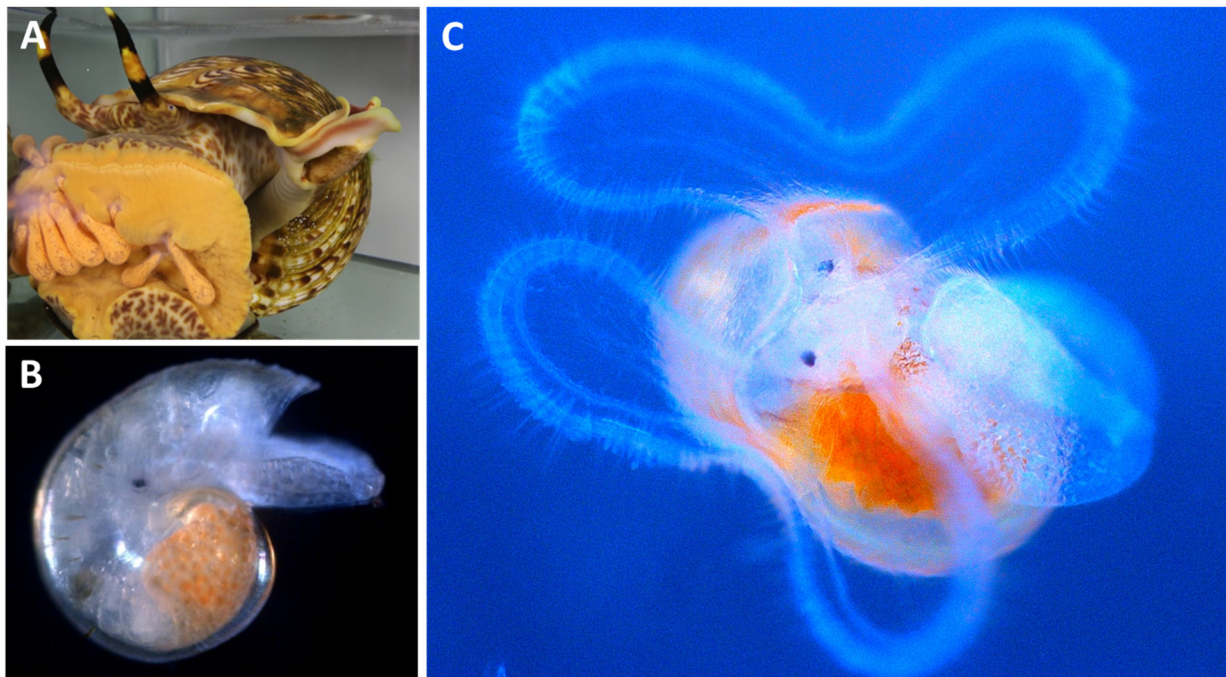
Table 2. Cont.

Incubation period (days)	49–56	-	35–60	55–63	52–68
Hatching success of capsules	-	0% unfertilized	43–96%	86–96%	-
Veligers per capsule	1140–1447	-	973–1459	2046–2110	-
Total veligers produced female <sup>−1</sup>	-	-	$0.26 \times 10^6$ – $1.47 \times 10^6$	$1.12 \times 10^6$ – $1.27 \times 10^6$	$\sim 0.8 \times 10^6$
Shell length at hatching (μm)	768–934	-	720–925	664–700	740
Temperature of larval rearing tank	-	-	-	-	24.5 °C
Larval diet	-	-	-	Immediately post hatching: <i>Isochrysis zhanjiangensis</i> , <i>Chaetoceros muelleri</i> and <i>Phaeodactylum tricornutum</i> (1:1:1, $2.0$ – $3.0 \times 10^4$ cells mL <sup>−1</sup> ). Two weeks post hatching: formulated brine shrimp flakes (52% protein, 8% crude fat, 5% crude fiber, and 7% moisture) at a rate of 0.3 mg L <sup>−1</sup> every other day.	<i>Isochrysis galbana</i> , <i>Diacronema lutheri</i> , <i>Nannochloropsis oceanica</i> , <i>Dunaliella</i> sp.
Other conditions	32–34 PSU		34–36 PSU 0.7 veliger mL <sup>−1</sup>		
Settlement	None at 30 days	-	None at 300 days	None at 140 days	None at 83 days

All eggs within the ootheca have an equal chance of undergoing embryogenesis as there are no nurse cells [81]. This post-fertilization process occurs within the egg capsule and can take anywhere from 35 to over 60 days [25,76,78,79]. Throughout this incubation period the female does not feed. She exhibits maternal care, using her foot muscle to clean the outer surface of the egg capsule, thereby preventing biofouling [76,87], and physically protect the oothecae from predation [81,88–90]. Other females in the vicinity may also protect and care for the clutch [81,87].

*C. tritonis* embryos gastrulate at ~7 days post-fertilization (dpf). Trochophore development occurs between 9–12 dpf followed by protoconch I (or embryonic shell) formation at 15–18 dpf [76]. This development phase is typified by the formation of the first two shell whorls. As yolk reserves are depleted, there is an overall whitening of the egg capsules, their texture becoming granular. The two eyespots develop 25 dpf (Figure 2B), the operculum and foot begin to form at 29 dpf, and a larval (false) heartbeat can be detected at ~35 dpf [76]. After ~63 dpf, trochophores, having a shell length of between 664–934 µm, emerge from the ootheca through a terminal pore [81] and enter their planktotrophic phase.





**Figure 2.** The early life history stages of *Charonia tritonis*. (A) Adult female depositing egg capsules in the SeaSim laboratory at AIMS (Photo: Peter Thomas-Hall, AIMS), (B) side profile of 25-day post fertilization veliger showing yolk reserve (orange) and eye spot (black) (Photo: Tom Barker, AIMS) and (C) front view of 14-day post hatched veliger with two eye spots visible and velum extended (Photo: Thomas Armstrong, AIMS).

In captivity, a female *C. tritonis* has been observed to produce  $0.26\text{--}1.47 \times 10^6$  veligers per spawning season (Table 2). This level of fecundity, assuming it holds true for wild breeding females, raises the question: why are *C. tritonis* rare in locations where they have been actively protected by policy? The relative population densities on coral reefs of adult gastropod species which have planktonic and planktotrophic larval development compared to those with intracapsular development, i.e., Cypraeidae (pelagic phase 10–50 days) versus Volutidae, is reported to be 1:10 [91]. Therefore, larval survival in *Charonia* spp. is likely to be extremely low and/or their dispersal so great that settlement to any one reef, especially the natal spawning reef, is rare [92], possibly hindering population recovery [93].

A lack of understanding of the rudimentary requirements of the *C. tritonis* veliger, including information regarding the biochemical and physiological processes that regulate adult reproduction, larval development and larval growth [25,94], have hampered attempts to rear them in captivity. A recent de novo assembly of transcriptomes from the *C. tritonis* cerebral ganglion identified 38 neuropeptide precursor genes encoding for conserved molluscan neuropeptides, including several associated with reproduction [74]. Future studies with a focus on de novo whole-genome sequencing of the *C. tritonis* genome and additional transcriptomic studies targeting the functional characterisation of these conserved molluscan neuropeptides are needed to decode the *C. tritonis* reproductive neuroendocrine pathway [95] and better understand their social behaviour. In addition, complementary genetic studies to maximize egg and embryo viability and survival of veliger and juveniles are needed ([96] and references therein). For example, genomic estimated breeding values established based on genome-wide single nucleotide polymorphisms and growth traits (i.e., shell length, height, width, and weight, and body weight), has imparted significant growth advantages to offspring of the commercially important freshwater triangle sail mussel, *Hyriopsis cumingii* [97]. Such knowledge of *C. tritonis* will promote the development of more reliable aquaculture methods to support stock enhancement and will be especially important should it prove an important conservation biocontrol agent against CoTS [98–101].

## 6. Juvenile Growth, Development and Morphological Relationships

The veliger of Ranellidae, Cymatidae and Charoniidae, including *C. tritonis*, hatch at an advanced protoconch stage I and complete their development in the water column [102]. They are teleplanic, having an extraordinarily long larval development phase capable of dispersing across oceans [103–105]. For example, the larval duration of *Fusitriton oregonensis* (Cymatiidae), from hatching to metamorphosis, can extend up to 4.5 years, the longest teleplanic larval period recorded for any marine organism [106].

The shell length of newly hatched *C. lampas* veliger measures 430 µm. For *C. variegata* the shell measures between 770–930 µm [79,86], with some specimens collected from the Atlantic exceeding 5000 µm [105]. Shell length of *C. tritonis* veligers maintained for over 140 days [76], 164 days [25,107] (Figure 2C) and 300 days [80] all progressively increased over time, reaching approximately 2000 µm. However, although shedding of the velar cilia was observed, none achieved the protoconch II phase [90,104] or successfully advanced to settlement [78], and factors such as the minimum shell size required for the transition remain unknown.

Attainment of settlement competency relies on numerous factors including a minimum shell size, sufficient energy reserves and the development of specific receptors and neural connections [108,109]. Even once competency is achieved these veliger can halt growth and limit calcification enabling them to remain planktonic and, endowed with four large velar lobes extending up to 10 times the diameter of the larval shell length, transit oceans [103,105,110–113] presumably until they encounter a suitable and often highly specific settlement cue [114–119]. High density monocultures of various commercially important molluscan bivalves, i.e., oysters, clams, scallops, etc., can be induced to settle with high success when presented with various substrates and/or environmental chemical cues (Table 3). Late development stage teleplanic Tonnoidea larvae captured in ocean plankton tows have metamorphosed and settled in aquaria, with biofilms on the tank walls speculated to be the source of the settlement signal [103,110]. Some gastropod juveniles start as ectoparasites and there is direct evidence larval settlement in these species is induced by waterborne cues from their adult (mostly sedentary algae, sponge and coral) prey [120], although for Tonnoidea veligers there remains only indirect evidence. For example, larvae of *Monoplex* (*M. aquatilis*, *M. nicobaricus*, and *M. pilearis*) and *Gutturium muricinum* (both previously *Cymatium*) will settle in the presence of adult tridacnid clam prey [121]. Unidentified juvenile gastropods, speculated to be those of *C. tritonis*, have been reported to settle and parasitize starfish, especially *Echinaster lozonius* and *Linckia multifora* [64]. Overall, there is only indirect evidence that Tonnoidea veligers rely on the odor of their future prey as a settlement cue [122]. For *C. tritonis* the cues that induce settlement remain elusive [25] (Table 3).

The application of -omics techniques has identified the molecular mechanisms and settlement cues for a range of gastropod veliger [95]. Recently, reference *C. tritonis* transcriptomes have been derived from adult tissues [37,74,148] and early life developmental stages (embryo and veliger) [101]. A diversity of rhodopsin-like G protein-coupled receptors (GPCRs), all representing candidate olfactory receptors, were located within adult cephalic tentacles, supporting earlier studies showing *C. tritonis* use chemosensing to locate CoTS prey [16,37]. In addition, several GPCR genes were identified as being unique to veligers providing insight into the chemosensory capacity of this early life stage with possible function in settlement. While such findings are beginning to address the knowledge gaps, further investigations of *C. tritonis* are warranted to establish gene function, identify candidate settlement cues and explore their possible application in aquaculture and conservation.

**Table 3.** Inducers of metamorphosis and settlement for gastropod veliger larvae (updated and modified [123]). Species for which data is limited to only settlement in presence of live prey (i.e., chemical has not been identified) have been omitted here, but are listed in [123]. Cues tested for *Charonia tritonis* [25] but found to be ineffective are listed as a comparison.

Species	Compound	Solution/Dose/Time/ % Metamorphosis	Reference
<i>Concholepus concholepus</i>	Adult conspecific shells covered in barnacles	Up to 4–5 days, 100%	[124]
<i>Crepidula fornicata</i>	20 mM KCl	50% settlement after 30–50 min	[125]
	Adult conspecific conditioned water	40% settlement after 50 min	[125]
	Conspecific pedal mucus	25% settlement after 50 min	[125]
	Raise KCl to 20 mM	55%, Highest settlement in those fed <i>Isochrysis</i> sp. ( $4 \times 10^5$ cells/larva/day)	[126]
	Elevated KCl above background by 15–20 mM	50% within 4 h	[127]
	Tested serotonin, dopamine and FMRFamide ( $10^{-5}$ M/L)	Measured whether larvae go up (serotonin) or down (dopamine, FMRFamide) in the water column	[128]
	Dibromomethane (DBM)	90–100% metamorphosis at 5000 ppm, combined DBM and KCl	[129]
	Red algae extract, $\gamma$ -aminobutyric acid (GABA), Hydrogen peroxide	70–95% metamorphosis	[130,131]
<i>Aliger gigas</i>	Nursery habitat sediment, KCl		[132,133]
	Hydrogen peroxide ( $H_2O_2$ )	100% at 10 h in 50 $\mu$ M $H_2O_2$	[130]
	Extract of <i>Laurencia poiteau</i> ; Phycoerythrins and related protein conjugants	88% metamorphosis	[132,134,135]
	Bromomethane	90% at 600 ppm	[136]
<i>Haliotis discus hannai</i> , <i>H. rufescens</i> <i>H. diversicolor</i> , <i>H. asinina</i>	conc KCl in normal seawater 9 mM	40% at 19 mM KCl	[136]
	$1 \times 10^{-6}$ M (final) GABA	37–99%	[137]
	Whole <i>Ulva australis</i> and <i>U. compressa</i> and <i>Amphiroa anceps</i> and <i>Corallina officinalis</i>	0.05–0.1 g wet wt algae or 1 cm <sup>2</sup> of 95% cover rock (CCA) added to 5 mL wells in 4 mL of seawater. CCA best (80%)	[138]
	Supplemented KCl	50% in 5–10 mM KCl (supplemented)	[139]
	GABA	40% $10^{-6}$ M GABA	[139]
	KCl, GABA	>40% 20 mM KCl, >75% $10^{-6}$ M GABA	[140]
	Biogenic amines	% metamorphosis at $10^{-6}$ M of GABA (98%), L-glutamate (80%), L-glutamine (0%), $\beta$ -alanine (16–68%)	[141]
	GABA, $\delta$ -aminovaleric acid (5-AVA), L-glutamic acid, monosodium glutamate (MSG)	$10^{-1}$ mM 5-AVA (62% at 6 h) > $10^{-3}$ mM GABA (58% at 72 h) > 25 mM MSG (50% at 72 h) > $10^{-3}$ mM L-glutamic acid (48% at 72 h).	[142]
	$10^{-3}$ , $10^{-4}$ , $10^{-5}$ , $10^{-6}$ M GABA	$10^{-6}$ M GABA at 2 days, 73%	[143]
	5 spp. Benthic diatoms ( <i>Navicula</i> spp. and <i>Nitzschia</i> spp.)	If fed 5 spp., at 2 days 90–94%	[143]
<i>Phestilla sibogae</i>	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	[144]
<i>Hermisenda crassicornis</i>	<i>Ectopleura crocea</i> water soluble secretion; GABA, choline, serotonin, glutamate, $K^+$ , $Cs^+$ .	induces high proportion of metamorphosis	[145]

Table 3. Cont.

Species	Compound	Solution/Dose/Time/ % Metamorphosis	Reference
<i>Adalaria proxima</i>	Presence of <i>Electra pilosa</i> ; peptide with low molecular weight (<500 kDa)		[146,147]
	Adult conspecific	5000 L tank with adult conspecific, >10,000 veliger, 0%	
	Adult conspecific conditioned water	45 L tank conditioned for 12 h with adult female conspecific, ~2000 veliger, 12 h, 0%	
	Conspecific intracapsular fluid	6-well plates; 6 veliger per well, 20 µL intracapsular fluid added to each well, 12 h, 0%	
	Adult prey	45 L tank, adult CoTS, ~2000 veliger, 12 h, 0%	
	Adult prey conditioned water	45 L tank conditioned for 12 h with adult CoTS, ~2000 veliger, 12 h, 0%	
	Adult prey mucous	6-well plates; 6 veliger per well, 20 µL CoTS mucous added to each well, 12 h, 0%	
	Juvenile prey	500 mL tank, 10× juvenile CoTS, ~2000 veliger, 12 h, 0%	
	Environmental cue: crustose coralline algae (CCA)	6-well plates; 6 veliger per well, CCA chip, 24 h, 0%	
	Environmental cue: CCA methanolic extract	6-well plates; 6 veliger per well, 5, 10 µL mL <sup>-1</sup> , 12 h, 0%	
<i>Charonia tritonis</i>	Sediment (1–1000 µm) from aquaria (live rock, coral, macroalgae, assemblage of other reef organisms)	500 mL tank, ~2000 veliger, 12 h, 0%	[25]
	Filtered (60 µm mesh) sediment from aquaria (live rock, coral, macroalgae, assemblage of other reef organisms)	500 mL tank, ~2000 veliger, 12 h, 0%	
	Multivitamin	500 mL roller tank, ~2000 veliger, 0.05 multivitamin capsule, 12 h, 0%	
	KCl	500 mL tank, ~2000 veliger, 10, 20 mM, 12 h, 0%	
	Synthetic peptides: Serotonin, GLW-amide, WW-amide, APGW-amide, FRMF-amide, sCAP-amide, FF-amide, FF-amide 2, FV-amide, ADRYSFFGGL, Allotropin, Cerebrin, Conopressin, Myomodulin, KPGW-amide, GnRH, Egg laying hormone, Dopamine, L-DOPA	6-well plates; 6 veliger per well, 10 µM mL <sup>-1</sup> , 12 h, 0%	

The post-settlement biology, including juvenile growth rates, of some marine gastropods is understood. In newly settled juvenile *Cabestana spengleri* (Tonnoidea: Cymatiidae), growth rates have been estimated at 0.3 mm (shell length) day<sup>-1</sup> and *C. muricinum* at 0.3–0.4 mm day<sup>-1</sup> [149,150]. In contrast, the growth rate of recently settled juvenile *G. muricinum*, *M. aquatilis* and *M. pilearis* (Tonnoidea: Cymatiidae) is much higher, averaging 0.6–0.7 mm day<sup>-1</sup> for an extended period up to 6 weeks, the highest rates reaching 0.8–0.9 mm day<sup>-1</sup> [121]. Such high growth rates, coupled with an abundance of food, allow these tritons to achieve formation of the first varix, e.g., within 33 days of settlement for *G. muricinum* and between 50–57 days for *M. aquatilis* and *M. pilearis* [121]. Reaching this life stage is critical for reducing vulnerability to predators [151], but the factors that govern this transition remain a significant knowledge gap in the life cycle of *C. tritonis*. Similarly, adult growth rates are unreported [151].



## 7. Management of *Charonia tritonis*

### 7.1. Threats to Population Recovery

Throughout their habitat range *Charonia* spp., including *C. tritonis*, are considered uncommon, rare or with seriously depleted populations approaching extirpation [2,57,152,153]. Unregulated harvesting of *C. lampas* and *C. variegata* has severely impacted numbers in the Mediterranean Sea [154–156]. Similarly, in the 1950s *C. tritonis* were regularly observed in the Atlantic and Caribbean, but are now reported to be uncommon to rare throughout [55,157]. Anecdotal evidence indicates that *C. tritonis* were abundant on the GBR prior to incidental collection in the 1930s [6]. Between 1947 and 1960, income from commercial harvesting of Bêche-de-mer (sea cucumber) and *Rochia* spp. (a top-shelled sea snail commonly known as Trochus) in northern Australia was supplemented with *C. tritonis*, with anecdotal records indicating over 800 *C. tritonis* shells were collected from Cooktown to Palm Island in a single trip [8]. Based on these records, an estimated 10,000 *C. tritonis* shells were collected annually [8] and by the 1970s they were considered uncommon [7]. Trade statistics of ornamental shell collections and sales reveal there was a considerable increase in the volume of *C. tritonis* shells traded in the 1970s along with a further depletion of their populations on harvested reefs [9,158,159]. However, as insufficient scientific data exists for harvesting or trade figures, it is difficult to accurately determine whether their rarity today is a result of overexploitation alone.

Between 1966 and 1972, dive surveys conducted on over 130 GBR reefs located only 78 *C. tritonis* [160]. Another study surveying the reefs between Princess Charlotte Bay and the Palm Islands and spanning two years (1966–1968) only found 28 *C. tritonis* [6]. By the late 1980s, as part of the program to cull CoTS on the GBR, 30 divers making 90 dives over 2 weeks were successful in locating only 12 individuals [161]. Furthermore, a population density of <1 *C. tritonis* per km<sup>2</sup> was extrapolated based on a 12 month survey (430 h diving time; 1993 to 1994) of 12 GBR reefs between Port Douglas and Airlie Beach [162]. By 2016, divers of the ‘Targeted Crown-of-thorns Starfish Control Program’ reported sighting, on average, one *C. tritonis* triton per 10 day CoTS culling trip [163]. Similar anecdotal evidence extends to other countries. In the 1960s, local Tongan fisherman regularly collected up to seven *C. tritonis* per day, whereas by 1993, and despite a bounty, none were located over a two-month period [162]. During a 6-month survey of Guam reefs, divers sighted only seven *C. tritonis* [164]. Despite the Thailand Tropical Marine Mollusc Programme [165] listing *C. tritonis* as a ‘target’ species of interest, only three specimens were procured between 1997–1998. Such anecdotal evidence within the grey literature suggests extreme rarity, and at such low population densities, and as a dioecious species, the probability of encountering a mate and successful reproduction may be severely limited, even after the introduction of marine protected areas [166], as has been the case for the endangered Caribbean Queen conch, *Aliger* (formerly *Strombus*) *gigas* [167,168]. However, it should be noted that the cryptic and nocturnal nature of *C. tritonis* may impede visual counts during daylight hours and result in underestimated population estimates.

Chesher [164] hypothesized that the reduction in the standing stock of *C. tritonis* associated with over-harvesting might have been sufficient at the time for CoTS populations to rise above a critical minimum leading to conditions conducive to outbreaks. Modelling studies have since predicted that in higher numbers *C. tritonis* may suppress CoTS numbers and potentially limit population outbreaks [169–171], yet these models suffer from a lack of verified or adequate information describing the predator-prey dynamics between *C. tritonis* and CoTS [172] and rely on best guestimates of previous and current *C. tritonis* populations.

Collection of *C. tritonis* has been prohibited in Australia since 1983 [173], although illegal poaching has been reported on the GBR. In addition, as a demonstration of latent demand, *C. tritonis* shells have continued to be imported annually into Australia (David Savage, QNPWS pers. comm. in [162]) and more recently traded over the internet [174]. To secure its future, a proposal was submitted in 1993 to include *C. tritonis* on the CITES Appendix II list as a species that may become threatened or extinct unless trade is closely controlled. This proposal was unsuccessful due primarily to the lack of evidence on its biological and trade status, i.e., the

Berne criteria for listing could not be met [175–177]. Regardless, and independent of international agreement, many Indo-Pacific countries have banned the collection or exportation of *C. tritonis*: Australia (1969), India (1972), Seychelles (1969/1978), Fiji (1971), Indonesia (1987) and Philippines (2001). Other countries and jurisdictions, including Guam, Vanuatu and Kenya, have regulated collection [2,9,153–156,178–182], yet several *Charonia* spp. continue to be illegally traded in large volumes [2,183,184]. In countries where collection is not banned, *C. tritonis* are deemed to be locally extinct or extremely rare, i.e., Thailand [57].

With *C. tritonis* now protected on the GBR, the presumption is that populations are slowly returning to pre-1960 levels yet predicting population recovery timeframes is challenging as little is known of the natural pressures they face. In the Caribbean, predation on *C. variegata* by rays (*Aetobatus* sp.) and turtles (*Caretta caretta* and *Eretmochelys imbricata*) has been observed, these predators crushing the shells [55]. Groups of moribund and dead *C. variegata* were also observed; their opercula found near their intact shells with no obvious cause of death, although *Octopus* sp. was ruminated [55]. Living and dead shells have been observed to be badly pitted by bioeroding boring sponges of the genus *Cliona* [55,185], and X-ray has revealed the extent of internal damage sustained by larger (presumably older) specimens [185]. While such infestations have been observed in other gastropods [186] and found to be responsible for extensive shell damage in larger *C. tritonis* shells it is not known whether they cause mortality. Aside from these natural pressures, anthropogenic and environmental stressors present a real and continuing threat to all *C. tritonis* life stages: eggs [187], larval development [188,189], larval diet [190], adult growth [191], shell [192,193] and predator-prey interactions [194]. The cumulative impacts of these, together with the shell still being highly coveted by collectors and the long planktotrophic development phase, may slow recovery to a point where *C. tritonis* numbers will never be naturally restored. A genetic study of *Columbella adansonii* (Family Columbellidae), which also has planktotrophic development, revealed no phylogeographic structure, low interpopulational variance, low genetic diversity and a lack of spatial structure in the distribution of the genetic diversity confirming pelagic larval dispersal to be a critical factor driving high genetic connectivity [195]. Similarly, pelagic larval dispersal was established as the primary factor driving the high level of genetic connectivity in *Talisman scrobilator* (Family Bursidae) over vast distances and throughout its habitat [196]. Unfortunately, no such data is available for *C. tritonis*. Targeted conventional and eDNA surveys, in combination with population connectivity studies and further research into the planktotrophic and juvenile life phases, are essential to assess the gene flow between local and regional *C. tritonis* populations and determine the influence of pelagic larval dispersal. Revealing the pattern of genetic connectivity in *C. tritonis* is highly relevant for its conservation and is particularly important if the population is reliant on the influx of planktotrophic larvae from regions where the shell continues to be overexploited.

## 7.2. Aquaculture and Stock Enhancement Potential

Food security and pharmaceutical biodiscovery has driven the development of aquaculture programs for over 36 marine gastropods (Table 4), including several endangered species [122,197–201]. Some of these programs have also been instrumental in species' conservation. For example, native populations of *A. gigas* have been severely depleted throughout the Caribbean to the point of being threatened and several aquaculture programs to restock these for commercial harvesting have now been established [135,166,199,202–206]. Similarly, wild populations of *Rochia nilotica* in Vanuatu and Vietnam have been successfully replenished through captive breeding [207,208]. More recently, *Ostrea lurida* aquaculture programs have been established along the west coast of North America, with the primary aim being conservation of the species and recovery of locally extinct communities to restore ecosystem functions; harvesting being a secondary (i.e., future) consideration [209].



**Table 4.** Marine mollusks which are produced at commercial scale through aquaculture. Modified from [210,211]. <sup>c</sup> carnivore, <sup>h</sup> herbivore, <sup>d</sup> detritivore, <sup>f</sup> filter feeder, \* conservation achieved.

Group	Species
Bivalvia (44)	
Oysters <sup>d/f</sup>	<i>Ostrea edulis</i> , <i>O. chilensis</i> , <i>O. conchaphila</i> , <i>Magallana gigas</i> , <i>Crassostrea virginica</i> , <i>Saccostrea glomerata</i>
Mussels <sup>d/f</sup>	<i>Mytilus edulis</i> , <i>M. galloprovincialis</i> , <i>M. chilensis</i> , <i>Perna canaliculus</i> , <i>Anodonta cygnea</i> , <i>Aulacomya atra</i> , <i>Choromytilus chorus</i> , <i>Modiolus</i> spp.
Scallops <sup>d/f</sup>	<i>Mizuhopecten yessoensis</i> , <i>Aequipecten opercularis</i> , <i>A. (Agropecten) irradians</i> , <i>Argopecten purpuratus</i> , <i>Mimachlamys varia</i> , <i>Pecten maximus</i>
Clams <sup>d/f</sup>	<i>Mercenaria mercenaria</i> , <i>Corbicula fluminea</i> , <i>Anadara broughtonii</i> , <i>Cyclina sinensis</i> , <i>Venus verrucosa</i> , <i>Donax</i> spp., <i>Mya arenaria</i> , <i>Leukoma staminea</i> , <i>Saxidomus gigantea</i> , <i>Tresus nuttallii</i>
Carpet shells <sup>d/f</sup>	<i>Ruditapes decussatus</i> , <i>Ruditapes philippinarum</i> , <i>Venerupis corrugata</i> , <i>Polititapes rhomboides</i>
Razor clams <sup>d/f</sup>	<i>Sinomovacula</i> spp., <i>Ensis ensis</i> , <i>Panopea abrupta</i>
Cockles <sup>d/f</sup>	<i>Tegillarca granosa</i> , <i>Cerastoderma edule</i> , <i>Cardiidae</i>
Pen shell clams <sup>d/f</sup>	<i>Atrina</i> spp.
Gastropoda (+5)	
Snails	<i>Rapana</i> spp. <sup>c</sup> , <i>Babylonia</i> spp. <sup>d/c</sup> , <i>Buccinum undatum</i> <sup>c</sup> , <i>Aliger gigas</i> <sup>d/h,*</sup> , <i>Strombus pugilis</i> <sup>d/h</sup> , <i>Rochia nilotica</i> <sup>h,*</sup> , <i>Stromboidea</i> <sup>h/d</sup>
Abalone <sup>h</sup>	<i>Haliotis rufescens</i> , <i>H. discus</i> , <i>H. tuberculata</i>
Cephalopoda (1)	
Octopus <sup>c</sup>	<i>Octopus</i> spp.

There are four critical biological stages which require optimization for successful gastropod aquaculture: (1) broodstock procurement, (2) seed (egg and larvae) production, (3) juvenile nursery culture, and (4) sub-adult grow-out to commercial size. However, almost all successful aquaculture programs involve species that are easily collected, spawn year-round, and have lecithotrophic non-feeding larvae that hatch, settle within days, and quickly transition to herbivorous juveniles achieving a minimum market size in 2–3 years [211–216].

Adult *C. tritonis* are rare in the wild, yet they can be collected in sufficient numbers (typically under permit) to establish a broodstock population [25,76,78,217]. Broodstock will breed spontaneously in captivity, with both fertilization and larval hatching readily achieved (Table 2). However, the husbandry requirements of the planktotrophic larvae are substantial, and reliant on suitably nutritional adult and larval diets, the latter typically a cocktail of phyto- and zooplankton [218,219]. Aquaria-reared *C. tritonis* veliger will actively hunt and ingest mixed microalgae, copepod nauplii and adults, artemia nauplii and adult rotifers [25], yet this diet was found to be deficient or suboptimal. Veliger survived for up to 300 days but there was no evidence of larval growth, development or settlement. *C. lampas* veliger fed a diet of diatom and *Artemia salina* survived for 21 days [156]. *C. lampas* (*sauliae*) fed *Chaetoceros simplex* var. *calcitrans*, *Isochrysis galbana*, and *Diacronema lutheri* achieved the highest larval survival rate (23% at 15 °C) and shell growth ( $408 \pm 21.52 \mu\text{m}$  to  $625 \pm 19.76 \mu\text{m}$ ) over 60 days [220]. In this instance, significant increases in larval survival and growth rates were also achieved when the broodstock (i.e., parental) diet included the preferred starfish prey, *Asterias amurensis* [221]. Marine larvae, including the planktotrophic larvae of many gastropod species [133,135], rely on a hierarchy of environmental sensory cues to locate suitable settlement sites and initiate metamorphosis (Table 3) [222–224]. The critical challenge in rearing *C. tritonis* for stock enhancement remains the identification of these chemical cues (likely mediated by chemosensory receptors [94]) that trigger the cascade of intercellular signaling events and induce metamorphosis and settlement.

Comparative transcriptomic, proteomic and metabolomic (i.e., multi-omics) techniques have proven critical to revealing the underlying molecular mechanisms that regulate hatching, growth, settlement and metamorphosis of commercially and scientifically important molluscan larvae [95], including *Aplysia*, *Biomphalaria*, *Haliotis*, *Cornu*, *Lottia*, *Lymnaea* and *Aliger* [225–228]. Proteomic, transcriptomic and associated expression profiling studies of *A. gigas* have provided significant insight into the reproductive mechanisms and genetic factors that underpin successful spawning in wild populations [226,229]. Furthermore, microsatellite analysis of Caribbean populations separated by 600 km found they were not panmictic (i.e., having limited gene flow) even though the veliger are capable of remaining in the plankton for up to two months and susceptible to environmental factors that promote larval dispersal. Overall, a global deficit of gene heterozygosity was detected, with only four stock populations identified, a finding that led to a reassessment of both local and regional management and conservation efforts [227]. Mitogenomic and transcriptomic resources, based on both larval and adult life stages, have been established for *C. tritonis* and are now revealing information regarding reproduction, and larval development, growth, and competency [37,66,74,94]. However, sequencing the complete nuclear genome and establishing genetic connectivity and diversity of *C. tritonis* is essential for identifying critical stock populations to guide local and/or regional conservation efforts, and to develop species-specific aquaculture methodologies for potential stock enhancement.

## 8. Predator-Prey Dynamics—*Charonia tritonis* and CoTS

### 8.1. Direct Interactions

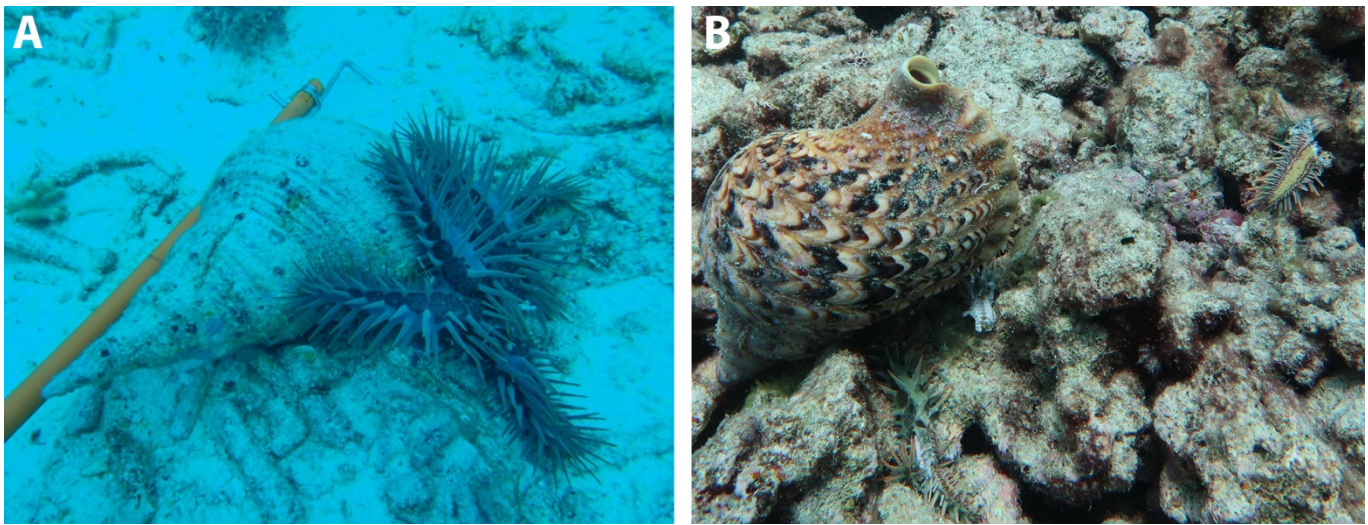
As pivotal as agents of natural selection, predators drive rapid evolution of key survival behaviors, defensive morphologies and chemical defenses in prey [230,231]. However, despite the various anti-predatory attributes of CoTS (reviewed in [232]) approximately 14 invertebrate and vertebrate species have been *observed* to hunt, attack or consume *live* adult CoTS [4,10,233,234] (Table 5). These predators are mostly generalized feeders and not obligate to CoTS, many preying on injured CoTS or autotomized tissues rather than healthy individuals [10,235].

**Table 5.** Predators observed to prey on healthy live juvenile, sub-adult and adult Crown-of-Thorns starfish. Modified from [4].

Taxa (Class)	Species	Reference
Anthozoa	<i>Stoichactis</i> sp.	[164,233,236,237]
	<i>Paracorynactis hoplites</i>	
	<i>Pseudocorynactis</i> sp.	
Polychaeta	<i>Pherecardia striata</i>	[235,238]
Gastropoda	<i>Charonia tritonis</i>	[239–242]
Malacostraca	<i>Hymenocera picta</i>	[235,242–244]
	<i>Tumidodromia dormia</i>	
Actinopterygii	<i>Epinephelus lanceolatus</i>	[10,164,239,241,245–251]
	<i>Lethrinus</i> spp.	
	<i>Cheilinus undulatus</i>	
	<i>Arothron hispidus</i> , <i>A. stellatus</i>	
	<i>A. nigropunctatus</i>	
	<i>Balistoides viridescens</i> <i>Pseudobalistes flavimarginatus</i>	

Although there is limited literature available documenting *in situ* predation by *C. tritonis* (reviewed by [4]), they have been observed by divers to hunt and feed on CoTS [7,239]. In addition, early field studies reported *C. tritonis* actively seeking and attacking caged CoTS [6]. Preferential predation of CoTS by *C. tritonis* was observed on Grubb and John Brewer reefs

even though *Linckia laevigata* (blue star) was also abundant [161]. Recently, opportunistic surveys in 2020 have photographed *C. tritonis* feeding on adult CoTS (Figure 3).



**Figure 3.** Observations of *Charonia tritonis* feeding on Crown-of-Thorns starfish (CoTS). (A) Horseshoe Reef, remnants of CoTS limbs evident (Photograph: Kate Osbourne, AIMS Voyage 27, 4 October 2018) and (B) Llewellyn Reef, 9 m, ~30 cm shell length [252]; Photograph: crew of Escape GBRMPA Voyage 43, 30 September 2020).

### 8.2. Hunting

Many species of Tonnoidea are specialist predators [33,35]. They are distinct from grazers, having a siphonal canal located within the anterior lip of the shell; the pallial mantle margin folds to fit the lip and directs inhalant water current to a highly developed osphradium containing chemoreceptors capable of detecting prey odors [253]. They also have a long pleurembolic proboscis that has been adapted to deliver, via insertion, toxins and acidic pH 2.0 saliva that are discharged from associated glands [33,254]. Such attacks can cause almost instant immobilization of prey and death, while for some marine gastropods the function of the proboscis is to activate parasitism, as is the case for *G. muricinum* preying on tridacnid clams [121].

*Charonia tritonis* primarily hunts at night. When hunting prey, they randomly sweep their tentacles from side to side. Upon detection of prey odor, this sweeping motion intensifies, and as the odor gradient strengthens, their velocity increases and movement becomes directional [16,37,55]. When in close proximity, the fully extended proboscis (up to 400 mm) perforates the outer skin of the prey targeting its central disc. Rapid paralysis is induced by injection with either a toxin or acidic saliva [55,255,256]. Once paralysed, the prey is held firm by the large muscular foot, after which it is completely enveloped in a thick mucus allowing the radula to rasp the CoTS, rendering the thorny outer skin ineffectual. CoTS secrete toxic hemolytic saponins [257–259] and other toxins into the water column [37] as a chemical defense [260–262] and this mucus likely functions to prevent entry of this toxic cocktail into mantle cavity where it could potentially cause damage to the delicate filaments of the monopectinate ctenidium.

Asterosaponins produced by many species of starfish act aposematically as a signal of unpalatability to potential predatory fish, [263–267], annelids, mollusks, arthropods and vertebrates [257,268–270]. Ultimately, they can prove lethal [262,267,271]. *C. tritonis*, however, are immune to these toxic saponins, readily feeding on live adult CoTS [37]. This immunity may arise from glycosidases. In the liver of *C. lampas*, the glycosidases  $\alpha$ -fucosidase,  $\beta$ -xylosidase and  $\beta$ -glucosidase breakdown the asterosaponins by cleaving off the oligosaccharide chain to yield the free non-toxic sterol [272,273]. The sulfur scavenging enzyme arylsulfatase, which is capable of catalysing the breakdown of sulphated saponins,



has also been detected in the salivary glands of *C. tritonis* [37]. This finding supports earlier studies of *C. tritonis* tissues, whereby the principal sterols of CoTS:  $\Delta^7$ -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%) [274], were isolated in significant amounts. Together, these chemical investigations provide indirect evidence for the dietary preference of *C. tritonis*, i.e., asteroids and specifically CoTS.

Not all attacks by *C. tritonis* on CoTS are immediately fatal. CoTS can autotomize the injured arm(s) and later regenerate them [38,64,164], yet observations in captivity have revealed many individuals that initially survive an incomplete *C. tritonis* attack ultimately perish if the proboscis has penetrated the outer skin [185].

### 8.3. Prey Preference

Prey preference is generally explained based on random encounter rates and capture success, with deviations from this indicative of selective predation. For many gastropods, simple encounter rates often fail to account for prey selection indicating they make behavioural diet selections [253,275,276]. For example, *C. (rubicunda) lampas* preys on the most abundant echinoderm within its habitat, but when offered a choice shows a preference for the asteroids *Patiriella regularis* and *Coscinasterias calamaria* [36]. This prey selection is linked to the well-developed chemosensory organs of the Tonnoidea, which enables them to discriminate between prey species and guide hunting. In a controlled aquarium experiment, *C. (rubicunda) lampas* exposed to odor from prey items placed in an upstream current respond with hunting behaviour [36]. Similarly, Y-maze aquarium experiments have shown that waterborne odors released by CoTS attract *C. tritonis* [37,217]. In experimental aquaria, predators are often maintained on a limited diet and may well become impacted by ‘ingestive conditioning’, hence extrapolation of results from controlled prey preference experiments is fraught with ambiguity [253,277,278]. A further consideration is the ability of predators to undergo dietary switching dependent on the abundance of the preferred prey species. When abundance is high relative to other prey species the number of attacks on and the percent mortality of the preferred prey species is disproportionately large, and disproportionately small when the prey species is relatively rare [279]. Whether this phenomenon influences the feeding preferences of *C. tritonis* remains to be established.

The natural diet of *Charonia* spp. is reported to be predominantly asteroids, followed by holothurians and, to a lesser extent, echinoids [36,55,280,281]. For *C. lampas*, its distribution in the Mediterranean is partially controlled by that of its prey *Holothuria forshali* and *Paracentrotus lividus* [282,283]. In New Zealand, *C. lampas* preferentially preys upon the most common and largest echinoderm in its habitat, *P. regularis* [36]. *C. lampas* presented with meal derived from 15 different species, revealed a preference for asteroid > holothurian > fish > crustacean > other species [284]. A similar preference gradient was observed in *C. lampas* presented with live prey over 30 days: asteroids > holothurian > echinoids, with no predation on mollusks [136]. Based on these findings *C. lampas* was identified as a possible biocontrol agent for the predatory starfish *Asterias amurensis* threatening the security of economically important shellfish fisheries.

Early reports of predation by *C. tritonis* indicated a preference for *Nardoa* sp. [6], although they were also observed to prey on *Stichopus* sp., *L. laevigata* [36] and sub-adult and adult CoTS [7]. This was supported by caged experiments whereby *C. tritonis* was observed preferentially feeding on asteroids other than CoTS if given a choice [239]. Regardless, *C. tritonis* ( $n = 15$ ) held in a fenced enclosure with 100 adult CoTS over three months consumed 1.5 CoTS week<sup>-1</sup> [6]. In another study, two *C. tritonis* consumed ten small and three large CoTS month<sup>-1</sup> [285,286]. Given infested reefs have higher number of CoTS, and that *C. tritonis* would presumably consume whichever echinoderm species they first encounter, these studies suggest they would feed more so on CoTS. Observations of *C. tritonis* feeding preferences in the laboratory confirm they favor asteroids, yet the preferred species appears to vary. When presented with live asteroids (CoTS, *Culcita novaeguineae* and *Echinaster*), echinoid (*Diadema setosum*) and holothurians (*Holothuria atra* and *Stichopus chloronotus*) [80],

a single adult *C. tritonis*, maintained in captivity for 2 years, preferentially hunted and consumed CoTS, while *C. novaeguineae* were only partially consumed. Both *H. atra* and *S. chloronotus* were also readily consumed, however, they induced symptoms of anesthesia in *C. tritonis* post-feeding [80]. When offered both CoTS and *Linckia* in equal numbers, *C. tritonis* attacked and consumed all CoTS entirely within 12 h of being introduced, whereas some *Linckia* remained untouched, suggesting a dietary preference for CoTS [161]. *C. tritonis* broodstock have been successfully maintained on CoTS, *C. novaeguineae*, *H. atra*, *S. chloronotus* [78] and *Stichopus horrens* [76]. Hunting behaviour was initiated 83% of the time for CoTS, 57% for *C. novaeguineae* and 24% for both *H. atra* and *S. chloronotus*. CoTS were completely devoured while the other three species were either very slowly or only partially consumed [78]. *Charonia tritonis*, fed solely on CoTS, have been observed to complete the entire hunt, attack and consumption of an adult CoTS within 4 h to 24 h [37]. Recent citizen science surveys of *C. tritonis* have observed feeding on CoTS, *Linckia* sp. and *C. novaeguineae* [252].

CoTS not only exhibit a strong predator avoidance reaction when in direct physical contact with *C. tritonis* [161], they also display a rapid fleeing response when exposed to *C. tritonis*-conditioned water; CoTS will actively move away from the source of the *C. tritonis* odor [16]. This chemosensory-driven escape response provides further evidence for CoTS as the preferred prey of *C. tritonis* and also supports earlier sightings of *C. tritonis* on CoTS infested reefs, feeding predominately on CoTS [6]. However, to determine the true potential of *C. tritonis* as a CoTS biocontrol agent, there remains a need to establish its full feeding spectrum and prey preference, as well as the ‘attractiveness’ of these alternate prey species to *C. tritonis*, through both physical presence and choice experiments. Furthermore, to predict the extent of collateral damage to non-CoTS prey populations, the proximity deterrence effects of physical presence (i.e., hunting and consumption) and/or odor (i.e., non-consumptive) of *C. tritonis* on the behaviour and mortality of these species needs to be established.

#### 8.4. Indirect Interactions

Prey population density is generally directly mediated by the predator via kill and consumption rates [287]. This process is often referred to as a density-mediated indirect interaction (DMII) and can impact on prey resources as well as other non-prey species [288–298]. In Trinidad, *C. variegata* have been observed hunting in pairs, methodically herding and attacking aggregated spawning *Echinaster sentus*. Individual prey was only partially consumed before the pair resumed hunting and feeding on yet more individuals. This DMII thereby exerted downward pressure on the entire *E. sentus* population [55]. The removal (either unintentional or deliberate) of such marine benthic predators can influence not only the population density of the predominate prey, but also lead to downstream effects on the broader benthic community [299]. The lack of accurate surveys of *C. tritonis* on the GBR pre- and post-exploitation makes it difficult to assess whether this same knock-on effect is a driver for the increased frequency and intensity of CoTS outbreaks.

The mere presence of predators in a community can have significant influence on prey, forcing them to modify their condition (i.e., alter a trait), including phenotype (body shape, armor and size), behaviour (refuge seeking), and physiology (chemical defenses), a process referred to as a trait-mediated indirect interaction (TMII) [300–311], regardless whether or not they consume prey items [312–316]. In essence, while modifying traits minimizes risk of predation, they may inadvertently result in sub-optimal performance of the prey, i.e., slowing and/or delaying growth and maturity [317]. In aquatic ecosystems, non-consumptive TMII effects generally exceed DMII consumptive effects [318,319]. Risk perception by prey, such as that displayed by CoTS in the presence of *C. tritonis*, therefore plays a dominant role in marine trophic interactions, both temporally and spatially, and influences ecosystem stability [319–323].

Quantitative data supporting the ecosystem-wide impacts of TMIs induced specifically by waterborne predator signals has been reported [231,294,317,324]. These chemically

mediated phenomena, referred to anecdotally as ‘landscapes of fear’ [312,319,325], are finding application in biocontrol strategies [317,326] including in the marine environment [327]. Regarding CoTS, when exposed to the waterborne chemical odor of *C. tritonis*, representing a short-lived but unpredictable high-risk situation [328–332], they exhibit predator avoidance behaviour [16]. The intensity, persistence [333,334], scale and direction [335,336] of the odor source provides prey with crucial information on immediate risk [337–340] and determines the predator’s zone of impact. Furthermore, chemoreceptor sensitivity and specificity is critical if the prey to discriminate such signals [341]. In this context, novel CoTS control technologies are being developed to exploit this predator avoidance behaviour [16,17].

#### 8.5. Attributes of a CoTS Biocontrol Agent

Biocontrol is the use of natural enemies to control pest species [342] and has been considered in the context of the marine environment. However, strategies used, especially the choice of predator, the practicality of implementation, and the scale of the effect required are serious issues that need to be overcome to effectively control marine pest species, particularly mobile ones such as CoTS [327,343].

Effective biocontrol agents generally have three attributes: prey specificity, a reproductive rate similar to that of the pest species, and capacity to thrive in the prey’s habitat [344]. Similarly, their implementation is usually via three main routes: classical, augmentation and conservation. However, Atalah et al. [327] has warned that “classical biocontrol based on the deliberate introduction of non-indigenous agents has a high risk of leading to adverse non-target effects in marine environments and cannot be justified”. Augmentative inundation strategies, which involve the periodic release of a natural enemy without establishing a permanent predator population, are more amenable to marine environments, while conservation strategies, which are more complex to implement, are considered the most acceptable and truly sustainable approach [24]. *C. tritonis*, being an indigenous species and a specialist predator of CoTS in their native range, is suited to the latter two strategies and deserves further investigation. For example, current (laboratory-derived) knowledge indicates the net predatory effect of *C. tritonis* on CoTS is largely due to (non-lethal) TMIs, yet because of their overexploitation it is not known to what extent they would also contribute to DMII should their population be returned to pre-exploitation numbers, although their status as a primary predator of the adult CoTS (e.g., targeted hunting and lethal consumption) suggests this is likely.

CoTS outbreaks represent a unique problem with respect to their pest status. CoTS are naturally endemic to the Indo-Pacific and play a beneficial role in promoting coral diversity. As such, efforts to control them are not focused on eradication, as is the case in most pest control programs, but rather suppression of populations. Although the drivers of CoTS outbreaks are still highly debated, the release of predation pressure because of over-exploitation of predators [345] means the implementation of augmentative inundation and conservation biocontrol strategies are likely to offer a sustainable approach to suppress CoTS populations in the longer term with the added advantage of restoring *C. tritonis* populations.

Gastropod species have been used, with varying degrees of success, as biocontrol agents (Table 6). Of note are the two predatory marine gastropods *Conus textile* and *Babylonia areolata*. Both have been investigated for their potential as biocontrol agents for *M. pulex*, a gastropod snail that feeds on the commercially important oyster *Pinctada fucata* [346,347], and found to be effective agents in reducing predation on the oyster. Most recently, the presence of *Vasula deltoidea* has been shown to significantly reduce *Coralliophila galea* corallivory and thus improve *Acropora cervicornis* survival [348]. As for these gastropods, *C. tritonis* possesses many of the biological and ecological traits required for a biocontrol agent (Table 7) and their potential to limit population outbreaks of CoTS is further supported by modelling and tracking studies [72,169–171]. Yet, lessons learnt from unsuccessful campaigns, such as that of *Euglandina rosea* which preferentially hunts



the native *Achatinella lila* over the invasive target pest *Lissachatina fulica* [349], need to be considered for *C. tritonis* to understand the likely impact to non-target endemic echinoderm species and the ecosystem as a whole.

**Table 6.** Gastropods deployed as biocontrol agents. Modified from [350], see references therein. Updated entries are individually referenced. \* denotes marine species, \*\* freshwater species.

Species	Target of Control; (N) = Unsuccessful, (Y) = Moderate Success, (P) = Potential	Genome of Gastropod	Mitogenome of Gastropod
<i>Babylonia areolata</i> *	<i>Monoplex pilearis</i> (Y) [346]—mitogenome reported [351]	No	Yes [352]
<i>Conus textile</i> *	<i>Monoplex pilearis</i> (Y) [346]	No	Yes [353]
<i>Edentulina affinis</i>	<i>Lissachatina fulica</i> (N)—mitogenome reported [354]	No	No
<i>Edentulina obesa bulimiformis</i>	<i>Lissachatina fulica</i> (N)	No	No
<i>Euglandina rosea</i>	<i>Lissachatina fulica</i> (N), <i>Cornu aspersum</i> (N), <i>Otala lactea</i> (N), <i>Rumina decollata</i> (N), <i>Slugs</i> (N)	No	No
<i>Tayloria kibweziensis</i>	<i>Lissachatina fulica</i> (N), <i>Cornu aspersum</i> (N), <i>Otala lactea</i> (N), <i>Rumina decollata</i> (N), <i>Slugs</i> (N)	No	No
<i>Tayloria quadrilateralis</i>	<i>Lissachatina fulica</i> (N)	No	No
<i>Gonaxis vulcani</i>	<i>Lissachatina fulica</i> (N)	No	No
<i>Gulella bicolor</i>	<i>Lissachatina fulica</i> (N), <i>Subulina octona</i> (N)	No	No
<i>Gulella wahlbergi</i>	<i>Lissachatina fulica</i> (N)	No	No
<i>Marisa cornuarietis</i> **	Freshwater weeds and snail vectors of schistosomes; <i>Biomphalaria glabrata</i> , <i>Biomphalaria pfeifferi</i> , <i>Bulinus tropicus</i> , <i>Bulinus truncatus</i> , <i>Hydrilla verticillata</i> , <i>Eichhornia crassipes</i> (Y)	No	Yes [355]
<i>Melanoides tuberculata</i> **	<i>Biomphalaria glabrata</i> , <i>Biomphalaria straminea</i> , <i>Biomphalaria havanensis</i> , <i>Biomphalaria peregrina</i> , <i>Biomphalaria helophia</i> (N)	No	No
<i>Natalina cafra</i>	<i>Lissachatina fulica</i> (N), <i>Otala lactea</i> (N), <i>Rumina decollata</i> (N), <i>Slugs</i> (N)	No	No
<i>Oleacina straminea</i>	<i>Lissachatina fulica</i> (N)	No	No
<i>Pomacea glauca</i> **	<i>Biomphalaria glabrata</i> (N), <i>Pistia stratiotes</i> (N)	No; available for <i>P. canaliculata</i>	No; available for <i>P. canaliculata</i> , <i>P. diffusa</i> & <i>P. maculata</i> [356–359]

Table 6. Cont.

Species	Target of Control; (N) = Unsuccessful, (Y) = Moderate Success, (P) = Potential	Genome of Gastropod	Mitogenome of Gastropod
<i>Ptychotrema walikalense</i>	<i>Lissachatina fulica</i> (N)	No	No
<i>Rumina decollata</i>	<i>Cornu aspersum</i> (N)	No	No
<i>Salasiella</i> sp.	<i>Lissachatina fulica</i> (N)	No	No
<i>Streptaxis contusus</i>	<i>Lissachatina fulica</i> (N)	No	No
<i>Tarebia granifera</i> **	<i>Biomphalaria havanensis</i> , <i>Biomphalaria peregrina</i> , <i>Biomphalaria helophila</i> (N)	No	No
<i>Vasula deltoidea</i> *	<i>Coralliophila galea</i> (Y), [348], <i>C. abbreviata</i> (P) [360]	No	No

**Table 7.** Summary of characteristics of *Charonia tritonis* and amenability to Crown-of-Thorns Starfish (CoTS) biocontrol. Concept modified from [361]. Prey specificity, predation efficiency, lifespan, and secretion of the ‘landscape of fear’ feature as key attributes. Amenability is ranked as limited (+), likely (++) and certain (+++).

Characteristic	Definition	<i>Charonia tritonis</i>	Ranking
Narrow host range [362,363]	Generalized predators; preference for the target pest population in the presence of alternate natural prey	Echinoderm specialists; preference for CoTS over other echinoderms not established	++
Climatic adaptability [364]	Adaptability to the introduced environment, including to environmental extremes	Endemic to GBR	+++
Synchrony with prey life cycle [365]	Should be present when the CoTS juveniles first emerge.	Long-lived; likely decades—unconfirmed	+++
	Self-replicating capacity; High reproductive potential with large numbers of offspring.	lays large clusters of capsules—2000 larvae per capsule	++
	Population growth rates; teleplanic long-lived oceanic larval phase	Likely slow—unconfirmed	+
	More than one generation is completed for each generation of the pest	annual spawner on GBR	++
	Longevity	Likely decades—unconfirmed	+++
Efficient search ability	Prey detection ability even when prey is scarce	Chemosensory capacity	+++
Short handling time	Higher predator consumption rates equate to greater number of attacks on prey. Small populations of efficient natural enemies may be more effective biocontrol agents than larger populations of less efficient species. Effective biocontrol agents reduce or suppress a pest population below a defined threshold.	Only eat 1–2 CoTS per week	+
Survival at low host (prey) density	The type of biocontrol used will depend on several factors for this to be effective	Will prey on other echinoderms in the absence of CoTS	+++

## 9. Future Prospects

Presented here is the current state of knowledge regarding the giant triton, *Charonia tritonis*, overfished throughout its Indo-Pacific habitat and now considered rare and endangered. With much of the knowledge limited to their morphology and anatomical biology, conservation efforts have focused on easy-to-implement local protection measures, however, these have been shown to be inconsistent, with some governments imposing a

strict no-take policy, while others none. In addition, population distributions, even within reef systems such as the well-studied GBR, are limited to historical records and recent opportunistic sightings, made even more difficult by their cryptic nature. Hence, there is no way of knowing if *C. tritonis* populations are recovering, static or continuing to decline. Extending traditional biogeographical surveys using molecular-based techniques, supported by a fully sequenced *C. tritonis* genome, will help establish their spatial extent and true numbers, providing a baseline against which future populations can be monitored.

On the GBR, there is no evidence demonstrating the regulation of exploitation (through a no take policy) or the designation of nature reserves (i.e., green ‘no-take’ zones) has increased *C. tritonis* numbers. Stock enhancement, usually through the introduction of advanced juveniles reared in ex situ breeding programs, can restore populations, and improve the success of conservation outcomes. Yet, attempts to rear *C. tritonis* in captivity have, to date, proven unsuccessful with larval growth and settlement key bottlenecks in the process. Knowledge of their reproductive and early life stage (veliger) biology, particularly the optimal larval diet and the factors that govern settlement, is crucial to overcome these. With little data available regarding the juvenile life stage, discovering when they transition to an echinoderm diet is also imperative (i.e., immediately upon settlement and coinciding with settlement of CoTS, or longer?).

Coral cover on the GBR continues to decline under the pressure of recurring CoTS outbreaks despite significant intervention. To avoid the tipping point beyond which most or all hard corals may disappear, conservation biocontrol, based on the use of an indigenous enemy, represents a promising complementary and sustainable solution to protect coral reefs from CoTS over their full geographical range. With supporting field and laboratory-based evidence suggesting a proclivity for CoTS (i.e., consumptive effect), the *C. tritonis* remains a biocontrol agent of interest. There is also mounting experimental evidence that the chemistry naturally exuded by *C. tritonis* modifies CoTS behaviour [16] (i.e., non-consumptive effect), with the application of such chemistry being considered within the CoTS IPM strategy. However, with predation levels low at 1 CoTS per week, and with the diffusive spread and dilution of chemosensory cues in the aquatic environment reliant on hydrodynamic parameters [366,367], neither trait in isolation is likely to impact on CoTS populations. However, the combination of non-consumptive and consumptive effects induced by the presence of *C. tritonis* is likely to have greater success in a proximity deterrence effect on CoTS in situ. This deterrence could promote effective dispersal or prevent aggregations of CoTS at opportune times (i.e., spawning events), thereby indirectly suppressing CoTS populations, especially those under the outbreak threshold. Stock densities of *C. tritonis* needed in such scenarios to elicit the desired affect remain to be determined. These knowledge gaps should be addressed with some urgency.

Mapping of population distributions against those of CoTS, based on knowledge of their predator-prey dynamics, will also establish evidence of the link (or not) with CoTS outbreaks, and if proven so, will improve predictions of future outbreaks and provide another tool (i.e., predator management) for the long-term sustainable control of CoTS populations.

**Author Contributions:** M.R.H. obtained funding. C.A.M. and M.R.H. conducted the literature review and wrote the original draft. C.A.M., M.R.H. and S.F.C. reviewed and edited further versions of the manuscript. All authors have read and agreed to the published version of the manuscript.

**Funding:** This project was funded by the Australian Government National Environmental Science Program Tropical Water Quality (NESP TWQ 2.1.1) Hub, and the Australian Federal Government Department of the Environment and Energy Reef 2050 Sustainability Plan Grant ID: 3600000775. The project was supported by the Australian Institute of Marine Science.

**Institutional Review Board Statement:** Not applicable.

**Informed Consent Statement:** Not applicable.

**Data Availability Statement:** Not applicable.

**Acknowledgments:** We thank Damien Burrows of James Cook University and Frederieke Kroon of AIMS for valuable input and suggestions to the NESP TWQ 2.1.1 report on which this work is based. We acknowledge the Wulgurukaba and Bindal people as the Traditional Owners of the land upon which this review was conducted.

**Conflicts of Interest:** The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

### Abbreviations

CoTS	Crown-of-Thorns starfish
dpf	days post-fertilization
eDNA	environmental Deoxyribonucleic acid
GBR	Great Barrier Reef
IPM	integrated pest management

### References

1. Morton, B. Triton's legacy. *Mar. Pollut. Bull.* **2012**, *64*, 891–892. [[CrossRef](#)] [[PubMed](#)]
2. Nijman, V.; Spaan, D.; Nekaris, A.-I.K. Largescale trade in legally protected marine mollusc shells from Java and Bali, Indonesia. *PLoS ONE* **2015**, *10*, e0140593. [[CrossRef](#)]
3. Haszprunar, G.; Vogler, C.; Wörheide, G. Persistent gaps of knowledge for naming and distinguishing multiple species of Crown-of-Thorns-Seastar in the *Acanthaster planci* species complex. *Diversity* **2017**, *9*, 22. [[CrossRef](#)]
4. Cowan, Z.-L.; Pratchett, M.; Messmer, V.; Ling, S. Known predators of Crown-of-Thorns starfish (*Acanthaster* spp.) and their role in mitigating, if not preventing, population outbreaks. *Diversity* **2017**, *9*, 7. [[CrossRef](#)]
5. Estes, J.A.; Terborgh, J.; Brashares, J.S.; Power, M.E.; Berger, J.; Bond, W.J.; Carpenter, S.R.; Essington, T.E.; Holt, R.D.; Jackson, J.B.C.; et al. Trophic downgrading of planet Earth. *Science* **2011**, *333*, 301–306. [[CrossRef](#)]
6. Endean, R. *Report on Investigations Made into Aspects of the Current Acanthaster planci (Crown-of-Thorns Starfish) Infestations on Certain Reefs of the Great Barrier Reef*; Fisheries Branch Queensland, Department of Primary Industries: Brisbane, Australia, 1969; pp. 1–35.
7. Endean, R.; Stalium, W. A study of some aspects of the Crown-of-thorns starfish (*Acanthaster planci*) infestations on reefs of Australia's Great Barrier Reef. *Atoll Res. Bull.* **1973**, *167*, 1–76. [[CrossRef](#)]
8. James, P. *Requiem for the Reef*; Foundation Press: Brisbane, Australia, 1976.
9. Wells, S.M.; Pyle, R.M.; Collins, N.M. *The International Union for Conservation of Nature Invertebrate Red Data Book*; International Union for Conservation of Nature: Gland, Switzerland, 1983.
10. Pratchett, M.S.; Caballes, C.F.; Rivera-Posada, J.A.; Sweatman, H.P.A. Limits to understanding and managing outbreaks of crown-of-thorns starfish (*Acanthaster* spp.). In *Oceanography and Marine Biology: An Annual Review*; Hughes, R., Hughes, D., Smith, I., Eds.; CRC Press: Boca Raton, FL, USA, 2014; pp. 133–200.
11. Babcock, R.C.; Plagányi, É.E.; Condie, S.A.; Westcott, D.A.; Fletcher, C.S.; Bonin, M.C.; Cameron, D. Suppressing the next crown-of-thorns outbreak on the Great Barrier Reef. *Coral Reefs* **2020**, *39*, 1233–1244. [[CrossRef](#)]
12. Babcock, R.C.; Dambacher, J.M.; Morello, E.B.; Plaganyi, E.E.; Hayes, K.R.; Sweatman, H.P.A.; Pratchett, M.S. Assessing different causes of Crown-of-Thorns starfish outbreaks and appropriate responses for management on the Great Barrier Reef. *PLoS ONE* **2016**, *11*, e0169048. [[CrossRef](#)] [[PubMed](#)]
13. Caballes, C.F.; Pratchett, M.S. Reproductive biology and early life history of the crown-of-thorns starfish. In *Echinoderms: Ecology, Habitats and Reproductive Biology*; Whitmore, E., Ed.; Nova Science Publishers: New York, NY, USA, 2014.
14. Uthicke, S.; Logan, M.; Liddy, M.; Francis, D.; Hardy, N.; Lamare, M. Climate change as an unexpected co-factor promoting coral eating seastar (*Acanthaster planci*) outbreaks. *Sci. Rep.* **2015**, *5*, 8402. [[CrossRef](#)]
15. Pratchett, M.S.; Caballes, C.F.; Wilmes, J.C.; Matthews, S.; Mellin, C.; Sweatman, H.P.A.; Nadler, L.E.; Brodie, J.; Thompson, C.A.; Hoey, J.; et al. Thirty years of research on Crown-of-Thorns Starfish (1986–2016): Scientific advances and emerging opportunities. *Diversity* **2017**, *9*, 41. [[CrossRef](#)]
16. Hall, M.R.; Kocot, K.M.; Baughman, K.W.; Fernandez-Valverde, S.L.; Gauthier, M.E.A.; Hatleberg, W.L.; Krishnan, A.; McDougall, C.; Motti, C.A.; Shoguchi, E.; et al. The crown-of-thorns starfish genome as a guide for biocontrol of this coral reef pest. *Nature* **2017**, *544*, 231–234. [[CrossRef](#)] [[PubMed](#)]
17. Høj, L.; Byrne, M.; Kroon, F.; Westcott, D. A Review of Biologically Based Control Technologies for Crown-of-Thorns Starfish: Options for Enhancing the Integrated Pest Management Approach. In *Report to the National Environmental Science Program; Reef and Rainforest Research Centre Limited*: Cairns, Australia, 2020; p. 133.
18. Collier, T.; van Steenwyk, R. A critical evaluation of augmentative biological control. *Biol. Control* **2004**, *31*, 245–256. [[CrossRef](#)]
19. Singh, S.P. *Some Success Stories in Classical Biological Control in India*; Asia-Pacific Association of Agricultural Research Institutions: Bangkok, Thailand, 2004; p. 73.
20. Stiling, P.; Cornelissen, T. What makes a successful biocontrol agent? A meta-analysis of biological control agent performance. *Biol. Control.* **2005**, *34*, 236–246. [[CrossRef](#)]

21. Van Driesche, R.G.; Carruthers, R.I.; Center, T.; Hoddle, M.S.; Hough-Goldstein, J.; Morin, L.; Smith, L.; Wagner, D.L.; Blossey, B.; Brancatini, V.; et al. Classical biological control for the protection of natural ecosystems. *Biol. Control* **2010**, *54*, S2–S33. [\[CrossRef\]](#)
22. Nicot, P.C. *Classical and Augmentative Biological Control against Diseases and Pests: Critical Status Analysis and Review of Factors Influencing Their Success*; International Organization for Biological and Integrated Control of Noxious Animals and Plants, West Palearctic Regional Section (IOBC/WPRS): Zurich, Switzerland, 2011; p. 184.
23. van Lenteren, J.C. The state of commercial augmentative biological control: Plenty of natural enemies, but a frustrating lack of uptake. *BioControl* **2011**, *57*, 1–20. [\[CrossRef\]](#)
24. Begg, G.S.; Cook, S.M.; Dye, R.; Ferrante, M.; Franck, P.; Lavigne, C.; Lövei, G.L.; Mansion-Vaquie, A.; Pell, J.K.; Petit, S.; et al. A functional overview of conservation biological control. *Crop Prot.* **2017**, *97*, 145–158. [\[CrossRef\]](#)
25. Motti, C.; Cummins, S.; Francis, D.; Hall, M.; Hillberg, A.; Klein, A.; Menéndez, P.; Rudd, D.; Thomas-Hall, P. *Charonia tritonis*: A natural biocontrol agent for crown-of-thorns starfish. In *Final Report Prepared for Reef2050 Grant Id: 3600000775*; Australian Institute of Marine Science: Townsville, Australia, 2019; p. 172.
26. Pratchett, M.S.; Caballes, C.F.; Cvitanovic, C.; Raymundo, M.L.; Babcock, R.C.; Bonin, M.C.; Bozec, Y.-M.; Burn, D.; Byrne, M.; Castro-Sanguino, C.; et al. Knowledge gaps in the biology, ecology, and management of the pacific crown-of-thorns sea star, *Acanthaster* sp., on Australia's Great Barrier Reef. *Biol. Bull.* **2021**, *241*, 330–346. [\[CrossRef\]](#)
27. Hall, M.R.; Motti, C.A.; Kroon, F.J. The potential role of the giant triton snail, *Charonia tritonis* (Gastropoda: Ranellidae) in mitigating population outbreaks of the crown-of-thorns starfish. In *NESP Project 2.1.1: Integrated Pest Management of Crown-of-Thorns Starfish*; Australian Institute of Marine Science: Townsville, Australia, 2018; pp. 1–52.
28. Ponder, W.F.; Colgan, D.J.; Healy, J.; Nützel, A.; Simone, L.R.L.; Strong, E.E. Caenogastropoda. In *Phylogeny and Evolution of the Mollusca*; Ponder, W., Lindberg, D.L., Eds.; University of California Press: Berkeley, CA, USA, 2008; pp. 331–383.
29. Ponder, W.F.; Lindberg, D.R.; Ponder, J.M. *Biology and Evolution of the Mollusca*; CRC Press: Boca Raton, FL, USA, 2019; Volume 1.
30. Bouchet, P.; Gofas, S. *Charonia*. World Register of Marine Species. Available online: <http://www.marinespecies.org/aphia.php?p=taxdetails&id=138425> (accessed on 10 September 2022).
31. Strong, E.E.; Puillandre, N.; Beu, A.G.; Castelin, M.; Bouchet, P. Frogs and tuns and tritons—A molecular phylogeny and revised family classification of the predatory gastropod superfamily Tonnoidea (Caenogastropoda). *Mol. Phylogenet. Evol.* **2019**, *130*, 18–34. [\[CrossRef\]](#)
32. Toscano, A.; Bentivegna, F.; Cirino, P. Holothurians' responses to attack by the tonnid gastropod *Tonna galea*. In *Echinoderm Research*; Scalera-Liaci, L., Ed.; CRC Press: London, UK, 1991; p. 204.
33. Morton, B. Prey capture, preference and consumption by *Linatella caudata* (Gastropoda: Tonnoidea: Ranellidae) in Hong Kong. *J. Molluscan Stud.* **1990**, *56*, 477–486. [\[CrossRef\]](#)
34. Cornman, I. Toxic properties of the saliva of *Cassis*. *Nature* **1963**, *200*, 88–89. [\[CrossRef\]](#)
35. Houbrick, J.R.; Fretter, V. Some aspects of the functional anatomy and biology of *Cymatium* and *Bursa*. *J. Molluscan Stud.* **1969**, *38*, 415–429.
36. Laxton, J.H. Feeding in some Australasian Cymatiidae (Gastropoda: Prosobranchia). *Zool. J. Linn. Soc.* **1971**, *50*, 1–9. [\[CrossRef\]](#)
37. Bose, U.; Wang, T.; Zhao, M.; Motti, C.A.; Hall, M.R.; Cummins, S.F. Multiomics analysis of the giant triton snail salivary gland, a crown-of-thorns starfish predator. *Sci. Rep.* **2017**, *7*, 6000. [\[CrossRef\]](#)
38. Morton, B. Foregut anatomy and predation by *Charonia lampas* (Gastropoda: Prosobranchia: Neotaenioglossa) attacking *Ophidaster ophidianus* (Asteroidea: Ophidiasteridae) in the Açores, with a review of triton feeding behaviour. *J. Nat. Hist.* **2012**, *46*, 2621–2637. [\[CrossRef\]](#)
39. Beu, A. The Mollusca of the genus *Charonia* (Family Cymatiidae). *Trans. R. Soc. N. Z.* **1970**, *11*, 205–223.
40. Dodge, H. A historical review of the mollusks of Linnaeus. Part 5 the genus *Murex* of the Class Gastropoda. *Bull. Am. Mus. Nat. Hist. N. Y.* **1957**, *113*, 73–224.
41. Beu, A.G.; Kay, A. Taxonomy of gastropods of the families Ranellidae (=Cymatiidae) and Bursidae. Part IV the *Cymatium pileare* complex. *J. R. Soc. N. Z.* **1988**, *18*, 185–223. [\[CrossRef\]](#)
42. Beu, A. Neogene tonnoidean gastropods of tropical and South America: Contributions to the Dominican Republic and Panama Paleontology projects and uplift of the Central American Isthmus. *Bull. Am. Paleontol.* **2010**, *377–378*, 1–550.
43. Vermeij, G.J.; Cambridge, M.A. *Biogeography and Adaptation: Patterns of Marine Life*; Harvard University Press: Cambridge, UK, 1978.
44. Wagner, P.J. Gastropod phylogenetics: Progress, problems and implications. *J. Paleontol.* **2001**, *75*, 1128–1140. [\[CrossRef\]](#)
45. Strong, E.E. Refining molluscan characters: Morphology, character coding and a phylogeny of the Caenogastropoda. *Zool. J. Linn. Soc.* **2003**, *137*, 447–554. [\[CrossRef\]](#)
46. Ponder, W.F.; Lindberg, D.R. Towards a phylogeny of gastropod molluscs—An analysis using morphological characters. *J. Zool. Soc.* **1997**, *119*, 83–265. [\[CrossRef\]](#)
47. Bigatti, G.; Sacristán, H.; Rodríguez, M.; Stortz, C.; Penchaszadeh, P. Diet, prey narcotization and biochemical composition of salivary gland secretions of the volutid snail *Odontocymbiola magellanica*. *J. Mar. Biol. Assoc. UK* **2010**, *90*, 959–967. [\[CrossRef\]](#)
48. Taylor, J.D.; Morris, N.J.; Taylor, C.N. Food specialization and the evolution of predatory prosobranch gastropods. *Palaeontology* **1980**, *23*, 375–409.
49. Coelho, A.C.S.; Matthwes, H.R.; Leal, J.H. Superfamily Tonnacea do Brasil. VI Família Cymatiidae (Mollusca, Gaqstropoda). *Arq. Mus. Nac. Riojan. Braz.* **1981**, *56*, 111–136.



50. Beu, A. Indo-West Pacific Ranellidae, Bursidae and Personidae (Mollusca: Gastropoda). A monograph of the New Caledonian fauna and revisions of related taxa. *Mem. Am. Mus. Nat. Hist.* **1998**, *178*, 1–255.
51. Fairweather, P.G. Correlations of predatory whelks with intertidal prey at several scales of space and time. *Mar. Ecol. Prog. Ser.* **1988**, *45*, 237–243. [[CrossRef](#)]
52. Wilson, B.R. *Australian Marine Shells. II Prosobranch Gastropods. Part One*; Odyssey Publishing: Perth, Australia, 1993.
53. Lai, K.-Y. The family Cymatiidae of Taiwan. *Bull. Malacol. Rep. China* **1989**, *14*, 107–128.
54. Clench, W.J.; Turner, R.D. The family Cymatiidae in the Western Atlantic. *Johnsonia* **1957**, *3*, 189–244.
55. Percharde, P.L. Observations on the gastropod, *Charonia variegata*, in Trinidad and Tobago. *Nautilus* **1972**, *85*, 84–92.
56. Atlas of Living Australia. Available online: [http://biocache.ala.org.au/occurrences/search?q=charoniatritonis#tab\\_mapView](http://biocache.ala.org.au/occurrences/search?q=charoniatritonis#tab_mapView) (accessed on 15 June 2017).
57. Nateewathana, A.; Aungtonya, C. The Indo-Pacific trumpet triton snail, *Charonis tritonis* L.: Morphometrics of a species on the verge of local extinction. *Phuket Mar. Biol. Cent. Spec. Publ.* **1994**, *13*, 137–140.
58. Kay, E.A. Pacific Island Marine Mollusks: Systematics. In *Marine Coastal Biodiversity in the Tropical Island Pacific Region*; Maragos, J.E., Peterson, M.N.A., Eldredge, L.G., Bardach, J.E., Takeuchi, H.F., Eds.; EastWest Center: Honolulu, HI, USA, 1995; pp. 135–159.
59. Kubota, S. Record of a rare species *Charonia tritonis* (Linnaeus, 1758) (Gastropoda: Ranellidae) from Shirahama, Wakayama Prefecture, central Honshu, Japan. *Molluscan Divers.* **2012**, *3*, 95–96.
60. Montoya, M. A 3000 mile range extension: *Charonia tritonis* in the Eastern Pacific. *Hawaii. Shell News* **1983**, *31*, 8.
61. Emerson, W.K. On the occurrence of *Charonia tritonis* in the eastern Pacific (Ranellidae: Cymatiinae). *Festivus* **1989**, *21*, 13–15.
62. Bouchet, F.; Héros, V.; Lozouet, F.P.; Maestrati, P. A quarter-century of deep-sea malacological exploration in the South and West Pacific: Where do we stand? How far to go? In *Tropical Deep-Sea Benthos 25*; Héros, V., Cowie, R.H., Bouchet, P., Eds.; Mémoires du Muséum National d'Histoire Naturelle: Paris, France, 2008; Volume 196.
63. Tröndlé, J.; Boutet, M. Inventory of marine molluscs of French Polynesia. *Atoll Res. Bull.* **2009**, *570*, 1–90. [[CrossRef](#)]
64. Paterson, J.C. Preliminary survey of the giant triton (*Charonia tritonis*) on selected reefs in the Cairns Region during January. In *Charonia Research Report to Great Barrier Reef Marine Park Authority COTSREC*; 1990; Available online: <https://charonia.wordpress.com/report-to-gbrmpa-1990/> (accessed on 13 March 2021).
65. Cho, I.-Y.; Kim, K.-Y.; Yi, C.H.; Kim, I.H.; Jung, Y.-H.; Hwang, S.-J.; Bae, J.; Yoon, M.; Kim, M.-S. Full-length mitochondrial genome of the triton trumpet *Charonia lampas* (Littorinimorpha: Ranellidae). *Mitochondrial DNA Part B Resour.* **2017**, *2*, 759–760. [[CrossRef](#)]
66. Klein, A.H. Establishment of Multi-Omics Resources for the Giant Triton Snail and the Silver-Lipped Pearl Oyster. Ph.D. Thesis, University of the Sunshine Coast, Sippy Downs, Australia, 2021.
67. Uthicke, S.; Lamare, M.; Doyle, J.R. eDNA detection of corallivorous seastar (*Acanthaster cf. solaris*) outbreaks on the Great Barrier Reef using digital droplet PCR. *Coral Reefs* **2018**, *37*, 1229–1239.
68. Adams, C.I.M.; Knapp, M.; Gemmell, N.J.; Jeunen, G.-J.; Bunce, M.; Lamare, M.D.; Taylor, H.R. Beyond biodiversity: Can environmental DNA (eDNA) cut it as a population genetics tool? *Genes Genomes Genet.* **2019**, *10*, 192. [[CrossRef](#)]
69. Allen, A.M.; Singh, N.J. Linking movement ecology with wildlife management and conservation. *Front. Ecol. Evol.* **2016**, *3*, 155. [[CrossRef](#)]
70. Supp, S.R.; Bohrer, G.; Fieberg, J.; La Sorte, F.A. Estimating the movements of terrestrial animal populations using broad-scale occurrence data. *Mov. Ecol.* **2021**, *9*, 60. [[CrossRef](#)]
71. Mueller, T.; Fagan, W.F. Search and navigation in dynamic environments—From individual behaviours to population distributions. *Oikos* **2008**, *117*, 654–664. [[CrossRef](#)]
72. Schlaff, A.; Menéndez, P.; Hall, M.; Heupel, M.; Armstrong, T.; Motti, C. Acoustic tracking of a large predatory marine gastropod, *Charonia tritonis*, on the Great Barrier Reef. *Mar. Ecol. Prog. Ser.* **2020**, *642*, 147–161. [[CrossRef](#)]
73. Pratchett, M.S.; Caballes, C.F.; Messmer, V.; Fletcher, C.S.; Westcott, D.A. Movement patterns of Pacific crown-of-thorns starfish (*Acanthaster cf. solaris*) linked to habitat structure and prey availability. In *Report to the National Environmental Science Program; Reef and Rainforest Research Centre Limited: Cairns, Australia, 2020*; p. 40.
74. Bose, U.; Suwansa-ard, S.; Maikaeo, L.; Motti, C.A.; Hall, M.R.; Cummins, S.F. Neuropeptides encoded within a neural transcriptome of the giant triton snail *Charonia tritonis*, a Crown-of-Thorns Starfish predator. *Peptides* **2017**, *98*, 3–14. [[CrossRef](#)] [[PubMed](#)]
75. Moomjian, L.; Nystrom, S.; Rittschof, D. Behavioral responses of sexually active mud snails: Kariomones and pheromones. *J. Chem. Ecol.* **2003**, *29*, 497–501. [[CrossRef](#)] [[PubMed](#)]
76. Zhang, L.-P.; Xia, J.-J.; Peng, P.-F.; Li, H.-P.; Luo, P.; Hu, C.-Q. Characterization of embryogenesis and early larval development in the Pacific triton, *Charonia tritonis* (Gastropoda: Caenogastropod). *Invertebr. Reprod. Dev.* **2013**, *57*, 237–246. [[CrossRef](#)]
77. Strathmann, M.F. *Reproduction and Development of Marine Invertebrates of the Northern Pacific Coast, Data and Methods for the Study of Eggs, Embryos and Larvae*; University of Washington Press: Seattle, WA, USA, 1987.
78. Nugranad, J.; Promjinda, K.; Varaibal, T.; Chantara, S. Reproduction of the trumpet triton *Charonia tritonis* in captivity. *Phuket Mar. Biol. Cent. Spec. Publ.* **2001**, *25*, 153–160.
79. Berg, C. Egg capsule and early veliger of *Charonia tritonis* (Linnaeus). *Veliger* **1971**, *13*, 298.
80. Nugranad, J.; Chantrapornsilp, S.; Varapibal, T. Feeding and spawning behaviour of the trumpet triton, *Charonia tritonis* in captivity. *Phuket Mar. Biol. Cent. Spec. Publ.* **2000**, *21*, 51–56.
81. Laxton, J.H. Reproduction in some New Zealand Cymatiida. *Zool. J. Linn. Soc.* **1969**, *48*, 237–253. [[CrossRef](#)]



82. Thorson, G. Reproductive and larval ecology of marine bottom invertebrates. *Biol. Rev.* **1950**, *25*, 1–45. [\[CrossRef\]](#)
83. Cañete, J.; Gallardo, G.; Céspedes, T.; Cárdenas, C.; Santana, M. Encapsulated development, spawning and early veliger of the ranellid snail *Fusitritonis magellanicus* (Röding, 1798) in the cold waters of the Magellan Strait, Chile. *Lat. Am. J. Aquat. Res.* **2012**, *40*, 914–928. [\[CrossRef\]](#)
84. Webber, H.H. Gastropoda: Prosobranchia. In *Reproduction in Marine Invertebrates*; Giese, A., Pearse, J., Eds.; Academic Press: New York, NY, USA, 1977; p. 369.
85. Kilburn, R.; Rippey, E. *Seashells of Southern Africa*; Macmillan: Johannesburg, South Africa, 1982.
86. Cazaux, C. Ponte et larves du gasteropode prosobranch *Tritonalia nodifer*. *Bull. Soc. Linn. Bordx.* **1972**, *11*, 143–148.
87. Motti, C.; (Australian Institute of Marine Science, Townsville, Australia). Personal Communications, Observed paternal care by adult *charonia tritonis* for egg capsules laid in captivity. Both males and females were observed in close proximity to the egg capsules. Egg capsules that were removed from the tank and maintained in separate aquaria showed greater amounts of biofouling. Overall rate of prey consumption dropped during mating, spawning and embryonic development. 2017.
88. D'Asaro, C.N. Egg capsules of prosobranch mollusks from South Florida and the Bahamas and notes on spawning in the laboratory. *Bull. Mar. Sci.* **1970**, *20*, 414–440.
89. Latigan, M.J. Some aspects of the breeding biology of *Charonia lampas pustulata* and *Mayena australasia gemmifera* under aquarium conditions. *Ann. Cape Prov. Mus. Nat. Hist.* **1976**, *11*, 47–53.
90. Riedel, F. A re-evaluation of the ontogeny of *Cabestana spengleri* (Perry, 1811). *Veliger* **1992**, *35*, 117–121.
91. Bouchet, P.; Lozouet, P.; Maestrati, P.; Heros, V. Assessing the magnitude of species richness in tropical marine environments: Exceptionally high numbers of molluscs at a New Caledonia site. *Biol. J. Linn. Soc. Lond.* **2002**, *75*, 421–436. [\[CrossRef\]](#)
92. Shuto, T. Larval ecology of prosobranch gastropods and its bearing on biogeography and paleontology. *Lethaia* **1974**, *7*, 239–256. [\[CrossRef\]](#)
93. Bode, M.; Bode, L.; Armsworth, P.R. Larval dispersal reveals regional sources and sinks in the Great Barrier Reef. *Mar. Ecol. Prog. Ser.* **2006**, *308*, 17–25. [\[CrossRef\]](#)
94. Klein, A.H.; Motti, C.A.; Hillberg, A.K.; Ventura, T.; Thomas-Hall, P.; Armstrong, T.; Barker, T.; Whatmore, P.; Cummins, S.F. Development and Interrogation of a Transcriptomic Resource for the Giant Triton Snail (*Charonia tritonis*). *Mar. Biotechnol.* **2021**, *23*, 501–515. [\[CrossRef\]](#)
95. Klein, A.H.; Ballard, K.R.; Storey, K.B.; Motti, C.A.; Zhao, M.; Cummins, S.F. Multi-omics investigations within the Phylum Mollusca, Class Gastropoda: From ecological application to breakthrough phylogenomic studies. *Brief. Funct. Genom.* **2019**, *18*, 377–394. [\[CrossRef\]](#)
96. Astorga, M.P. Genetic considerations for mollusk production in aquaculture: Current state of knowledge. *Front. Genet.* **2014**, *5*, 435. [\[CrossRef\]](#)
97. Wang, Z.; Hu, H.; Sun, T.; Li, X.; Lv, G.; Bai, Z.; Li, J. Genomic selection for improvement of growth traits in triangle sail mussel (*Hyriopsis cumingii*). *Aquaculture* **2022**, *561*, 738692. [\[CrossRef\]](#)
98. Mazurais, D.; Darias, M.; Zambonino-Infante, J.L.; Cahu, C.L. Transcriptomics for understanding marine fish larval development. *Can. J. Zool.* **2011**, *89*, 599–611. [\[CrossRef\]](#)
99. Li, H.; Zhang, B.; Huang, G.; Liu, B.; Fan, S.; Zhang, D.; Yu, D. Differential gene expression during larval metamorphic development in the Pearl Oyster, *Pinctada fucata*, based on transcriptome analysis. *Int. J. Genom.* **2016**, *2016*, 2895303. [\[CrossRef\]](#)
100. Song, H.; Yu, Z.-L.; Sun, L.-N.; Xue, D.-X.; Zhang, T.; Wang, H.-Y. Transcriptomic analysis of differentially expressed genes during larval development of *Rapana venosa* by digital gene expression profiling. *Genes Genomes Genet.* **2016**, *6*, 2181–2193.
101. Klein, A.; Zhao, M.; Motti, C.A.; Cummins, S. Gene expression analysis of the giant triton snail, *Charonia tritonis*, during larval development. In *Report Prepared for Reef2050 Grant Id: 3600000775*; Australian Institute of Marine Science: Townsville, Australia, 2019; p. 18.
102. Fioroni, P. Larval organs, larvae, metamorphosis and types of development of Mollusca, a comprehensive review. *Zool. Jahrbcher Abt. Anat. Ontog. Tiere* **1982**, *108*, 375–420.
103. Scheltema, R.S. The dispersal of larvae of shoal-water benthic invertebrate species over long distances by ocean currents. In *Fourth European Marine Biology Symposium, Bangor, North Wales, UK, 7–28 September 1969*; Cambridge University Press: Cambridge, UK, 1971.
104. Pechenik, J.A. Growth and energy balance during the larval lives of three prosobranch gastropods. *J. Mar. Biol. Ecol.* **1980**, *44*, 1–28. [\[CrossRef\]](#)
105. Scheltema, R.S. Larval dispersal as a means of genetic exchange between geographically separated populations of shallow water benthic marine gastropods. *Biol. Bull.* **1971**, *140*, 284–322. [\[CrossRef\]](#)
106. Strathmann, M.F.; Strathmann, R.R. An extraordinary long larval duration of 4.5 years from hatching to metamorphosis for teleplanic veligers of *Fusitriton oregonensis*. *Biol. Bull.* **2007**, *213*, 152–159. [\[CrossRef\]](#) [\[PubMed\]](#)
107. Motti, C.A.; Cummins, S.; Armstrong, T.; Barker, T.; Hillberg, A.; Schlawinsky, M.; Thomas-Hall, P. *Charonia tritonis* larval rearing: Progress report Jan 2018. In *Report Prepared for Reef2050 Grant Id: 3600000775*; Australian Institute of Marine Science: Townsville, Australia, 2018; p. 43.
108. Hadfield, M.G. Metamorphosis in marine molluscan larvae: An analysis of stimulus and response. In *Settlement and Metamorphosis of Marine Invertebrate Larvae*; Chia, F., Rice, M., Eds.; Elsevier: North-Holland, The Netherlands, 1978; pp. 165–175.

109. Hadfield, M.G.; and Strathmann, M.F. Variability, flexibility and plasticity in life histories of marine invertebrates. *Oceanol. Acta* **1996**, *19*, 323–334.
110. Lebour, M.V. The eggs and larvae of some prosobranchs from Bermuda. *Proc. Zool. Soc. Lond.* **1945**, *114*, 462–489. [[CrossRef](#)]
111. Scheltema, R.S. Biological interactions determining larval settlement in marine invertebrates. *Thalass. Jugosl.* **1974**, *10*, 263–296.
112. Pechenik, J.A.; Scheltema, R.S.; Eyster, L.S. Growth stasis and limited shell calcification in larvae of *Cymatium pathenopeum* during trans-Atlantic transport. *Science* **1984**, *224*, 1097–1099. [[CrossRef](#)]
113. Richter, G. Die gehauseentwicklung bei den Larven der Cymatiiden (Prosobranchia: Tonnacea). *Arch. Molluskenkd. Senckenberg. Nat. Ges.* **1984**, *115*, 125–141.
114. Scheltema, R.S. Long distance dispersal by planktonic larval of shoal-water benthic invertebrates among Pacific Islands. *Bull. Mar. Sci.* **1986**, *39*, 241–256.
115. Hadfield, M.G.; Carpizo-Ituarte, E.J.; del Carmen, K.; Nedved, B.T. Metamorphic competence, a major adaptive convergence in marine invertebrate larvae. *Am. Zool.* **2001**, *41*, 1123–1131. [[CrossRef](#)]
116. Dalesman, S.; Rundle, S.D.; Coleman, R.A.; Cotton, P.A. Cue association and antipredator behaviour in a pulmonate snail, *Lymnaea stagnalis*. *Anim. Behav.* **2006**, *71*, 789–797. [[CrossRef](#)]
117. Lesoway, M.P.; Page, L.R. Growth and differentiation during delayed metamorphosis of feeding gastropod larvae: Signatures of ancestry and innovation. *Mar. Biol.* **2008**, *153*, 723–734. [[CrossRef](#)]
118. Page, L.R. Molluscan larvae: Pelagic juveniles or slowly metamorphosing larvae. *Biol. Bull.* **2009**, *216*, 216–225. [[CrossRef](#)]
119. Martel, A.L.; Tremblay, R.; Toupoint, N.; Olivier, F.; Myrand, B. Veliger size at metamorphosis and temporal variability in prodissoconch II morphometry in the blue mussel (*Mytilus edulis*): Potential impact on recruitment. *J. Shellfish. Res.* **2014**, *33*, 443–455. [[CrossRef](#)]
120. Ritson-Williams, R.; Shjegstad, S.M.; Paul, V.J. Larval metamorphosis of *Phestilla* spp. in response to waterborne cues from corals. *J. Exp. Mar. Biol. Ecol.* **2009**, *375*, 84–88. [[CrossRef](#)]
121. Govan, H. *Cymatium Muricinum and Other Ranellid Gastropods: Major Predators of Cultured Tridacnid Clams*; Intern Centre for Living Aquatic Resources Management: Manila, Philippines, 1995.
122. Heslinga, G.A.; Watson, T.C.; Isamu, T. Cultivation of giant clams: Beyond the hatchery. In *The First Asian Fisheries Forum*; Maclean, J., Dizon, L., Hosillos, L., Eds.; Asian Fisheries Society: Manila, Philippines, 1986; pp. 53–58.
123. Bornancin, L.; Bonnard, I.; Mills, S.C.; Banaigs, B. Chemical mediation as a structuring element in marine gastropod predator-prey interactions. *Nat. Prod. Rep.* **2017**, *34*, 644–676. [[CrossRef](#)] [[PubMed](#)]
124. Manríquez, P.H.; Navarrete, S.A.; Rosson, A.; Castilla, J.C. Settlement of the gastropod *Concholepas concholepas* on shells of conspecific adults. *J. Mar. Biol. Assoc. UK* **2004**, *84*, 651–658. [[CrossRef](#)]
125. Cahill, A.E.; Koury, S.A. Larval settlement and metamorphosis in a marine gastropod in response to multiple conspecific cues. *PeerJ* **2016**, *4*, e2295. [[CrossRef](#)] [[PubMed](#)]
126. Padilla, D.K.; McCann, M.J.; Glenn, M.M.; Hooks, A.P.; Shumway, S.E. Effect of food on metamorphic competence in the model system *Crepidula fornicata*. *Biol. Bull.* **2014**, *227*, 242–251. [[CrossRef](#)]
127. Pechenik, J.A.; Heyman, W.D. Using KCl to determine size at competence for larvae of the marine gastropod *Crepidula fornicata*. *J. Mar. Biol. Ecol.* **1987**, *112*, 27–38. [[CrossRef](#)]
128. Penniman, J.R.; Doll, M.K.; Pires, A. Neural correlates of settlement in veliger larvae of the gastropod, *Crepidula fornicata*. *Invertebr. Biol.* **2013**, *132*, 14–26. [[CrossRef](#)]
129. Taris, N.; Comtet, T.; Stolba, R.; Lasbleiz, R.; Pechenik, J.A.; Viard, F. Experimental induction of larval metamorphosis by a naturally-produced halogenated compound (bromomethane) in the invasive mollusc *Crepidula fornicata*. *J. Mar. Biol. Ecol.* **2010**, *393*, 71–77. [[CrossRef](#)]
130. Boettcher, A.A.; Dyer, C.; Casey, J.; Targett, N.M. Hydrogen peroxide induced metamorphosis of queen conch, *Strombus gigas*: Tests at the commercial scale. *Aquaculture* **1997**, *148*, 247–258. [[CrossRef](#)]
131. Boettcher, A.A.; Targett, N.M. Role of chemical inducers in larval metamorphosis of Queen conch, *Strombus gigas*: Relationship to other marine invertebrate systems. *Biol. Bull.* **1998**, *194*, 132–142. [[CrossRef](#)]
132. Davis, M.; Heyman, W.D.; Harvey, W.; Withstandley, C.A. A comparison of two inducers, KCl and *Laurencia* extracts and techniques for the commercial scale induction of metamorphosis in queen conch, *Strombus gigas* larvae. *J. Shellfish. Res.* **1990**, *9*, 67–73.
133. Cob, Z.C.; Arshad, A.; Bujang, J.S.; Muda, W.L.W.; Ghaffar, M.A. Metamorphosis induction of the dog conch *Strombus canarium* using cues associated with conch nursery habitat. *J. Appl. Sci.* **2010**, *10*, 628–635. [[CrossRef](#)]
134. Siddall, S.E. Biological and economic outlook for hatchery production of queen conch. In *Proceedings of the 35th Gulf and Caribbean Fisheries Institute*, Miami, FL, USA, 11–13 November 1982; pp. 46–53.
135. Davis, M.; Stoner, A.W. Trophic cues induce metamorphosis of queen conch larvae (*Strombus gigas*). *J. Exp. Mar. Biol. Ecol.* **1994**, *180*, 83–102. [[CrossRef](#)]
136. Kang, K.H.; Kim, J.M. The predation of trumpet shell, *Charonia* sp. on eight different marine invertebrate species. *Aquac. Res.* **2004**, *35*, 1202–1206. [[CrossRef](#)]
137. Searcy-Bernal, R.; Anguiano-Beltrán, C. Optimizing the concentration of gamma-aminobutyric acid (GABA) for inducing larval metamorphosis in the Red Abalone *Haliotis rufescens* (Mollusca: Gastropoda). *J. World Aquac. Soc.* **1998**, *29*, 463–470. [[CrossRef](#)]

138. Huggett, M.J.; de Nys, R.; Williamson, J.E.; Heasman, M.; Steinberg, P.D. Settlement of larval blacklip abalone, *Haliotis rubra*, in response to green and red algae. *Mar. Biol.* **2005**, *147*, 1155–1163. [CrossRef]
139. Li, H.; Lin, W.; Zhang, G.; Cai, Z.; Cai, G.; Chang, Y.; Xing, K. Enhancement of larval settlement and metamorphosis through biological and chemical cues in the abalone *Haliotis diversicolor supertexta*. *Aquaculture* **2006**, *258*, 416–423. [CrossRef]
140. Bryan, P.J.; Qian, P.Y. Induction of larval attachment and metamorphosis in the abalone *Haliotis diversicolor*. *J. Exp. Mar. Biol. Ecol.* **1998**, *223*, 39–51. [CrossRef]
141. Morse, D.E. Recent progress in larval settlement and metamorphosis: Closing the gaps between molecular biology and ecology. *Bull. Mar. Sci.* **1990**, *46*, 465–483.
142. Stewart, P.; Soonklang, N.; Stewart, M.J.; Wanichanon, C.; Hanna, P.J.; Poomtong, T.; Sobhon, P. Larval settlement of the tropical abalone, *Haliotis asinina* Linnaeus, using natural and artificial chemical inducers. *Aquac. Res.* **2008**, *39*, 1181–1189. [CrossRef]
143. Sawatpeera, S.; Krauatrachue, M.; Sonchaeng, P.; Upatham, S.; Rojanasarampkit, T. Settlement and early growth of abalone larvae *Haliotis asinina* in response to the presence of diatoms. *Veliger* **2004**, *47*, 91–99.
144. Pires, A.; Croll, R.P.; Hadfield, M.G. Catecholamines modulate metamorphosis in the opisthobranch gastropod *Phestilla sibogae*. *Biol. Bull.* **2000**, *198*, 319–331. [CrossRef]
145. Avila, C.; Tamse, C.T.; Kuzirian, A.M. Induction of metamorphosis in *Hermisenda crassicornis* larvae (Molluscs: Nudibranchia) by GABA, choline and serotonin. *Invertebr. Reprod. Dev.* **1996**, *29*, 127–141. [CrossRef]
146. Lambert, W.; Todd, C. Evidence for a water-borne cue inducing metamorphosis in the dorid nudibranch mollusc *Adalaria proxima* (Gastropoda: Nudibranchia). *Mar. Biol.* **1994**, *120*, 265–271. [CrossRef]
147. Lambert, W.J.; Todd, C.D.; Hardege, J.D. Partial characterization and biological activity of a metamorphic inducer of the dorid nudibranch *Adalaria proxima* (Gastropoda: Nudibranchia). *Invertebr. Biol.* **1997**, *116*, 71. [CrossRef]
148. Zhang, G.; Xu, M.; Zhang, C.; Jia, H.; Zhang, H.; He, M.; Liu, W. Comparative transcriptomic and expression profiles between the foot muscle and mantle tissues in the giant triton snail *Charonia tritonis*. *Front. Physiol.* **2021**, *12*, 632518. [CrossRef]
149. Laxton, J.H. Shell growth in some New Zealand Cymatiidae (Gastropoda: Prosobranchia). *J. Exp. Mar. Biol. Ecol.* **1970**, *4*, 250–260. [CrossRef]
150. Perron, F.E.; Heslinga, G.A.; Fagolimus, J.O. The gastropod *Cymatium muricinum*, a predator on juvenile tridacnid clams. *Aquaculture* **1985**, *48*, 211–221. [CrossRef]
151. Vermeij, G.J.; Signor, P.W. The geographic, taxonomic and temporal distribution of determinate growth in marine gastropods. *Biol. J. Linn. Soc. Lond.* **1992**, *47*, 233–247. [CrossRef]
152. Hombre, S.E.; Gonzalez, J.B.; Baguinbin, D.M.; Balisco, R.A.T.; Dolorosa, R.G. Preliminary checklist of marine gastropods and bivalves in the Kalayaan Island group Palawan, Western Philippines. *Philipp. J. Syst. Biol.* **2016**, *10*, 25–34.
153. Salm, R.V. Conservation of Marine Resources in Seychelles. In *Report to International Union for Conservation of Nature and Natural Resources*; United Nations Environment Program: Nairobi, Kenya, 1978; p. 52.
154. Council of Europe. CETS No. 104 Convention on the Conservation of European Wildlife and Natural Habitats. In *European Treaty Series*; Council of Europe: Bern, Switzerland, 1979; pp. 1–26.
155. European Community. Council Decision of 22 October on concluding the protocol concerning specially protected areas and biological diversity in the Mediterranean and on accepting the annexes to that protocol Barcelona Convention Official 14-12-1999. *J. Eur. Communities* **1999**, *322*, 1–17.
156. Cavallaro, M.; Navarra, E.; Danze, A.; Danze, G.; Muscolino, D.; Giarratana, F. Mediterranean triton *Charonia lampas lampas* (Gastropoda: Caenogastropoda): Report on captive breeding. *Acta Adriat.* **2016**, *57*, 263–272.
157. Marler, G.; Marler, L. Triton's triumph. *Sea Front.* **1982**, *28*, 354–356.
158. McClanahan, T.R. Kenyan coral reef-associated gastropod fauna: A comparison between protected and unprotected reefs. *Mar. Ecol. Prog. Ser.* **1989**, *53*, 11–20. [CrossRef]
159. Chesher, R.; Poulsen, A. A key predator on coral reefs a favoured prey for shell collector. *Giant Triton Aust. Shell News* **1993**, *83*, 1–2.
160. Sapp, J. *What Is Natural? Coral Reef Crisis*; Oxford University Press: Oxford, UK, 1999.
161. Paterson, J.C.; Poulsen, A.L. A study of *Charonia tritonis* on the Great Barrier Reef. Report to the Great Barrier Reef Marine Park Authority. 1988. Available online: <https://charonia.wordpress.com/report-to-gbrmpa-1988/> (accessed on 15 March 2021).
162. Poulsen, A.L. Coral reef gastropods—A sustainable resource? *Pac. Conserv. Biol.* **1995**, *2*, 142–145. [CrossRef]
163. Moon, S.; (Association of Marine Park Tourism Operators, Cairns, Australia). Personal Communications, 2016.
164. Chesher, D.P. Destruction of Pacific corals by the sea star *Acanthaster planci*. *Science* **1969**, *165*, 280–283. [CrossRef]
165. Tropical Marine Mollusc Programme. Workshop of the Tropical Marine Mollusc Programme. In *Research Bulletin (Sun Chirawit-thaya Thang Thale Phuket)*, 12–18 August 1991; Phuket Marine Biological Center: Wichit, Thailand, 1991.
166. Stoner, A.W. Evidence for a significant decline in Queen Conch in the Bahamas, including the population in a marine protected area. In *Proceedings of the 65th Gulf and Caribbean Fish Institute, Santa Marta, Colombia*, 5–9 November 2012; pp. 349–361.
167. Stoner, A.W.; Davis, M.; Bull, U.S. Experimental outplanting of juvenile queen conch, *Strombus gigas*: Comparisons of wild and hatchery-reared stocks. *Fish* **1994**, *92*, 390–411.
168. Stoner, A.W.; Ray-Culp, M. Evidence for Allee effects in an overharvested marine gastropod: Density dependent mating and egg production. *Mar. Ecol. Prog. Ser.* **2000**, *202*, 297–302. [CrossRef]
169. Antonelli, P.J.; Kazarinoff, N.D. Starfish predation of a growing coral reef community. *J. Theor. Biol.* **1984**, *107*, 667–684. [CrossRef]



170. Bradbury, R.H.; Hammond, L.S.; Moran, P.J.; Reichelt, R.E. Coral reef communities and the crown-of-thorns starfish: Evidence for quantitatively stable cycles. *J. Theor. Biol.* **1985**, *113*, 69–80. [CrossRef]
171. McCallum, H.I. Predator regulation of *Acanthaster planci*. *J. Theor. Biol.* **1987**, *127*, 207–220. [CrossRef]
172. Morello, E.B.; Plagányi, É.; Babcock, R.C.; Sweatman, H.; Hillary, R.; Punt, A.E. Model to manage and reduce crown-of-thorns starfish outbreaks. *Mar. Ecol. Prog. Ser.* **2014**, *512*, 167–183. [CrossRef]
173. Great Barrier Reef Marine Park Authority. *Great Barrier Reef Marine Park Regulations 2019: F2021L01190*; Office of Parliamentary Counsel: Canberra, Australia, 2019.
174. Nautical Crush Trading. Available online: <https://www.nauticalcrushtrading.com/triton-shell-1-triton-seashell-large-9--10-for-decor/> (accessed on 31 August 2022).
175. Chesher, R.H. *Charonia Tritonis*; Proposal for listing in Schedule II of CITES; Commonwealth of Australia: Canberra, Australia, 1993.
176. Convention in Trade in Endangered Species. *Inclusion of the Giant Triton Charonia Tritonis on Appendix II of the Convention in Trade in Endangered Species (CITES)*; Appendix 2; Commonwealth of Australia: Canberra, Australia, 1994.
177. Rosser, A.R.; Haywood, M.J. *Guidance for CITES Scientific Authorities: Checklist to Assist in Making Non-Detriment Findings for Appendix II Exports*; International Union for Conservation of Nature: Gland, Switzerland; Cambridge, UK, 2002; p. 146.
178. Kay, E.A. The Conservation Biology of Molluscs. In *Occasional Paper of the Survival Commission No 9*; International Union for Conservation of Nature: Gland, Switzerland, 1995; p. 81.
179. Weis, A.; Dunning, M.; Gaffney, P. Ecological assessment of Queensland's Marine Specimen Shell Collection Fishery. In *A Report to the Australian Government Department of the Environment and Heritage on the Ecological Sustainable Management of a Small Scale Highly Selective Hand and Shell Dredge Collection Fishery*; Queensland Government Department of Primary Industries and Fisheries: Brisbane, Australia, 2004; p. 30.
180. United Nations Environment Program. *Decision IG.19/12. Annex II. Amendments of the list of Annexes II and III of the Protocol concerning Specially Protected Areas and Biological Diversity in the Mediterranean*; United Nations Environment Program: Brussels, Belgium, 2009. Available online: [https://wedocs.unep.org/bitstream/handle/20.500.11822/10181/09ig19\\_08\\_annex2\\_19\\_12\\_eng.pdf](https://wedocs.unep.org/bitstream/handle/20.500.11822/10181/09ig19_08_annex2_19_12_eng.pdf) (accessed on 6 May 2021).
181. *Fisheries Act 2014*; Laws of Seychelles; ILO: Geneva, Switzerland, 2014; pp. 1–29.
182. Palawan Council for Sustainable Development. Approving the 2014 updated list of terrestrial and marine wildlife in Palawan and their categories pursuant to Republic Act 9147, otherwise known as the Wildlife Resources Conservation and Protection Act of 2001. In *Palawan Council for Sustainable Development Resolution No. 15–521*; Republic of the Philippines Republic Act 7611: Palau, Philippines, 2015; pp. 1–18.
183. PCSD. Illegal Traders of Endangered Wildlife, Caught. Available online: <https://pcsd.gov.ph/3323/> (accessed on 1 November 2021).
184. Convention on the Conservation of European Wildlife and Natural Habitats Standing Committee. Presumed large-scale exploitation and marketing of protected marine shelled molluscs in Greece. In *Proceedings of the Convention on the Conservation of European Wildlife and Natural Habitats. Standing Committee 38th Meeting*, Strasbourg, France, 27–30 November 2018.
185. Motti, C. The shells of captive *Charonia tritonis* snails were observed to be biofouled to various degrees with organisms including crustose coralline algae and boring sponges. Extensive pitting was observed in the older whorls, some pitting was observed by X-ray in the more recent whorls. In captivity, observations have revealed CoTS that initially survive an incomplete *C. tritonis* attack ultimately perish within 12–48 h if the proboscis has penetrated the outer skin. Unpublished data. 2022.
186. Stefaniak, L.M.; McAtee, J.; Shulman, M.J. The costs of being bored: Effects of a clonid sponge on the gastropod *Littorina littorea* (L.). *J. Exp. Mar. Biol. Ecol.* **2005**, *327*, 103–114. [CrossRef]
187. Noiset, F.; Comtet, T.; Legrand, E.; Bordey, F.; Davout, D.; Martin, S. Does encapsulation protect embryos from the effects of ocean acidification? The example of *Crepidula fornicata*. *PLoS ONE* **2014**, *9*, e93021. [CrossRef] [PubMed]
188. Padilla, D.K.; Charifson, D.; Liguori, A.; McCarty-Glenn, M.; Rosa, M.; Rugila, A. Factors affecting gastropod larval development and performance: A systematic review. *J. Shellfish. Res.* **2018**, *37*, 851–867. [CrossRef]
189. Bogan, S.N.; McMahon, J.B.; Pechenik, J.A.; Pires, A. Legacy of multiple stressors: Responses of gastropod larvae and juveniles to ocean acidification and nutrition. *Biol. Bull.* **2019**, *236*, 159–173. [CrossRef] [PubMed]
190. Pechenik, J.A.; Tyrell, A.S. Larval diet alters larval growth rates and post-metamorphic performance in the marine gastropod *Crepidula fornicata*. *Mar. Biol.* **2015**, *162*, 1597–1610. [CrossRef]
191. Lu, J.; Shi, Y.; Wang, S.; Chen, H.; Cai, S.; Feng, J. NMR-based metabolomic analysis of *Haliotis diversicolor* exposed to thermal and hypoxic stresses. *Sci. Total Environ.* **2016**, *545–546*, 280–288. [CrossRef]
192. Coleman, D.W.; Byrne, M.; Davis, A.R. Molluscs on acid: Gastropod shell repair and strength in acidifying oceans. *Mar. Ecol. Prog. Ser.* **2014**, *509*, 203–211. [CrossRef]
193. Harvey, B.P.; Agostini, S.; Wada, S.; Inaba, K.; Hall-Spencer, J.M. Dissolution: The Achilles' heel of the triton shell in an acidifying ocean. *Front. Mar. Sci.* **2018**, *5*, 371. [CrossRef]
194. Guiden, P.W.; Bartel, S.L.; Byer, N.W.; Shipley, A.A.; Orrock, J.L. Predator-prey interactions in the anthropocene: Reconciling multiple aspects of novelty. *Trends Ecol. Evol.* **2019**, *34*, 616–627. [CrossRef] [PubMed]
195. Modica, M.V.; Russini, V.; Fassio, G.; Oliverio, M. Do larval types affect genetic connectivity at sea? Testing hypothesis in two sibling marine gastropods with contrasting larval development. *Mar. Environ. Res.* **2017**, *127*, 92–101. [CrossRef] [PubMed]

196. Crocetta, F.; Caputi, L.; Paz-Sedano, S.; Tanduo, V.; Vazzana, A.; Oliverio, M. High genetic connectivity in a gastropod with long-lived planktonic larvae. *J. Molluscan Stud.* **2020**, *86*, 42–55. [\[CrossRef\]](#)
197. Dwiono, S.A.P.; Makaputi, P.C.; Pradina, D.A. A hatchery for the topshell (*T. niloticus*) in Eastern Indonesia. In *Trochus: Status, Hatchery Practice and Nutrition*. ACIAR Proceedings No. 79; Lee, C., Lynch, P., Eds.; Australian Centre for International Agricultural Research: Canberra, Australia, 1997; pp. 33–37.
198. Guo, X.; Ford, S.E.; Zhang, F. Molluscan aquaculture in China. *J. Shellfish. Res.* **1999**, *18*, 19–31.
199. Davis, M. Queen conch (*Strombus gigas*) culture techniques for research, stock enhancement and grow-out markets. In *Recent Advances in Marine Biotechnology, Seaweeds and Invertebrates, Aquaculture Part A Seaweeds and Invertebrates*; Fingerman, M., Nagabhushanam, R., Eds.; Science Publishers: Endfield, CT, USA, 2000; Volume 4.
200. Dwiono; Pradina, S.A.P.; Makatipu, P.C. Spawning and seed production of the green snail (*Turbo marmoratus* L.) in Indonesia. *Secr. Pac. Community Trochus Inf. Bull.* **2001**, *7*, 9–13.
201. Katsanevakis, S.; Lefkaditou, E.; Galinou-Mitsoudi, S.; Koutsoubas, D.; Zenetos, A. Molluscan species of minor commercial interest in the Hellenic seas: Distribution, exploitation and conservation status. *Mediterr. Mar. Sci.* **2008**, *9*, 77–118. [\[CrossRef\]](#)
202. Laughlin, R.A.; Weil, E. Queen conch mariculture and restoration in the Archipiélago de Los Roques: Preliminary results. In *Proceedings of the 35th Gulf and Caribbean Fisheries Institute*, Miami, FL, USA, 11–13 November 1982; pp. 64–72.
203. Glazer, R.A.; Delgado, G.A.; Kidney, J.A. Estimating Queen Conch (*Strombus gigas*) home ranges using acoustic telemetry: Implications for the design of marine fishery reserves. *Gulf Caribb. Res.* **2003**, *14*, 79–89. [\[CrossRef\]](#)
204. Spring, A.; Davis, M. Recommendations for culturing juvenile Queen Conch, *Strombus gigas*, for restocking and commercial purposes. In *Proceedings of the 58th Gulf and Caribbean Fish Institute*, San Andres, Colombia, 7–11 November 2005; pp. 781–787.
205. Delgado, G.A.; Glazer, R.A. Interactions between translocated and native queen conch *Strombus gigas*: Evaluating a restorative strategy. *Endanger. Species Res.* **2007**, *3*, 259–266.
206. McCarthy, K. *A Review of Queen Conch (Strombus gigas) Life History*; Sustainable Fisheries Division, Ed.; SEDAR 14DW4; National Marine Fishery Service: Miami, FL, USA, 2008.
207. Crowe, T.P.; Lee, C.L.; McGuinness, K.A.; Amos, M.J.; Dangeubun, J.; Dwiono, S.A.P.; Makatipu, P.C.; Manuputty, J.; N’guyen, F.; Pakoa, K.; et al. Experimental evaluation of the use of hatchery-reared juveniles to enhance stocks of the topshell *Trochus niloticus* in Australia, Indonesia and Vanuatu. *Aquaculture* **2002**, *206*, 175–197. [\[CrossRef\]](#)
208. Hoang, D.H.; Tuan, V.S.; Hoa, N.X.; Sang, H.M.; Lu, H.D.; Tuyen, H.T. Experiments on using hatchery-reared *Trochus niloticus* juveniles for stock enhancement in Vietnam. *SPC Trochus Inf. Bull.* **2007**, *13*, 13–18.
209. Ridlon, A.D.; Wasson, K.; Waters, T.; Adams, J.; Donatuto, J.; Fleener, G.; Froehlich, H.; Govender, R.; Kornbluth, A.; Lorda, J.; et al. Conservation aquaculture as a tool for imperiled marine species: Evaluation of opportunities and risks for Olympia oysters, *Ostrea lurida*. *PLoS ONE* **2021**, *16*, e0252810. [\[CrossRef\]](#) [\[PubMed\]](#)
210. FAO. The state of world fisheries and aquaculture 2016. In *Contributing to Food Security and Nutrition for All*; Food and Agriculture Organization of the United Nations: Rome, Italy, 2016; p. 200.
211. Castell, L. Gastropod Molluscs. In *Aquaculture: Farming Aquatic Animals and Plants*; Lucas, J.S., Southgate, P.C., Eds.; Blackwell Publishing Ltd.: Oxford, UK, 2012; pp. 567–582.
212. Nash, W.J. *Hatchery Production of Trochus (Trochus niloticus) in Vanuatu: A Review of the Existing Facilities and a Manual of Rearing Techniques Appropriate for a Small-Scale Hatchery*; Food and Agriculture Organisation: Tasmania, Australia, 1989.
213. Chaitanawisuti, N.; Kritsanapuntu, A. Growth and production of hatchery-reared juvenile spotted babylon *Babylonia areolata* Link 1807 cultured to marketable size in intensive lowthrough and semi-closed recirculating water systems. *Aquac. Res.* **2000**, *31*, 415–419. [\[CrossRef\]](#)
214. Chaitanawisuti, N.; Kritsanapuntu, A.; Natsukari, Y.; Kathinmai, S. Effects of different types of substrate on growth and survival of juvenile spotted babylon, *Babylonia areolata* Link 1807 reared to marketable size in a flow-through seawater system. *Asian Fish. Sci.* **2001**, *14*, 279–284. [\[CrossRef\]](#)
215. Clarke, P.J.; Komatsu, T. Successful culture and release of trochus in Solomon Islands. *SPC Trochus Inf. Bull.* **2001**, *8*, 11–14.
216. Amos, M.J.; Purcell, S.W. Evaluation of strategies for intermediate culture of *Trochus niloticus* (Gastropoda) in sea cages for restocking. *Aquaculture* **2003**, *218*, 235–249. [\[CrossRef\]](#)
217. Hall, M.R.; Bose, U.; Cummins, S.F.; Motti, C.A.; Wang, T.; Zhao, M.; Roberts, R.; Smith, M.; Rotgans, B.A.; Wyeth, R.C.; et al. *The Crown-of-Thorns Secretome: Towards a Control Technology*; Australian Government Department of the Environment: Townsville, Australia, 2016; pp. 1–312.
218. Franz, D.R. Opisthobranch culture. In *Culture of Marine Invertebrates*; Smith, W., Chanley, M., Eds.; Plenum Press: New York, NY, USA, 1971; pp. 245–256.
219. Bertram, D.; Strathmann, R. Effects of maternal and larval nutrition on growth and form of planktotrophic larvae. *Ecology* **1998**, *79*, 315–327. [\[CrossRef\]](#)
220. Seon, S.C.; Kim, J.M.; Jung, C.-G.; Yun, S.J.; Kang, K.H. Influence of water temperature on spawning induction, larval and spat rearing of trumpet shell, *Charonia lampas sauliae*. *Korean J. Malacol.* **2005**, *21*, 107–111.
221. Kang, K.; Kim, M.; Hong, H.; Cha, G.; Sui, Z. Feeding broodstocks different starfish diets affect growth and survival of larvae of trumpet shell (*Charonia lampas sauliae* Reeve 1844). *J. Ocean. Univ. China* **2016**, *15*, 861–865. [\[CrossRef\]](#)
222. Kingsford, M.J.; Leis, J.M.; Shanks, A.; Lindeman, K.C.; Morgan, S.G.; Pineda, J. Sensory environments, larval abilities and local self-recruitment. *Bull. Mar. Sci.* **2002**, *70*, 309–340.

223. Hay, M.E. Marine chemical ecology: Chemical signals and cues structure marine populations, communities, and ecosystems. *Annu. Rev. Mar. Sci.* **2009**, *1*, 193–212. [\[CrossRef\]](#)
224. Hadfield, M.G. Biofilms and marine invertebrate larvae: What bacteria produce that larvae use to choose settlement sites. *Ann. Rev. Mar. Sci.* **2011**, *3*, 453–470. [\[CrossRef\]](#) [\[PubMed\]](#)
225. Knudsen, B.; Kohn, A.B.; Nahir, B.; McFadden, C.; Moroz, L. Complete DNA sequence of the mitochondrial genome of the sea-slug, *Aplysia californica*: Conservation of the gene order in Euthyneura. *Mol. Phylogenet. Evol.* **2006**, *38*, 459–469. [\[CrossRef\]](#)
226. Spade, D.J.; Griffitt, R.J.; Liu, L.; Brown-Peterson, N.J.; Kroll, K.J.; Feswick, A.; Glazer, R.A.; Barber, D.S.; Denslow, N.D. Queen conch (*Strombus gigas*) testis regresses during the reproductive season at nearshore sites in the Florida Keys. *PLoS ONE* **2010**, *5*, e12737. [\[CrossRef\]](#) [\[PubMed\]](#)
227. Márquez, E.; Landínez-García, R.M.; Ospina-Guerrero, S.P.; Segura, J.A.; Prada, M.; Castro, E.; Correa, J.L.; Borda, C. Genetic analysis of Queen Conch *Strombus gigas* from the Southwest Caribbean. In Proceedings of the 65th Gulf and Caribbean Fisheries Institute, Santa Marta, Colombia, 5–9 November 2012; pp. 410–416.
228. Simakov, O.; Marletaz, F.; Cho, S.-J.; Edsinger-Gonzales, E.; Havlak, P.; Hellsten, U.; Kuo, D.-H.; Larsson, T.; Lv, J.; Arendt, D.; et al. Insights into bilaterian evolution from three spiralian genomes. *Nature* **2013**, *493*, 526–531. [\[CrossRef\]](#)
229. Dominguez-Perez, D.; Lippolis, J.; Dennis, M.; Miller, B.; Tiley, K.; Vasconcelos, V.; de Almeida, A.M.; Campos, A. The queen conch (*Lobatus gigas*) proteome: A valuable tool for biological studies in marine gastropods. *Protein J.* **2019**, *38*, 628–639. [\[CrossRef\]](#)
230. Tollrian, R.; Harvell, C.D. *The Ecology and Evolution of Inducible Defenses*; Princeton University Press: Princeton, NJ, USA, 1999.
231. Khater, M.; Murariu, D.; Gras, R. Predation risk tradeoffs in prey: Effects on energy and behaviour. *Theor. Ecol.* **2016**, *9*, 251–268. [\[CrossRef\]](#)
232. Motti, C.A.; Bose, U.; Roberts, R.E.; McDougall, C.; Smith, M.K.; Hall, M.R.; Cummins, S.F. Chemical ecology of chemosensation in Asteroidea: Insights towards management strategies of pest species. *J. Chem. Ecol.* **2018**, *44*, 147–177. [\[CrossRef\]](#)
233. Moran, P.J. The *Acanthaster* phenomenon. *Annu. Rev. Oceanogr. Mar. Biol.* **1986**, *24*, 379–480.
234. Birkeland, C.; Lucas, J. *Acanthaster planci: Major Management Problems of Coral Reefs*; CRC Press: Boca Raton, FL, USA, 1990.
235. Glynn, P.W. An amphinomid worm predator of the crown-of-thorns sea star and general predation on asteroids in eastern and western Pacific coral reefs. *Bull. Mar. Sci.* **1984**, *35*, 54–71.
236. Bos, A.R.; Gumanao, G.S.; Salac, F.N. A newly discovered predator of the crown-of-thorns starfish. *Coral Reefs* **2008**, *27*, 581. [\[CrossRef\]](#)
237. Bos, A.R.; Mueller, B.; Gumanao, G.S. Feeding biology and symbiotic relationships of the corallimorpharian *Paracorynactis hoplites* (Anthozoa: Hexacorallia). *Raffles Bull. Zool.* **2011**, *59*, 245–250.
238. Glynn, P.W. *Acanthaster* population regulation by a shrimp and a worm. In *Proceedings 4th International Coral Reef Symposium, 18–22 May 1981*; Marine Science Center, University of the Philippines: Manila, Philippines, 1982; pp. 607–612.
239. Pearson, R.G.; Endean, R. A preliminary study of the coral predator *Acanthaster planci* on the Great Barrier Reef. *Qld Fish. Branch Fish. Notes* **1969**, *3*, 27–55.
240. Endean, R. Population explosions of *Acanthaster planci* and associated destruction of hermatypic corals in the Indo-west Pacific region. In *Biology and Geology of Coral Reefs*; Jones, O., Endean, R., Eds.; Academic Press: New York, NY, USA, 1973; pp. 389–438.
241. Ormond, R.F.G.; Campbell, A.C.; Head, S.H.; Moore, R.J.; Rainbow, P.R.; Saunders, A.P. Formation and breakdown of aggregations of the Crown-of-Thorns starfish, *Acanthaster planci* (L.). *Nature* **1973**, *246*, 167–168. [\[CrossRef\]](#)
242. Alcalá, A.C. The sponge crab *Dromidiopsis dormia* as a predator of the crown of thorns starfish. *Siliman J.* **1974**, *21*, 174.
243. Brown, T.; Willey, K. *Crown of Thorns: The Death of the Great Barrier Reef?* Angus and Robertson: Sydney, Australia, 1972.
244. Glynn, P.W. Interactions between *Acanthaster* and *Hymenocera* in the field and laboratory. In Proceedings of the 3rd International Coral Reef Symposium, Miami, FL, USA, May 1977; pp. 209–215.
245. Owens, D. *Acanthaster planci* starfish in Fiji: Survey of incidence and biological studies. *Fiji Agric. J.* **1971**, *33*, 15–23.
246. Wilson, B.R.; Marsh, L.M. Seasonal behaviour of a ‘normal’ population of *Acanthaster* in Western Australia. In *Proceedings of the Crown-of-Thorns Starfish Seminar, 6th September 1974*; Australian Government Publishing Service: Brisbane, Australia, 1975; pp. 167–179.
247. Endean, R. Destruction and recovery of coral reef communities. In *Biology and Geology of Coral Reefs*; Jones, O., Endean, R., Eds.; Academic Press: New York, NY, USA, 1976; pp. 215–254.
248. Ormond, R.; Bradbury, R.; Bainbridge, S.; Fabricius, K.; Keesing, J.; de Vantier, L.; Medlay, A.; Steven, A. Test of a model of regulation of crown-of-thorns starfish by fish predators. In *Acanthaster and the Coral Reef: A Theoretical Perspective*; Bradbury, R., Ed.; Springer: Heidelberg, Germany, 1990; pp. 189–207.
249. Keesing, J.K.; Halford, A.R. Field measurement of survival rates of juvenile *Acanthaster planci*: Techniques and preliminary results. *Mar. Ecol. Prog. Ser.* **1992**, *85*, 107–114. [\[CrossRef\]](#)
250. Sweatman, H.P.A. A field study of fish predation on juvenile crown-of-thorns starfish. *Coral Reefs* **1995**, *14*, 47–53. [\[CrossRef\]](#)
251. Kroon, F.; (Australian Institute of Marine Science, Townsville, Australia). Personal Communications, Adult pufferfish (*Arothron hispidus*) were observed attacking and feeding on juvenile CoTS in aquaria studies. 2017.
252. Godoy, D.; Pacific Marine Group, Townsville, Australia. Personal Communications, Observations of *Charonia tritonis* feeding on Crown-of-Thorns starfish and *Linckia* sp. on the Great Barrier Reef. 2020.
253. Hughes, R.N. *A Functional Biology of Marine Gastropods*; Croom Helm: London, UK, 1986.



254. Littlewood, D.T.J. Pests and predators of cultivated mangrove oysters. In *Oyster Culture in the Caribbean*; Newkirk, G.F., Field, B.A., Eds.; International Mollusc Culture Research Centre: Halifax, NS, Canada, 1991; pp. 109–146.
255. Endean, R. Aspects of molluscan pharmacology. In *Chemical Zoology. Mollusca*; Flor-Kin, M., Scheer, N.Y., Eds.; Academic Press: New York, NY, USA, 1972; pp. 421–466.
256. Hall, M. Playing on Fears: Exploring the Use of the Pacific Triton for Mitigating Crown-of-Thorns Starfish Outbreaks. Australian Institute of Marine Science (AIMS). Available online: [http://www.aims.gov.au/docs/media/featured-content.html/-/asset\\_publisher/Ydk18I5jDwF7/content/playing-on-fears-exploring-the-use-of-the-pacific-triton-for-mitigating-crown-of-thorns-starfish-outbreaks](http://www.aims.gov.au/docs/media/featured-content.html/-/asset_publisher/Ydk18I5jDwF7/content/playing-on-fears-exploring-the-use-of-the-pacific-triton-for-mitigating-crown-of-thorns-starfish-outbreaks) (accessed on 6 June 2016).
257. Mackie, A.M.; Singh, H.T.; Fletcher, T.C. Studies on the cytolytic effects of seastar (*Marthasterias glacialis*) saponins and synthetic surfactants in the plaice *Pleuronectes platessa*. *Mar. Biol.* **1975**, *29*, 307–314. [\[CrossRef\]](#)
258. Andersson, L.; Bohlin, L.; Iorizzi, M.; Riccio, R.; Minale, L.; Moreno-López, W. Biological activity of saponins and saponin-like compounds from starfish and brittle-stars. *Toxicon* **1989**, *27*, 179–188. [\[CrossRef\]](#)
259. Francis, G.; Kerem, Z.; Makkar, H.P.; Becker, K. The biological action of saponins in animal systems: A review. *Br. J. Nutr.* **2002**, *88*, 587–605. [\[CrossRef\]](#)
260. Sharmin, F.; Koyama, T.; Koyama, H.; Ishizaki, S. Cholesterol-binding ability of saponin from Japanese starfish. *J. Food Sci. Technol.* **2020**, *58*, 3056–3064. [\[CrossRef\]](#) [\[PubMed\]](#)
261. Kitagawa, I.; Kobayashi, M. Saponin sapogenol XXVI. Steroidal saponins from the starfish *Acanthaster planci* L. (crown of thorns). Structure of major saponin thornasteroside A. *Chem. Pharm. Bull.* **1978**, *26*, 1864–1873. [\[CrossRef\]](#)
262. Lucas, J.S.; Hart, R.J.; Howden, M.E.; Salathe, R. Saponins in eggs and larvae of *Acanthaster planci* (L.) (Asteroidea) as chemical defences against planktivorous fish. *J. Exp. Mar. Biol. Ecol.* **1979**, *40*, 155–165. [\[CrossRef\]](#)
263. Montgomery, J.; Carlton, G.; Bodznick, D. Error-driven motor learning in fish. *Biol. Bull.* **2002**, *203*, 238–239. [\[CrossRef\]](#)
264. Prokofeva, N.G.; Chaikina, E.L.; Kicha, A.A.; Ivanchina, N.V. Biological activities of steroid glycosides from starfish. *Comp. Biochem. Physiol. Part B Biochem. Mol. Biol.* **2003**, *134*, 695–701. [\[CrossRef\]](#)
265. Podolak, I.; Galanty, A.; Sobolewska, D. Saponins as cytotoxic agents: A review. *Phytochem. Rev.* **2010**, *9*, 425–474. [\[CrossRef\]](#)
266. Thakur, M.; Melzig, M.F.; Fuchs, H.; Weng, A. Chemistry and pharmacology of saponins: Special focus on cytotoxic properties. *Bot. Targets Ther.* **2011**, *1*, 19–29.
267. Van Dyck, S.; Caulier, G.; Todesco, M.; Gerbaux, P.; Fournier, I.; Wisztorski, M.; Flammang, P. The triterpene glycosides of *Holothuria forskali*: Usefulness and efficiency as a chemical defense mechanism against predatory fish. *J. Exp. Biol.* **2011**, *214*, 1347–1356. [\[CrossRef\]](#)
268. Hashimoto, Y.; Yasumoto, T. Confirmation of saponin as a toxic principle of starfish. *Bull. Jpn. Soc. Sci. Fish.* **1960**, *26*, 1132–1138. [\[CrossRef\]](#)
269. Mackie, A.M.; Singh, H.T.; Owen, J.M. Studies on the distribution, biosynthesis and function of steroidal saponins in echinoderms. *Comp. Biochem. Physiol. B Biochem. Mol. Biol.* **1977**, *56*, 9–14. [\[CrossRef\]](#)
270. Komori, T. Toxins from the starfish *Acanthaster planci* and *Asterina pectinifera*. *Toxicon* **1997**, *35*, 1537–1548. [\[CrossRef\]](#)
271. Narita, H.; Nara, M.; Baba, K.; Ohgami, H.; Ai, T.K.; Noguchi, T.; Hashimoto, K. Effect of feeding a trumpet shell, *Charonia sauliae*, with toxic starfish. *Food Hyg. Saf. Sci.* **1984**, *25*, 251–255. [\[CrossRef\]](#)
272. Fukuda, M.; Egami, F. b-Xylosidase from the liver of *Charonia lampas* II. b-Xylosidase and b-glucosidase. *J. Biochem.* **1969**, *66*, 157–164. [\[CrossRef\]](#) [\[PubMed\]](#)
273. Butters, T.D.; Scudder, P.; Rotsaert, J.; Petursson, S.; Fleet, G.W.J.; Willenbrock, F.W.; Jacob, G.S. Purification to homogeneity of *Charonia lampas* a-fucosidase by using sequential ligand-affinity chromatography. *Biochem. J.* **1991**, *279*, 189–195. [\[CrossRef\]](#)
274. Teshima, S.; Kanazawa, A.; Hyodo, S.; Ando, T. Sterols of the triton, *Charonia tritonis*. *Comp. Biochem. Physiol. B Biochem. Mol. Biol.* **1979**, *64*, 225–228. [\[CrossRef\]](#)
275. Broom, M.J. A preliminary investigation into prey species preference by the tropical gastropods *Natica maculosa* and *Thais carnifera*. *J. Molluscan Stud.* **1983**, *49*, 43–52. [\[CrossRef\]](#)
276. Reichelt, R.E.; Kohn, A.J. Feeding and distribution of predatory gastropods on some Great Barrier Reef platforms. In Proceedings of the 5th International Coral Reef Congress, Tahiti, French Polynesia, 27 May–1 June 1985; pp. 191–196.
277. Jory, D.E.; Carriker, M.R.; Iversen, E.S. Preventing predation in molluscan aquaculture: An overview. *J. World Maric. Soc.* **1984**, *15*, 421–432. [\[CrossRef\]](#)
278. Gutiérrez, R.M.; Gallardo, C.S. Prey attack, food preference and growth in juveniles of the edible muricid snail, *Chorus giganteus*. *Aquaculture* **1999**, *174*, 69–79. [\[CrossRef\]](#)
279. Murdoch, W.W. Switching in general predators: Experiments on predator specificity and stability of prey populations. *Ecol. Monogr.* **1969**, *39*, 335–354. [\[CrossRef\]](#)
280. Russo, G.F.; Fasulo, G.; Toscano, A.; Toscano, F. On the presence of triton species (*Charonia* spp.) (Mollusca, Gastropoda) in the Mediterranean Sea: Ecological considerations. *Boll. Malacol.* **1990**, *26*, 91–104.
281. Doxa, C.K.; Papadakis, I.; Kentouri, M.; Divanach, R. Feeding preference of the Giant triton (*Charonia tritonis variegata*) and its contribution to the conservation of the marine environment. In *AQUA 2006: Linking Tradition & Technology*; World Aquaculture Society: Florence, Italy; Baton Rouge, LA, USA, 2006; p. 263.
282. Kisch, B.S. Further note on *Charonia lampas*. *J. Conchol.* **1952**, *23*, 266.
283. Kisch, B.S. Further observations on *Charonia lampas*. *J. Conchol.* **1949**, *23*, 84.

284. Doxa, C.K.; Kentouri, M.; Divanach, P. Feeding of *Charonia sequezea* (Arada & Benoit, 1870) on natural prey and alternative foods. *J. Molluscan Stud.* **2012**, *79*, 76–78.
285. Birkeland, C. The faustian traits of crown-of-thorns starfish. *Am. Sci.* **1989**, *77*, 155–163.
286. Birkeland, C. The influence of echinoderms on coral reef communities. In *Echinoderm Studies*; Jangoux, M., Lawrence, J., Eds.; Balkema: Rotterdam, The Netherlands, 1989; pp. 1–77.
287. Trussell, C.C.; Ewanchuk, P.J.; Bertness, M.D. Trait-mediated effects in rocky intertidal food chains: Predator risk cues alter prey feeding rates. *Ecology* **2003**, *84*, 629–640. [[CrossRef](#)]
288. Turner, A.M.; Mittelbach, G.G. Predator avoidance and community structure: Interactions among piscivores, planktivores and plankton. *Ecology* **1990**, *71*, 2241–2254. [[CrossRef](#)]
289. Legault, C.; Himmelman, J.H. Relation between escape behaviour of benthic invertebrates and the risk of predation. *J. Exp. Mar. Biol. Ecol.* **1993**, *170*, 55–74. [[CrossRef](#)]
290. Soluk, D.A. Multiple predator effects: Predicting combined functional response of stream fish and invertebrate predators. *Ecology* **1993**, *74*, 219–225. [[CrossRef](#)]
291. Dodson, S.I.; Crowl, T.A.; Peckarsky, B.L.; Kats, L.B.; Covich, A.P.; Culp, J.M. Non-visual communication in freshwater benthos: An overview. *J. N. Am. Benthol. Soc.* **1994**, *13*, 268–282. [[CrossRef](#)]
292. Swisher, B.J.; Soluk, D.A.; Wahl, D.H. Non-additive predation in littoral habitats: Influences of habitat complexity. *Oikos* **1998**, *81*, 30–37. [[CrossRef](#)]
293. Bruno, J.F.; Bertness, M.D. Habitat modification and facilitation in benthic marine communities. In *Marine Community Ecology*; Bertness, M.D., Gaines, S.D., Hay, M.E., Eds.; Sinauer Associates: Sunderland, MA, USA, 2001.
294. Werner, E.; Peacor, S. A review of trait-mediated indirect interactions in ecological communities. *Ecology* **2003**, *5*, 1083–1100. [[CrossRef](#)]
295. Abrams, P.A. Habitat choice in predator-prey systems: Spatial instability due to interacting adaptive movements. *Am. Nat.* **2007**, *169*, 581–594. [[CrossRef](#)]
296. Ferrer, R.P.; Zimmer, R. Community ecology and the evolution of molecules of keystone significance. *Biol. Bull.* **2012**, *223*, 167–177. [[CrossRef](#)] [[PubMed](#)]
297. Ferrer, R.P.; Zimmer, R.K. Molecules of keystone significance: Crucial agents in ecology and resource management. *Bioscience* **2013**, *63*, 428–438. [[CrossRef](#)]
298. Murray, J.A.; Wyeth, R.C. Introduction to the symposium-chemicals that organize ecology: Towards a greater integration of chemoreception, neuroscience organismal biology and chemical ecology. *Integr. Comput. Biol.* **2015**, *55*, 444–446. [[CrossRef](#)]
299. Tewfik, A. Losing the Shell Game: Consequences of Seascapes without Predatory Gastropods. In Proceedings of the 67th Gulf and Caribbean Fisheries Institute, Christ Church, Barbados, 3–7 November 2014; pp. 331–338.
300. Brown, K.M.; Alexander, J.E. Group foraging in a marine gastropod predator: Benefits and costs to individuals. *Mar. Ecol. Prog. Ser.* **1994**, *112*, 97–105. [[CrossRef](#)]
301. Abrams, P.A. Implications of dynamically variable traits for identifying, classifying and measuring direct and indirect effects in ecological communities. *Am. Nat.* **1995**, *146*, 112–134. [[CrossRef](#)]
302. Schmitz, O.J.; Berckerman, A.; O'Brien, K.M. Behaviourally mediated trophic cascades: Effects of predation risk on food web interactions. *Ecology* **1997**, *78*, 1388–1399. [[CrossRef](#)]
303. Pinnegar, J.K.; Polunin, N.V.C.; Francour, P.; Badalamenti, F.; Chemello, R.; Harmelin-Vivien, M.L.; Hereu, B.; Milazzo, M.; Zabala, M.; D'anna, G.; et al. Trophic cascades in benthic ecosystems: Lessons for fisheries and protected-marine areas. *Environ. Conserv.* **2000**, *27*, 179–200. [[CrossRef](#)]
304. Bernot, R.; Turner, A. Predatory identity and trait-mediated indirect effects in a littoral food web. *Oecologia Aquat.* **2001**, *129*, 139–146. [[CrossRef](#)]
305. Dill, L.M.; Heithaus, M.R.; Walter, C.J.s. Behaviourally mediated indirect interactions in marine communities and their conservation implications. *Ecology* **2003**, *84*, 1151–1157. [[CrossRef](#)]
306. Witman, J.D.; Genovese, S.J.; Bruno, J.F.; McLaughlin, J.W.; Pavlin, B.I. Massive prey recruitment and the control of rocky subtidal communities on large spatial scales. *Ecol. Monogr.* **2003**, *73*, 441–462. [[CrossRef](#)]
307. Bolnick, D.I.; Preisser, E.L. Resource competition modifies the strength of trait-mediated predator-prey interactions: A meta-analysis. *Ecology* **2005**, *86*, 2771–2779. [[CrossRef](#)]
308. Toscano, B.J.; Griffen, B.D. Trait-mediated functional responses: Predator behavioural type mediates prey consumption. *J. Anim. Ecol.* **2014**, *83*, 1469–1477. [[CrossRef](#)]
309. Hall, A.E.; Kingsford, M.J. Variation in the population demographics of *Scolopsis bilineatus* in response to predators. *Coral Reefs* **2016**, *35*, 1173–1185. [[CrossRef](#)]
310. Morgan, S.G.; Gavem, S.A.; Lipus, A.C.; Grabiell, M.; Miner, B.G. Trait-mediated indirect interactions among residents of rocky shore tidepools. *Mar. Ecol. Prog. Ser.* **2016**, *552*, 31–46. [[CrossRef](#)]
311. Ng, G.; Gaylord, B. The legacy of predators: Persistence of trait-mediated indirect effects in an intertidal food chain. *J. Exp. Mar. Biol. Ecol.* **2020**, *530–531*, 151416. [[CrossRef](#)]
312. Luttbeg, B.; Kerby, J.L. Are scared prey as good as dead? *Trends Ecol. Evol.* **2005**, *20*, 416–418. [[CrossRef](#)]

313. Peckarsky, B.L.; Abrams, P.A.; Bolnick, D.I.; Dill, L.M.; Grabowski, J.H.; Luttbeg, B.; Orrock, J.L.; Peacor, S.D.; Preisser, E.L.; Schmitz, O.J.; et al. Revisiting the classics: Considering nonconsumptive effects in textbook examples of predator-prey interactions. *Ecology* **2008**, *89*, 2416–2425. [[CrossRef](#)] [[PubMed](#)]
314. Peckarsky, B.L.; Kerans, B.L.; McIntosh, A.R.; Taylor, B.W. Predator effects on prey population dynamics in open systems. *Oecologia* **2008**, *156*, 431–440. [[CrossRef](#)] [[PubMed](#)]
315. Orrock, J.L.; Sih, A.; Dill, L.M.; Grabowski, J.H.; Peacor, S.D.; Peckarsky, B.L.; Preisser, E.L.; Vonesh, J.R.; Werner, E.E. Predator effects in predator-free space: The remote effects of predators on prey. *Open Ecol. J.* **2010**, *3*, 22–30. [[CrossRef](#)]
316. Paterson, R.A.; Pritchard, D.W.; Cick, J.T.A.; Alexander, M.E.; Hatcher, M.J.; Dunn, A.M. Predator cue studies reveal strong trait-mediated effects in communities despite variation in experimental designs. *Anim. Behav.* **2013**, *86*, 1301–1313. [[CrossRef](#)]
317. Schmitz, O.J.; Krivan, K.; Ovadia, O. Trophic cascades: The primacy of trait-mediated indirect interactions. *Ecol. Lett.* **2004**, *7*, 153–163. [[CrossRef](#)]
318. Turner, A.M.; Bernot, R.J.; Boes, C.M. Chemical cues modify species interactions: The ecological consequences of predator avoidance by freshwater snails. *Oikos* **2000**, *88*, 148–158. [[CrossRef](#)]
319. Preisser, E.L.; Bolnick, D.I.; Benard, M.F. Scared to death? The effects of intimidation and consumption in predator-prey interactions. *Ecology* **2005**, *86*, 501–509. [[CrossRef](#)]
320. Dill, L.M. Animal decision making and its ecological consequences: The future of aquatic ecology and behaviour. *Can. J. Zool.* **1987**, *65*, 803–811. [[CrossRef](#)]
321. Fletcher, W.J. Interactions among subtidal Australian sea urchins, gastropods and algae: Effects of experimental removals. *Ecol. Monogr.* **1987**, *57*, 89–109. [[CrossRef](#)]
322. Shurin, J.B.; Borer, E.T.; Seabloom, E.W.; Anderson, K.; Blanchette, C.A.; Broitman, B.; Cooper, S.D.; Halpern, B.S. A cross-ecosystem comparison of the strength of trophic cascades. *Ecol. Lett.* **2002**, *5*, 785–791. [[CrossRef](#)]
323. Schultz, J.A.; Cloutier, R.N.; Côte, I. Evidence for a trophic cascade on rock reefs following sea star mass mortality in British Columbia. *PeerJ* **2016**, *4*, e1980. [[CrossRef](#)] [[PubMed](#)]
324. Freeman, A. Size-dependent trait-mediated indirect interactions among sea urchin herbivores. *Behav. Ecol.* **2005**, *17*, 182–187. [[CrossRef](#)]
325. Preisser, E.L.; Bolnick, D.I. The many faces of fear: Comparing the pathways and impacts of nonconsumptive predator effects on prey populations. *PLoS ONE* **2008**, *3*, e2465. [[CrossRef](#)] [[PubMed](#)]
326. Deletre, E.; Schatz, B.; Bourguet, D.; Chandre, F.; Williams, L.; Ratnadass, A.; Martin, T. Prospects for repellent in pest control: Current developments and future challenges. *Chemoecology* **2016**, *26*, 127–142. [[CrossRef](#)]
327. Atalah, J.; Hopkins, G.A.; Fletcher, L.M.; Castinel, A.; Forrest, B.M. Concepts for biocontrol in marine environments: Is there a way forward? *Manag. Biol. Invasions* **2015**, *6*, 1–12. [[CrossRef](#)]
328. Lima, S.L.; Bednekoff, P.A. Temporal variation in danger drives antipredator behaviour: The predation risk allocation hypothesis. *Am. Nat.* **1999**, *153*, 649–659. [[CrossRef](#)]
329. Lima, S.L. Putting predators back into behavioral predator-prey interactions. *Trends Ecol. Evol.* **2002**, *17*, 70–75. [[CrossRef](#)]
330. Fryxell, J.M.; Mosser, A.; Sinclair, A.R.; Packer, C. Group formation stabilizes predator-prey dynamics. *Nature* **2007**, *449*, 1041–1043. [[CrossRef](#)]
331. Ferrari, M.C.; Sih, A.; Chivers, D.P. The paradox of risk allocation: A review and prospectus. *Anim. Behav.* **2009**, *78*, 579–585. [[CrossRef](#)]
332. Khater, M.; Murariu, D.; Gras, R. Contemporary evolution and genetic change of prey as a response to predator removal. *Ecol. Inform.* **2014**, *22*, 13–22. [[CrossRef](#)]
333. Zimmer, R.K.; Butman, C.A. Chemical signaling processes in the marine environment. *Biol. Bull.* **2000**, *198*, 168–187. [[CrossRef](#)]
334. Buskirk, J.V.; Krügel, A.; Kunz, J.; Miss, F.; Stamm, A. The rate of degradation of chemical cues indicating predation risk: An experiment and review. *Ethology* **2014**, *120*, 942–949. [[CrossRef](#)]
335. Gerlach, G.; Atema, J.; Kingsford, M.; Black, K.; Miller-Sims, V. Smelling home can prevent dispersal of reef fish larvae. *Proc. Natl. Acad. Sci. USA* **2007**, *104*, 858–863. [[CrossRef](#)]
336. Atema, J.; Brönmark, C.; Hansson, L.A. Aquatic odor dispersal fields: Opportunities and limits of detection, communication and navigation. In *Chemical Ecology in Aquatic Systems*; Brönmark, C., Hansson, L.A., Eds.; Oxford University Press: Oxford, UK, 2012; pp. 1–18.
337. Kats, L.B.; Dill, L.M. The scent of death: Chemosensory assessment of predation risk by prey animals. *Ecoscience* **1998**, *5*, 361–394. [[CrossRef](#)]
338. Mirza, R.S.; Chiver, D.P. Learned recognition of heterospecific alarm signals: The importance of a mixed predator diet. *Ethology* **2001**, *107*, 1007–1018. [[CrossRef](#)]
339. McCarthy, T.M.; Dickey, B.F. Mediated effects of injured prey on behavior of both prey and predators. *Behavior* **2002**, *139*, 585–602.
340. Gras, R.; Devaurs, D.; Wozniak, A.; Aspinnall, A. An individual based evolving predator-prey ecosystem simulation using fuzzy cognitive map as behavior model. *Artif. Life* **2009**, *15*, 423–463. [[CrossRef](#)] [[PubMed](#)]
341. Wicher, D. Functional and evolutionary aspects of chemoreceptors. *Front. Cell. Neurosci.* **2012**, *6*, 48. [[CrossRef](#)]
342. Beirner, B.P. Biological control and its potential. *World Rev. Pest Control* **1967**, *6*, 7–20.
343. Lafferty, K.; Kuris, A. Biological control of marine pests. *Ecology* **1996**, *77*, 1989–2000. [[CrossRef](#)]

344. Snyder, N.F.R.; Derrickson, S.R.; Beissinger, S.R.; Wiley, J.W.; Smith, T.B.; Toone, W.D.; Miller, B. Limitations of captive breeding in endangered species recovery. *Conserv. Biol. Pract.* **1996**, *10*, 338–348. [\[CrossRef\]](#)
345. Kroon, F.J.; Barneche, D.R.; Emslie, M.J. Fish predators control outbreaks of Crown-of-Thorns Starfish. *Nat. Commun.* **2021**, *12*, 6986. [\[CrossRef\]](#)
346. Zhou, Y.; Pan, J. A preliminary study on biological control of *Cymatium*, a predator of *Pinctada martensis*. *J. Trop. Oceanol.* **2001**, *3*, 20–22.
347. Malavé, C.; Freitas, L.; Lodeiros, C.; Mendoza, J.; Troccoli, L.; Dale, A.W. Annual recruitment, predation rates and biocontrol of *Linatella caudata* (Mollusca: Gastropoda) in suspended enclosure culture of the pearl oyster *Pinctada imbricata*. *Aquaculture* **2012**, *354–355*, 75–83. [\[CrossRef\]](#)
348. Delgado, G.A.; Sharp, W.C. Capitalizing on an ecological process to aid coral reef ecosystem restoration: Can gastropod trophodynamics enhance coral survival? *Coral Reefs* **2020**, *39*, 319–330. [\[CrossRef\]](#)
349. Holland, B.S.; Chock, T.; Lee, A.; Sugiura, S. Tracking behavior in the snail *Euglandina rosea*: First evidence of preference for endemic vs. Biocontrol target pest species in Hawaii. *Am. Malacol. Bull.* **2012**, *30*, 153–157. [\[CrossRef\]](#)
350. Cowie, R.H. Can snails ever be effective and safe biocontrol agents? *Int. J. Pest Manag.* **2001**, *47*, 23–40. [\[CrossRef\]](#)
351. Cunha, R.L.; Grande, C.; Zardoya, R. Neogastropod phylogenetic relationships based on entire mitochondrial genomes. *BMC Evol. Biol.* **2009**, *9*, 210. [\[CrossRef\]](#)
352. Xiong, G.; Wang, X.Q.; Kang, L.; Ma, X.; Zhu, D.L.; Wang, L.M.; Wu, Q.S.; Zeng, Z.N. The complete mitochondrial genome of the *Babylonia areolata*. *Mitochondrial DNA Part A DNA Mapp. Seq. Anal.* **2016**, *27*, 645–646.
353. Chen, P.-W.; Hsiao, S.-T.; Chen, K.-S.; Tseng, C.-T.; Wu, W.-L.; Hwang, D.-F. Mitochondrial DNA sequence of *Conus textile* (Neogastropoda: Conidae). *Mitochondrial DNA Part B Resour.* **2016**, *1*, 508–509. [\[CrossRef\]](#)
354. He, Z.P.; Dai, X.B.; Zhang, S.; Zhi, T.T.; Lun, Z.R.; Wu, Z.D.; Yang, T.B. Complete mitochondrial genome of the giant African snail, *Achatina fulica* (Mollusca: Achatinidae): A novel location of putative control regions (CR) in the mitogenome within Pulmonate species. *Mitochondrial DNA Part A DNA Mapp. Seq. Anal.* **2016**, *27*, 1084–1085. [\[CrossRef\]](#) [\[PubMed\]](#)
355. Wang, M.; Qiu, J.W. Complete mitochondrial genome of the giant ramshorn snail *Marisa cornuarietis* (Gastropoda: Ampullariidae). *Mitochondrial DNA Part A DNA Mapp. Seq. Anal.* **2016**, *27*, 1734–1735.
356. Yang, Q.; Liu, S.; Song, F.; Li, H.; Liu, J.; Liu, G.; Yu, X. The mitochondrial genome of *Pomacea maculata* (Gastropoda: Ampullariidae). *Mitochondrial DNA Part A DNA Mapp. Seq. Anal.* **2016**, *27*, 2895–2896. [\[CrossRef\]](#) [\[PubMed\]](#)
357. Zhou, X.; Chen, Y.; Zhu, S.; Xu, H.; Liu, Y.; Chen, L. The complete mitochondrial genome of *Pomacea canaliculata* (Gastropoda: Ampullariidae). *Mitochondrial DNA Part A DNA Mapp. Seq. Anal.* **2016**, *27*, 884–885.
358. Liu, C.; Zhang, Y.; Ren, Y.; Wang, H.; Li, S.; Jiang, F.; Yin, L.; Qiao, X.; Zhang, G.; Qian, W. The genome of the golden apple snail *Pomacea canaliculata* provides insight into stress tolerance and invasive adaptation. *GigaScience* **2018**, *7*, giy101. [\[CrossRef\]](#)
359. Yang, H.; Zhang, J.E.; Xia, J.; Yang, J.; Guo, J.; Deng, Z.; Luo, M. Comparative characterization of the complete mitochondrial genomes of the three apple snails (Gastropoda: Ampullariidae) and the phylogenetic analyses. *Int. J. Mol. Sci.* **2018**, *19*, 3646. [\[CrossRef\]](#) [\[PubMed\]](#)
360. Sharp, W.; Delgado, G. Predator-prey interactions between the corallivorous snail *Coralliophila abbreviata* and the carnivorous deltoid rock snail *Thais deltoidea*. *Biol. Bull.* **2015**, *229*, 129–133. [\[CrossRef\]](#)
361. Barratt, B.I.P.; Berndt, L.A.; Dodd, S.L.; Ferguson, C.M.; Hill, R.L.; Kean, J.M.; Teulon, D.A.J.; Withers, T.M. Biocontrol Information Resource for EPA Applicants. Available online: <http://www.b3nz.org/birea/> (accessed on 12 September 2022).
362. Symondson, W.O.C.; Sunderland, K.D.; Greenstone, M.H. Can generalist predators be effective biocontrol agents? *Annu. Rev. Entomol.* **2002**, *47*, 561–594. [\[CrossRef\]](#)
363. Brodeur, J. Host specificity in biological control: Insights from opportunistic pathogens. *Evol. Appl.* **2012**, *5*, 470–480. [\[CrossRef\]](#)
364. Hellmann, J.J.; Byers, J.E.; Bierwagen, B.G.; Dukes, J.S. Five potential consequences of climate change for invasive species. *Conserv. Biol.* **2008**, *22*, 534–543. [\[CrossRef\]](#)
365. Cheah, C.A.S.-J.; McClure, M.S. Seasonal synchrony of life cycles between the exotic predator, *Pseudoscyrmus tsugae* (Coleoptera: Coccinellidae) and its prey, the hemlock woolly adelgid *Adelges tsugae* (Homoptera: Adelgidae). *Agric. For. Entomol.* **2000**, *2*, 241–251. [\[CrossRef\]](#)
366. Webster, D.R.; Weissburg, M.J. The Hydrodynamics of Chemical Cues Among Aquatic Organisms. *Annu. Rev. Fluid Mech.* **2009**, *41*, 73–90. [\[CrossRef\]](#)
367. Motti, C.; Vasile, R.; Robson, B.; Høj, L.; Wang, C.; Craik, D.; Degnan, B.; Degnan, S.; Cummins, S.; Martini, A.; et al. Deployment of semiochemical control agents to manage Crown-of-Thorns starfish populations. In *A Report to the Australian Government by the COTS Control Innovation Program*; Australian Institute of Marine Science: Townsville, Australia, 2022; p. 80.