



Perspective

The future of utilising semiochemical pest control methods to manage the destructive crown-of-thorns starfish outbreaks on coral reefs

Richard J. Harris^{a,*}, d'Artagnan L. Barnard^b, Gillian Paxton^c, Stewart Lockie^c,
David J. Craik^b, Scott F. Cummins^d, Conan K. Wang^b, Cherie A. Motti^a

^a Australian Institute of Marine Science (AIMS), Cape Cleveland, 4810, Australia

^b Institute for Molecular Bioscience (IMB), ARC Centre of Excellence for Innovations in Peptide and Protein Science, The University of Queensland, Brisbane, 4072, Australia

^c The Cairns Institute, James Cook University (JCU), Cairns, 4870, Australia

^d Centre for Bioinnovation, University of the Sunshine Coast (UniSC), Sippy Downs, Queensland 4556, Australia

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ABSTRACT

The Crown-of-Thorns Starfish (*Acanthaster* cf. *solaris*; CoTS) is arguably the most destructive non-human animal to coral reefs, significantly impeding coral survival in the face of the foremost effects of climate change and coral bleaching. Controlling the unprecedented number of CoTS outbreaks and damage on reef systems is vital for the survival of the reef ecosystem. The emergent strategy of using semiochemicals in terrestrial pest control management, due to their environmentally friendly nature, has generated interest in their application to control populations of this destructive species. However, there have been only a limited number of studies on promising semiochemical applications within aquatic systems. This Perspectives Review provides a much-needed outlook of CoTS chemosensory and semiochemical repertoire, how we might hypothetically utilise semiochemicals with regard to modifying CoTS behaviours and discusses future research directions and the scope for innovative semiochemical technologies with the aim of sustainably controlling CoTS populations, thereby mitigating their devastating outbreaks and destruction of coral reef systems.

1. Introduction

The Crown-of-Thorns starfish (CoTS; *Acanthaster* spp. complex (Haszprunar et al., 2017)) threatens the biodiversity and ecological infrastructure of reef ecosystems via the degradation and consumption of hard (Scleractinian) corals (Birkeland, 1989a; Birkeland and Lucas, 1990; Colgan, 1987; De'Ath et al., 2012). These starfish were once grouped as *Acanthaster planci*, but recent evidence suggests that they are in fact a multispecies complex (Haszprunar et al., 2017; Haszprunar and Spies, 2014). The most notorious and arguably the most problematic of the species complex, *Acanthaster* cf. *solaris*, is native to tropical Indo-Pacific coral reefs, extending from Australia (specifically the Great Barrier Reef; GBR), Fiji, French Polynesia (Bora Bora, Moorea, Raiatea, and Tahiti), Japan, Marshall Islands, Micronesia, Papua New Guinea, Philippines, Vanuatu and Vietnam (Uthicke et al., 2024). A significant increase in the number of periodic CoTS outbreaks across the expanse of the Indo-Pacific, more prevalently across the GBR and South-East Asia, has raised concerns regarding the future health of many of these reef

ecosystems (Birkeland and Lucas, 1990; Pratchett et al., 2017a). More recently, *Acanthaster* spp. have begun to cause issues on reefs deemed outbreak-free, such as in the Gulf of Oman (United Arab Emirates) which similarly to major Indo-Pacific reefs, are also subject to increasing anthropogenic disturbances (Seveso et al., 2024).

The biggest threat to coral reef systems remains climate change. However, large losses of coral due to the unpredictable occurrence of CoTS population outbreaks and unprecedented consumption means that coral are fighting, and seemingly losing, on multiple battlefronts, which leaves them little respite and even less time to adapt to changing climate conditions. Therefore, being able to control the CoTS burden might give coral a greater chance of adapting and becoming more resilient to climate impacts. In light of the on-going threat of CoTS outbreaks to reef systems, there is a collective call for urgent and major actions from governments and environmental managers as well as largescale governmental and stakeholder research funded programs (including culling and monitoring programs) operating across research institutes to help solve the CoTS crisis (GBRMPA, 2020; GBRMPA, 2022; GBRF,

* Corresponding author.

E-mail address: r.harris@aims.gov.au (R.J. Harris).

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2024a; GBRF, 2024b).

1.1. The Crown-of-Thorns problem and current control methods

Due to their destructive capacity, there are some misconceptions that CoTS are an invasive pest species. In fact, they are endemic to the reef systems they inhabit and play a vital role in ecosystem dynamics (Fabricius and Fabricius, 1992; Yuasa et al., 2021). They are a natural boom-and-bust species, whereby their adult populations cycle through large fluctuations of increase, supported by a plentiful supply of their preferred coral prey, and then collapse as this prey becomes limited (Uthicke et al., 2009). Under natural conditions, these boom-and-bust cycles are likely beneficial to the reef ecosystem, but with the frequency of major outbreaks increasing from every 50–80 years to approximately every 15–17 years (Condie et al., 2018; Babcock et al., 2020), there is widespread concern, particularly since it is estimated to take 10–25 years for coral reefs to recover from mass bleaching events (Lourey et al., 2000). Several hypotheses have proposed anthropogenic sources, such as increasing terrestrial run-off of agricultural chemicals and nutrients, reduction in natural predators, or a combination of these (Pratchett et al., 2017a; Birkeland, 1982), as drivers of more frequent outbreaks. To date, these hypotheses have gone unresolved and provide no clear answer on how best to stem the issue. Therefore, without intervention and prevention strategies to moderate outbreaks, the health of reef systems will continue to decline.

Some authors have questioned the impact of culling on aquatic ecosystems (Bowen, 2011; Altenritter et al., 2022), including whether mass killing of CoTS is currently the correct solution - especially given there remains a lack of unequivocal scientific evidence for how and why CoTS outbreaks occur - and what the mass killing of CoTS means from a functional perspective to the broader reef ecosystem (Bellwood et al., 2024; Li et al., 2024). It has been suggested that one of the vital ecological roles CoTS play might be the consumption of highly competitive, fast growing coral (*Acropora* spp.) that in turn can promote slower-growing coral species, thereby increasing the diversity and productivity across a reef ecosystem (Bellwood et al., 2024; Porter, 1972). Bellwood et al., (2024) posed the question “are we in effect, actively preventing the establishment of diverse, resilient reefs by culling *Acropora* consuming CoTS?”

Despite the persistent knowledge gaps regarding CoTS functional role on reef ecosystems, coral loss due to climate change remains a real and on-going concern, and the confounding factor of CoTS coral consumption is preventing reefs from adapting fast enough to changing climate conditions. Therefore, attempting to control CoTS in the present is still a priority if we are to build reef resilience and buy time for adaptation. Government intervention has been a key factor in establishing CoTS culling programs, which are economically expensive and labour intensive, with the Australian Government investing USD\$70 million between 2012 and 2022 (Pratchett et al., 2019), and the Japanese Government investing today’s equivalent of USD\$2.5 billion in 1970, the latter for a negligible future impact (Pratchett et al., 2019; Yamaguchi, 1986).

To date, in situ manual culling is the most effective method for controlling CoTS outbreaks (Pratchett et al., 2019; Pratchett et al., 2014; Westcott et al., 2020; Matthews et al., 2024). To achieve this, efforts initially involved hand collection of adults and disposal on land (Pratchett et al., 2019; Yamaguchi, 1986), requiring significant manual labour and handling of CoTS (Boström-Einarsson et al., 2018; Boström-Einarsson and Rivera-Posada, 2016; Moutardier et al., 2015; Rivera-Posada et al., 2014). Contemporary methods involving the injection of adult CoTS in situ with chemicals are now common practice. Originally, the chemicals used were copper sulphate and then sodium bisulphate; however, to ensure mortality, CoTS had to be manually injected upwards of 30 times over different body areas (Rivera-Posada et al., 2011a; Rivera-Posada et al., 2011b), which did not represent a viable long-term solution. Nowadays, the most effective culling chemicals are bile salts

(Rivera-Posada et al., 2014) or weak acids such as acetic (Boström-Einarsson and Rivera-Posada, 2016) and citric acid (Buck et al., 2016). These usually require a single injection (10 mL), which acts rapidly to kill CoTS. Bile salts have proven more effective as they also induce an immune response that leads to cell apoptosis (Grand et al., 2014). Although culling by injection has proven to be effective at reducing CoTS densities and minimising environmental impacts, it remains a labour-intensive and time-consuming approach (Birkeland and Lucas, 1990; Pratchett et al., 2019; Westcott et al., 2020). Although research has identified the specific habitat types in which smaller juveniles live (i. e., within spur and groove systems and the underside of coral rubble) (Wilmes et al., 2020), the expanse of these habitats and their camouflage means there is not yet an effective culling method available to impact on these subpopulations (Birkeland and Lucas, 1990; Yamaguchi, 1973).

Recent narrative has identified the need to improve the effectiveness of the current culling effort on the GBR, either through expansion of the existing on-water CoTS Control Program (GBRMMPA, 2024) or development of new methods (Pratchett et al., 2021a). Amongst concepts under investigation, modification of CoTS behaviour has been suggested as a factor to exploit toward development of new biotechnologies for inclusion in the CoTS Integrated Pest Management Program (Hall et al., 2017). The sensory perceptions of vision (photoreception) are known in CoTS (Beer et al., 2016; Petie et al., 2016a; Petie et al., 2016b), however, it is their chemosensory perceptions (detection of chemical cues) that are vital to their ecology and the primary mode of communication and environmental sensation (Motti et al., 2018). Due to this understanding, and supported by recent commentaries (Pratchett et al., 2021a; Hall et al., 2017; Motti et al., 2018; Høj et al., 2020; Motti et al., 2022a), the inclusion of semiochemical technologies in the control of CoTS outbreaks is gaining traction. It is time to consider a targeted perspective on CoTS (and more specifically *A. cf. solaris*) semiochemicals.

2. A concise overview of semiochemicals

In the past 50 years, in an attempt to move away from the environmental consequences of pesticides (Sharma et al., 2019a), major efforts have been made to develop more efficient, safer, and environmentally friendly forms of chemical pest control methods (Zhou et al., 2024). Investigations into the use of semiochemicals (a chemical mixture emitted from an organism that changes the behaviour of the receiver) as alternatives have led to a better understanding of semiochemical-mediated interactions between and within species, knowledge which is now being exploited to develop new biotechnologies in pest management programs.

Semiochemicals, derived from the Greek word *semeion*, meaning ‘signal’, are emitted molecules that provide ecological information. The interpretation of semiochemicals by an organism can elicit an innate (physiological or behavioural) or learned response (Law and Regnier, 1971; Nordlund and Lewis, 1976; Freas and Cheng, 2022). Since chemicals and chemical mixtures can have a myriad of conformational chemical structures, concentrations, and combinations of molecules, the information they transmit can be highly specific to their source, providing information such as sex, species, location, age, etc. (Law and Regnier, 1971; Regnier, 1971; Whittaker and Feeny, 1971; Karlson and Lüscher, 1959). Typically, semiochemicals are detected by chemoreceptors, including G-protein-coupled receptors (GPCRs) and ionotropic glutamate receptors (Bargmann, 2006; Buck and Axel, 1991; Croset et al., 2010), and once detection occurs, a signal cascade modulates a specific physiological or behavioural change. Semiochemicals are categorised based on whether they are intraspecific (pheromones and signal mixtures) or interspecific (allelochemicals) in their mode of action (Law and Regnier, 1971; Nordlund and Lewis, 1976; Wyatt, 2010; Wyatt, 2014). Pheromones and allelochemicals can be further subdivided based on their functional roles in a given environment (Fig. 1). Although there are defining singular molecules that elicit a semiochemical behaviour, it is likely that a complex combination of

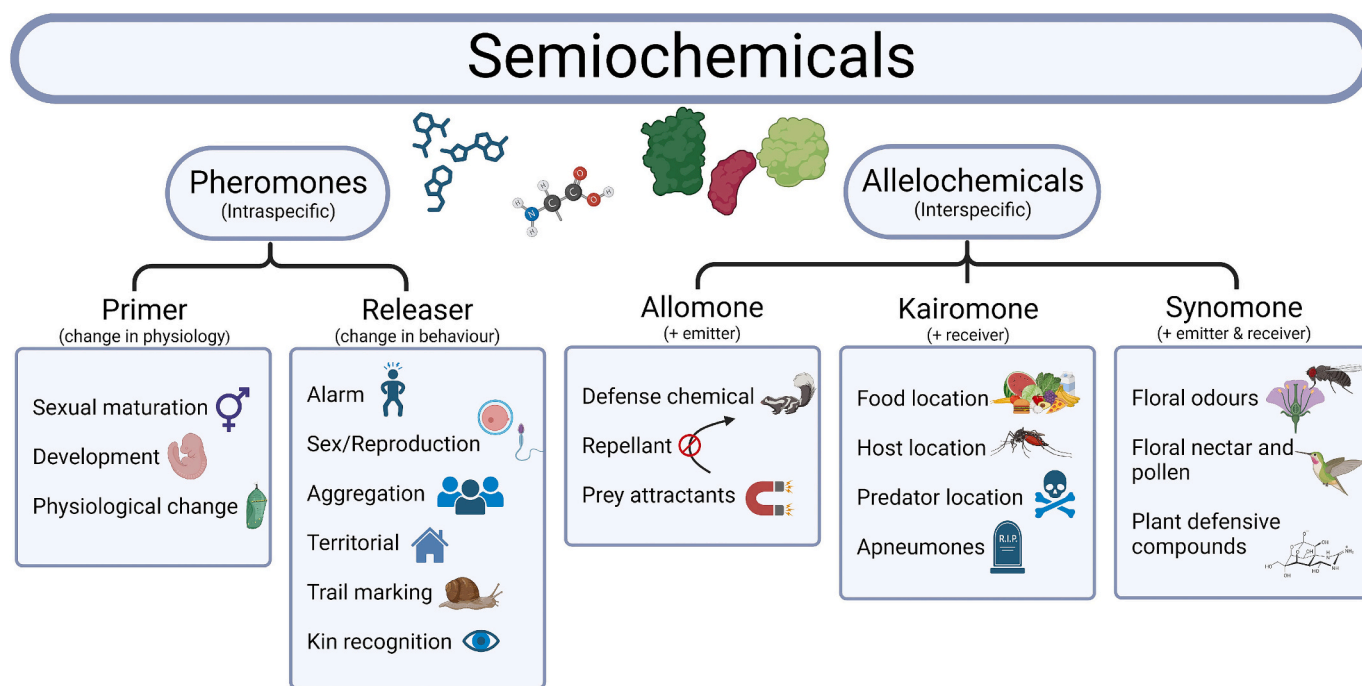


Fig. 1. A schematic diagram of semiochemical distinctions. Figure created using [Biorender.com](https://biorender.com).

molecular components is what creates the specificity or potency of the signal (Wyatt, 2010; Christensen et al., 1989).

2.1. Pheromones and signal mixtures

Pheromones, currently defined as, “molecules that are evolved signals, in defined ratios in the case of multiple component pheromones, which are emitted by an individual and received by a second individual of the same species, in which they cause a specific reaction” (see (Wyatt, 2010) modified from (Karlson and Lüscher, 1959)). Most pheromones are not a single molecule, but more likely a species-specific ratio of combined molecules that create a variety of effects that are context and receiver dependent. In most cases pheromones seem to induce an innate response, but in some instances learning of this mixture to elicit a behaviour is required (Wyatt, 2014).

There are two types of pheromonal effect: primer and releaser (Law and Regnier, 1971; Wilson, 1963). Primer pheromones alter physiological processes *within* the receiver, which elicit changes in behaviour over time (Law and Regnier, 1971), whilst releaser pheromones prompt a rapid behavioural response (Law and Regnier, 1971). Pheromones can also have both a primer and releaser effect as evidenced by pheromones found in goldfish (Stacey, 2014; Stacey, 2011).

Wyatt (2010) made a distinction between pheromones and what he termed ‘signal mixtures’, defined as “a variable chemical mixture (a subset of the molecules in an animal’s chemical profile) learned by other conspecifics and used to recognize an animal as an individual or as a member of a particular social group”. This review will avoid utilising the term signal mixture as (i) it could be argued that pheromones are an integral part of all signal mixtures, and (ii) the review’s intention is only to distinguish semiochemicals on a species-specific scale, not an individual scale.

2.2. Allelochemicals

Allelochemicals, chemical signals that work on an interspecific scale, are subdivided into allomones, kairomones, and synomones depending upon their beneficial nature to the receiver and/or emitter (Nordlund and Lewis, 1976; Whittaker and Feeny, 1971; Dicke and Sabelis, 1988). Allomones provide a benefit for the emitter but are detrimental to the

receiver (Nordlund and Lewis, 1976; Dicke and Sabelis, 1988). Such instances can be found in predator-deterrent exocrine secretions of skunks (Andersen et al., 1982; Wood et al., 2002), cockroaches (Brossut, 1983; Turnbull and Fashing, 2002), and some ticks (Yoder et al., 1993). Prey attractants/chemical mimicry are also common allomones (Haynes et al., 2002; Yeagan, 1988). Kairomones are semiochemicals that are detrimental to the emitter but are beneficial to the receiver (Nordlund and Lewis, 1976; Dicke and Sabelis, 1988). Kairomones are usually involved in the detection of a source such as food, predators, or deceased organic matter (apneumones/necromones). A prime example is host detection in haematophagous insects, such as mosquitos, whereby a plethora of compounds emitted by a host provide directional and species cues (Bernier et al., 2000; Gillies, 1980; Kemme et al., 1993; Price et al., 1979; Takken et al., 1997). Synomones provide a collaborative benefit to both the emitter and the receiver (Nordlund and Lewis, 1976; Dicke and Sabelis, 1988). Instances of synomones are largely found in pollinating plants where food, shelter, or a reproductive advantage is exchanged for pollen dispersal (Nishida, 2000; Tan et al., 2002).

It should also be noted that semiochemical definitions might be context dependent definitions since a pheromone of one species might act as an allelochemical to another species (Wyatt, 2014). As an example, a kairomone (see below for definition) might simply be a ‘prey odour’ and not a specific product of an evolved chemoreceptive trait on the receiver (Wyatt, 2014). Furthermore, some of these definitions continue to be debated, and one application of a definition might not necessarily be applicable across different groups of organisms, e.g., definitions of how insect semiochemicals work might not represent how chemical signalling works for mammals. Regardless of these semantic debates, for the purposes of this Perspective, these terms will be used as defined above. It is important to understand these terms as their definitions give rise to how the chemicals are utilised in association with an organism’s biology and ecology.

3. The use of semiochemicals as pest control agents

Pest management has arguably focused mainly around two methods: chemical pesticides and natural enemy biocontrol (NEB). Pesticides, although effective, can have harmful environmental consequences due

to their lack of specificity, sometimes extreme toxicity (DeLorenzo et al., 2001; Mostafalou and Abdollahi, 2017; Murty, 1986), environmental contamination (Carvalho, 2017; Meftaul et al., 2020), and tendency to become ineffective due to the target organism's evolving resistance (Mota-Sanchez et al., 2002; Georghiou, 1972). Conversely, NEB regulates pest populations via the introduction of native and/or more often non-native predators, parasites, pathogens, and competitors (Hajek and Eilenberg, 2018). Despite being natural and more ecologically friendly than pesticides, the introduction of NEB poses various challenges. For example, many NEB agents have inadvertently had disastrous ecological effects on non-target species through predation (Havens et al., 2012; Henderson, 1992; Louda, 2002; Shine, 2010; Margaritora et al., 2001) and competition (Shine, 2010; Carvalho et al., 2008); ultimately altering biodiversity and ecological balance. These limitations have motivated investigations into semiochemicals and have greatly improved understanding of semiochemical-mediated interactions between and within organisms. Indeed, semiochemicals have since emerged as promising and sustainable alternatives to conventional pest control methods and have played a pivotal role in the development of sustainable pest management strategies over the past 60 years (Heuskin et al., 2011; Pickett et al., 1997; Witzgall et al., 2010).

Owing to their biological and ecological functions, semiochemicals avoid the major concerns surrounding both pesticides and NEB agents as they are non-toxic, species- and sex-specific (Koczor et al., 2022; Szöcs et al., 1993), do not bioaccumulate (Stewart and Baker, 2012), have low concentration detection rates and half-lives (Stewart and Baker, 2012; Fine and Sorensen, 2008; Sorensen et al., 2005; Sorensen et al., 2003; Li et al., 2002; Covicristov and Halls, 2019), no resistance/desensitisation, and do not require the introduction of native and/or non-native natural enemies. Semiochemicals are versatile enough to be used alone or in conjunction with other methods, such as NEB and manual removal, and as needed.

Within regulatory frameworks, semiochemicals as control agents are now being considered as toxicologically inactive substances with fewer

restrictions than pesticides (Weatherston and Stewart, 2002; OECD, 2017). However, when developing semiochemical-based control strategies, it is necessary to integrate the induced behaviour, biological function, and intended target specificity. Therefore, five main control strategies have been proposed (Fig. 2):

- 'Pull' strategy - Attractants (foraging kairomones, sex and aggregation pheromones, apneumones) can be deployed to lure individuals to a point-source for trapping and aid in manual removal. This can help entice cryptic or deep-residing individuals who are usually difficult to detect or reach for manual removal strategies.
- 'Push' strategy - Repellents (prey kairomones, alarm pheromones, necromones (cues associated with organismal death/decay) implemented to push individuals from an area or deter them from entering/re-entering, thereby disrupting aggregations.
- 'Push-pull' strategy - The combined use of repellents and attractants designed to push individuals from one region and simultaneously or subsequently pull them to another for trapping and/or removal.
- 'Predator enhancement' strategy: Attractants (prey kairomones, prey apneumones) deployed to lure natural predators into the area to increase the rates of predation upon the pest.
- 'Mating disruption' strategy: Utilisation of pheromones that can cause asynchronous spawning/ reproduction or disrupt the physiological mechanisms that determine reproductive cycles and timings.

The commercial application of semiochemical-based pest control has seen substantial progress in a variety of terrestrial systems including intensive agriculture, horticulture, subsistence farming, stored-products, forests, along with private use in households and gardens (Pickett et al., 1997; Witzgall et al., 2010). Major breakthroughs can be found across such insect pest species as Ambrosia and bark beetles (Curculionidae weevils; subfamilies: Scolytinae and Platypodinae), Eurasian spongy moth (*Lymantria dispar* and subspecies), codling moth, (*Cydia pomonella*), pink bollworm (*Pectinophora gossypiella*), boll weevil

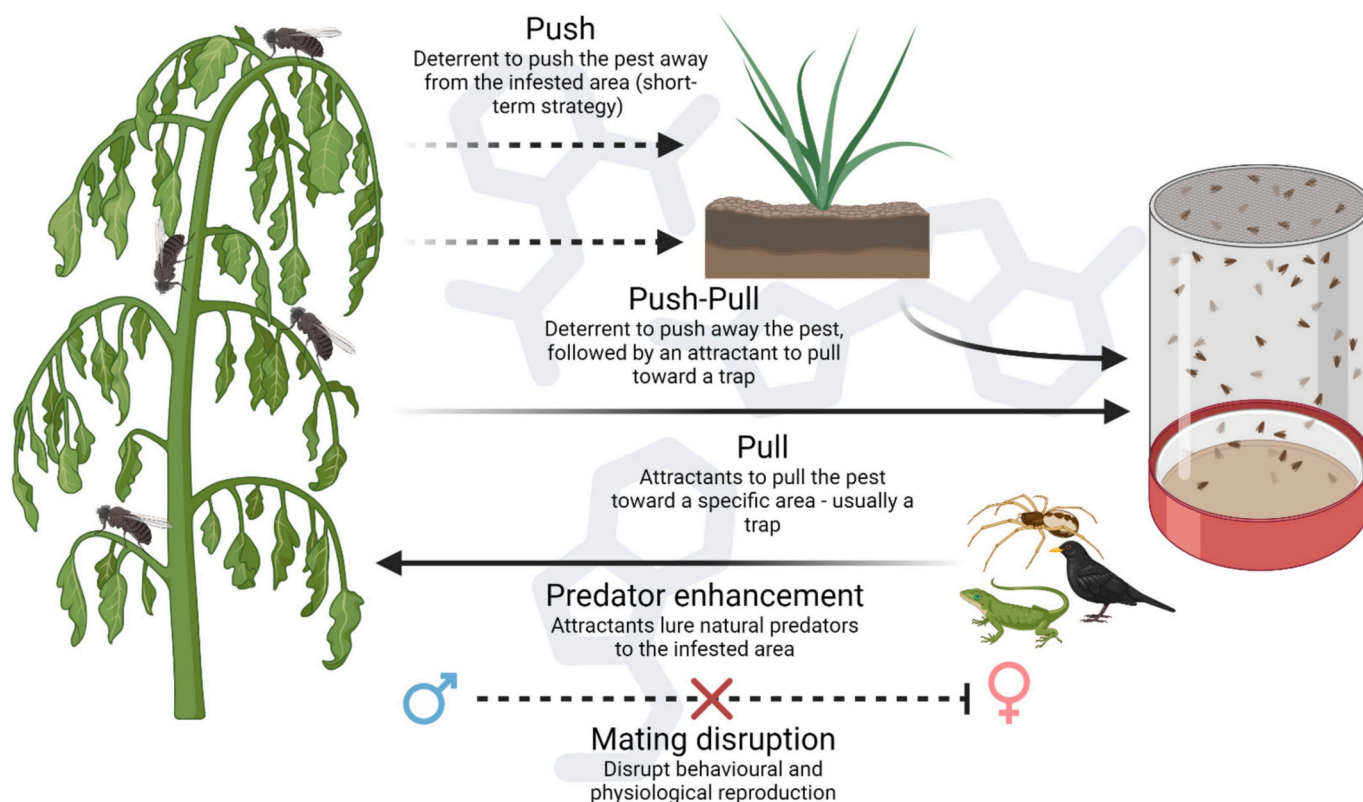


Fig. 2. Diagram outlining five strategies for semiochemical pest control. Image created in Biorender.com.

(*Anthonomus grandis*), etc. For in-depth commentaries see (Witzgall et al., 2010; Agelopoulos et al., 1999; El-Ghany, 2019; Mitchell, 2012; Progar et al., 2014; Sharma et al., 2019b).

Similar semiochemical applications to solve management quandaries within the aquatic environment have also been explored, e.g., aquaculture of Masu salmon (*Oncorhynchus masou masou*) (Kamio et al., 2022) and sea cucumber (*Holothuria arguinensis*) (Marquet et al., 2018), however, as only a small proportion of aquatic pest species have received research attention, semiochemical-based strategies to manage these are far less mature. Despite this, promising advances have been made. Much of the research on controlling aquatic pest species through semiochemical intervention has been in freshwater systems focussing on globally invasive and ecosystem habitat disrupting species including the invasive sea lamprey (*Petromyzon marinus*) (Barber and Steeves, 2020), common carp (*Cyprinus carpio*) (Stacey, 2014; Lim and Sorensen, 2011; Lim and Sorensen, 2012; Sorensen et al., 2019; Sorensen et al., 1988; Lowe et al., 2000), signal crayfish (*Pacifastacus leniusculus*) and red swamp crayfish (*Procambarus clarkia*) (Stebbing et al., 2003; Stebbing et al., 2004; Stebbing et al., 2010; Zhou et al., 2023; Blake and Hart, 1993; Blake and Hart, 1995; Gherardi et al., 2011). All examples focus on conspecific pull strategies exploiting sex pheromones. For example, male sea lamprey release 3-keto-petromyzonol sulfate (Li et al., 2002; Brant et al., 2015; Johnson et al., 2009; Johnson et al., 2013) that induces the migratory behaviour of sexually mature females toward males (Brant et al., 2015; Fredricks et al., 2021); female carp emit prostaglandin $F_{2\alpha}$ (PGF $_{2\alpha}$) (Lim and Sorensen, 2011; Lim and Sorensen, 2012; Irvine and Sorensen, 1993) and when implanted with PGF $_{2\alpha}$ females have been deployed as a pheromonal bait to mediate the trapping of males (Lim and Sorensen, 2012); mestranol concentrations released by female *Pr. clarkia* are directly proportional to the strength of male attraction (Zhou et al., 2023); and the urine of female *Pa. leniusculus* induces attraction behaviour in males (Stebbing et al., 2003). In the marine aquaculture context, research efforts have focused on controlling parasitic sea louse (*Lepeophtheirus salmonis*) in caged salmon farms (Mordue and Birkett, 2009) applying a push-pull strategy; non-host fish (*Scophthalmus maximus*) semiochemicals are used to 'push' *L. salmonis* away from salmon cages (Bailey et al., 2006) whilst virgin preadult II female *L. salmonis* cues (Ingvarsdóttir et al., 2002a) and host fish (*Salmo salar*) semiochemicals isophorone and 6-methyl-5-hepten-2-one (Bailey et al., 2006; Devine et al., 2000; Ingvarsdóttir et al., 2002b) are utilised to attract *L. salmonis* into traps. For more in-depth commentaries regarding the utility of semiochemicals in controlling these aquatic pest species see (Stacey, 2014; Stacey, 2011; Sorensen et al., 2019; Stebbing et al., 2003; Stebbing et al., 2004; Stebbing et al., 2010; Zhou et al., 2023; Mordue and Birkett, 2009; Fissette et al., 2024; Fissette et al., 2021; Hume et al., 2020; Oyama et al., 2020; Sorensen and Hoye, 2007; Sorensen and Johnson, 2016).

To date, there are no working examples of semiochemical interventions in the marine environment, especially within such revered systems as coral reefs. Thus, the following perspectives and hypotheses considered in the context of CoTS control are solely inferred from prior knowledge regarding successful and moderately successful examples in terrestrial and freshwater systems and from simulated marine aquaria, and until future research investigates these avenues further, it remains unclear as to how semiochemical pest intervention might work within the marine environment.

4. CoTS life history and ecology in brief

4.1. Reproduction and fertilisation

Acanthaster spp. are highly fecund dioecious broadcast spawners, whereby females can produce in excess of 100 million eggs per season and usually spawn synchronously (Babcock et al., 2016; Caballes and Pratchett, 2014). Higher fecundity seems to correlate to larger body size, with the ratio of gonadal tissue weight to body weight also exponentially

increased, all of which suggests reproduction is a high priority (Kettle and Lucas, 1987). Fertilisation rates of *A. cf. solaris* can reach up to 83 % success during a major spawning event (Babcock and Mundy, 1992). Gonad development, aggregation, and subsequent spawning occurs in the warmer months of the year (Pratchett et al., 2014). However, even though chemical cues that allow for synchronous spawning are likely the most parsimonious explanation, they remain to be determined.

4.2. Planktonic larval stages

After external fertilisation occurs, zygotes undergo cleavage division into the blastula stage (Fig. 3, (Birkeland and Lucas, 1990; Deaker and Byrne, 2022)). Transition to the gastrula stage sees free-swimming larvae hatch and utilise ciliary movements to swim to the surface (Birkeland and Lucas, 1990; Yamaguchi, 1973). Development then proceeds via two major planktonic larval phases (i) the bipinnaria, which develops from endogenous resources from the egg, and (ii) the brachiolaria, which is the planktonic feeding stage of development (Caballes and Pratchett, 2014). Even under food limited conditions, brachiolaria can survive for several weeks, being capable of drifting on currents to where food sources might be available.

4.3. Larval settlement and benthic juvenile lifestyle

Larval settlement occurs in the late brachiolaria stage (approx. 11 days post-fertilisation), the current premise being that this is induced by environmental cues, such as their main food source crustose coralline algae (CCA) and the associated microbial communities (Neil et al., 2022; Doll et al., 2023a). Metamorphosis of the brachiolaria stage into the five-armed juvenile stage (0.3–0.7 mm diameter) occurs via the absorption of the anterior larval body (Yamaguchi, 1973). Three weeks post-metamorphosis, more arms begin to grow, and the body colour changes to pink, which confers camouflage matching the environmental CCA they feed upon (Birkeland and Lucas, 1990; Yamaguchi, 1973) (Fig. 3). This cryptic lifestyle, in combination with nocturnal habits, suggests an evolved adaptation to avoid visual predators such as fish (Zann et al., 1987).

Although CCA is ubiquitous across reefs, CoTS larvae seem to have

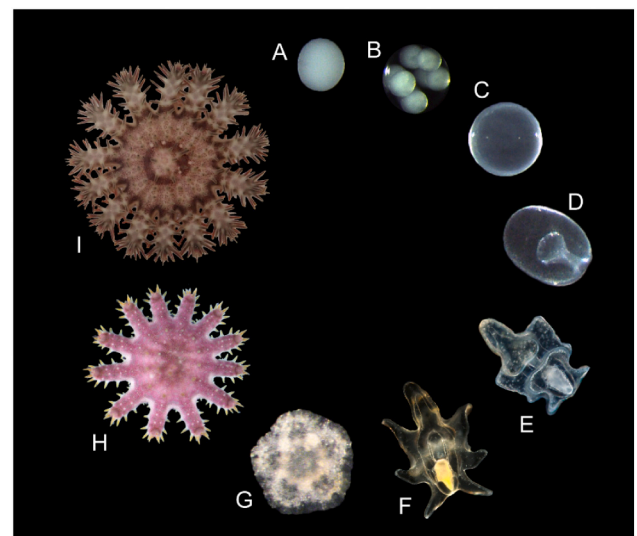


Fig. 3. The life history of CoTS. (A) an unfertilised egg [approx. 220 µm], (B) the eight-cell stage, (C) a blastula, (D) a gastrula with the archenteron, (E) a feeding bipinnaria with fully developed digestive tract [0.5–0.8 mm], (F) a brachiolaria with anterior arms used for benthic settlement [1–1.5 mm], (G) a newly settled juvenile [0.3–0.7 mm], (H) the older herbivorous stage juvenile, and (I) the corallivorous stage [>8 mm]. Figure adapted from Deaker & Byrne (2022) under the Creative Commons Attribution License 4.0 (CC BY-NC-ND).

some preferential settlement to specific CCA species (Doll et al., 2023a) and the distribution and availability on reefs may restrict larval settlement and account for apparent patterns of CoTS outbreaks. If their preferred CCA is available, at around four to six months juveniles switch to corallivory and begin to rapidly grow (Zann et al., 1987; Yamaguchi, 1974). However other favourable conditions may also factor into this transition, e.g., better proximity of coral to their nursery habitat (Zann et al., 1987), increased coral abundance, reduced competition from adults, and lower predator numbers (Deaker et al., 2020a). Research suggests that herbivorous juvenile CoTS can subsist for up to 6 years, and likely longer, under laboratory conditions before switching to a coral diet with no loss in feeding competency or growth (Deaker et al., 2020a). This provides evidence for the 'hidden army' hypothesis of CoTS outbreaks, whereby juvenile CoTS only transition to coral feeding when conditions are favourable.

The cryptic lifestyle continues into the coral feeding stage until they reach >10 cm, where they then display aggregative behaviour, closely followed by sexual maturation and the adult phase (Zann et al., 1987). Some studies have suggested that the successive settlement of CoTS larvae on a particular reef might allow for better predicting future aggregations and infestations on that reef (Wilmes et al., 2020; Zann et al., 1987).

4.4. Adult feeding ecology

Adults can reach an average maximum size up to 70 cm in diameter, yet still maintain a flexible body that can effectively navigate small reef crevices (Birkeland, 1989a). With an eversible stomach that envelops the coral surface to consume them, an adult CoTS can devour in excess of $10 \text{ m}^2 \text{ yr}^{-1}$ of coral tissue (an outbreak can consume up to $1715 \text{ m}^2 \text{ yr}^{-1}$) (Foo et al., 2024), which is astonishing considering another corallivorous starfish, *Culcita novaeguineae*, consumes around $1.0 \text{ m}^2 \text{ yr}^{-1}$ (Foo et al., 2024; Glynn and Krupp, 1986). Adults show a preference for Scleractinian corals, particularly *Acropora* spp. However, when these stocks are depleted they will feed on *Pocilloporidae* spp. and *Porites* spp. (De'ath and Moran, 1998; Pratchett, 2007; Pratchett et al., 2009), which is problematic as there is not one singular species that needs protecting, putting multiple coral species at risk.

5. CoTS chemical ecology and potential semiochemicals for control

With positive advances in utilising semiochemical control agents within the aquatic environment, we consider here similar investigations where the application of innovative semiochemical control agents may have a newly profound impact. Foundational research into CoTS semiochemicals have revealed some promising avenues to pursue, with potential target candidates identified that may be successfully incorporated as pest control semiochemicals. Here, we consider the prospects and challenges of identifying and utilising semiochemicals for CoTS control with respect to their life stages, biochemical properties, behavioural functions, and molecular modes of action.

5.1. Disruption of reproduction

Mating disruption is the most commonly utilised method for insect pest management (Witzgall et al., 2010), whilst in the aquatic environment the research is still ongoing for such pests as the sea lamprey (*Petromyzon marinus*) where attempts are being made to (i) inhibit the female's ability to attract a mate and/or the male's searching behaviour, and (ii) lure the sea lamprey into a target area that has poor reproductive success (Fisette et al., 2021). Similar methods might be contemplated for CoTS as they are highly fecund mass spawners (Babcock and Mundy, 1992), likely a contributing factor to their significant population outbreaks (Babcock et al., 2016; Pratchett et al., 2021b). It has been observed that, within a localised population, spawning is a highly

synchronous seasonal event (Pratchett et al., 2014; Babcock and Mundy, 1992; Caballes and Pratchett, 2017), whereby the initiation of spawning by males typically leads to the initiation of female spawning (Pratchett et al., 2014; Pratchett et al., 2021b). However, some field observations have found that females can induce mass spawning events too (Babcock and Mundy, 1992). Thus, disruption of mass spawning events represents a key opportunity in the control of future CoTS populations, similar to that being considered in the control of nuisance fish (Sorensen and Johnson, 2016). Given the astronomical numbers of eggs produced by females, it could be argued that this reproduction phase, if controlled, offers a higher likelihood of population suppression, particularly for long-term control management and the prevention of future outbreaks.

In some aquatic organisms, spawning can be induced by the reception of sex pheromones (Hardege and Bentley, 1997; Dulka et al., 1987), a physiological attribute also observed in free-spawning starfish (Miller, 1989; Soong et al., 2005). Early laboratory studies have suggested that pheromone extractions from CoTS ovaries and testes initiate synchronised spawning in nearby starfish and elicit a movement response toward the chemical source (Beach et al., 1975). Yet, the identification of these pheromones remains undiscovered and it is unclear if these pheromones are sex-specific, i.e., whether there is a suite of male pheromones that induce females to synchronously spawn, or vice versa.

The discovery of sex-specific gene expression of some proteins, including putative olfactory receptors within CoTS (Hall et al., 2017; Roberts et al., 2018; Roberts et al., 2017), highlights the potential for identification and utilisation of sex-specific pheromones to disrupt reproduction as a population control strategy. Sex-specific pheromones (such as those that initiate the neuroendocrine relaxin-like gonad-stimulating peptide (RGP) cascade (Smith et al., 2017; Smith et al., 2019)) might allow for strategies that could hypothetically induce premature and/or asynchronous spawning. A CoTS RGP (Aso-RGP) has been identified, and a synthetic analogue, when injected or exposed to extracted gonads, has been shown to successfully induce spawning in adult CoTS (Mita et al., 2022). Being able to induce artificial spawning in one sex could lead to asynchronous spawning, lowering successful fertilisation rates which would reduce the number of successful larval settlements thereby controlling future CoTS population numbers. The problem with this scenario is that it is currently not possible to distinguish between males and females in situ, and does not solve the intensive labour issue since injections to deliver the agent would still be required.

Further, a metabolomic study demonstrated that under starved conditions, L-glutamic acid is produced within the radial nerve of CoTS (Smith et al., 2018). L-glutamic acid is a known spawning inhibitor in some starfish (Mita, 2017), and an ex vivo assay revealed this was also true for CoTS (Smith et al., 2018). Therefore, as an alternative to inducing premature or asynchronous spawning, strategies to inhibit spawning altogether should be considered. However, given that CoTS are native species, their eradication through complete reproductive inhibition is unlikely to be desirable from both an ecological and environmental management perspective, but limiting their reproductive output temporarily through deliberate on-off applications to sub-populations might aid in suppressing their numbers and prove a more sustainable approach.

Developing a method that induces asynchronous spawning after exposure to sex-specific pheromones might cause one sex to be reproductively exhausted, producing a minimal number of gametes during the prime spawning season, or producing out-of-season less viable gametes, consequently reducing the overall number of CoTS in subsequent generations as a long-term control strategy. Hypothetically, this artificial asynchronous spawning could lead to long-term reduction of CoTS numbers meaning that this method might only need to be utilised infrequently over multiple years.

It is clear that more research to decouple the interplay between biochemistry and reproduction within CoTS, including the identification of released pheromonal cues that induce spawning, is vital to better

assess the potential and also limitations of this type of long-term control method.

5.2. Larval settlement semiochemicals

Larval settlement is a vital ontogenetic transition for many marine invertebrates. Their vulnerability at such an early life stage means that successful settlement is critical for long-term survival. Semiochemical cues are a strategy in which larvae are induced to settle in a viable and safe habitat (Hadfield and Paul, 2001), and is evident across many echinoderm species (see reviews (Doll et al., 2022; Rittschof et al., 1998; Slattey, 2020; Steinberg et al., 2002; Morse, 1990)). These cues can be produced from food sources, suitable biotic host environments, and conspecific adults. Hence, the identification of larval settlement semiochemicals and deployment in settlement traps could provide an alternative solution for long-term control of CoTS by reducing the localised spread of high-density aggregations.

Studies have shown that the CoTS settlement process might be influenced by cues from CCA substrates, possibly those associated with certain microbial communities, which provide a food source for early life-stages (Doll et al., 2023a; Johnson and Sutton, 1994; Johnson et al., 1991; Pratchett et al., 2017b; Cowan et al., 2016a). Species such as *Lithothamnion cf. proliferum* have been shown to induce significant settlement of CoTS larvae (Doll et al., 2023b) and represent a possible target for semiochemical investigation. However, CCA also induces larval settlement for other marine organisms, including coral larvae (Heyward and Negri, 1999; Morse et al., 1988) and other echinoderms (Doll et al., 2022), and is therefore likely to be a non-specific settlement cue. Further research is still needed to determine the precise semiochemical and biological mechanisms that drive CoTS larval settlement, and whether these are indeed 'universal' or if certain CCA semiochemicals might provide a more selective means to settle CoTS.

Given that adult CoTS form large aggregations, it has been suggested that larval settlement might also be mediated by conspecific pheromonal cues (Chesher, 1969), with some fundamental pairwise choice larval experiments suggesting this might hold true, as significant movement of larvae toward adult CoTS-conditioned water has been observed (Cowan et al., 2016a). However, follow-up experiments revealed conflicting evidence for this hypothesis by showing that conspecific cues do not induce larval settlement and do not enhance settlement in the presence of known settlement inducing CCA (Doll et al., 2023b). Larval settlement is more likely to be induced by kairomones rather than pheromones because kairomones would reduce the likelihood of large aggregations of larvae settling in the same location which could lead to early life stage intraspecific competition. Understanding of how chemical cues influence larval movement is required to determine which semiochemicals should be considered as alternative control strategies, either alone or in combination with larval settlement cues to pull larvae to a specific area to artificially induce settlement for easy and targeted removal.

Other settlement experiments have shown that CoTS larvae preferentially avoid settling in areas with a high presence of predators (Cowan et al., 2016a). This information could be vital in incorporating 'push-pull' strategies whereby utilising predator semiochemicals to push larvae away from an area where they might otherwise settle, and then attract them to point source where they are then motivated to settle in subpar or artificial environments, i.e., on removable man-made structures for culling.

These studies have highlighted that, during the settlement stages, CoTS larvae are highly receptive to semiochemical cues that signal suitable settlement habitats. A better understanding of CoTS larval ecology and extensive investigation of semiochemical cues that induce larval settlement might provide a means to develop successful control strategies.

Some of the disadvantages of targeting CoTS larvae with semiochemicals include the finite time frame for intervention, i.e., deployment and the constant need for field evaluation of spawning and larval

dispersal. However, critically, the justification for culling larval numbers should also consider the fact that CoTS are not an invasive species and likely play a vital ecological role when population numbers are at equilibrium within the reef system. Hence, on the GBR, as the main objective is not the complete eradication of CoTS, deployment of larval semiochemical control agents should target management of numbers at initiation reefs to achieve an ecologically sustainable level to minimise downstream environmental and socio-economic impacts (GBRMPA, 2020; Westcott et al., 2020).

5.3. Adult and juvenile aggregation semiochemicals

Aggregating behaviour in mature adults can provide density-dependent benefits that are key to survival and reproduction (Stamps, 1988; Pitcher et al., 1998; Cheney, 1972). Aggregation is typically initiated by attraction semiochemicals to signal a desirable environment or a transition to more favourable habitats for conspecifics (Buxton et al., 2020) or mating. Aquatic animals rely on detection of water-soluble pheromones, however, as their diffusion rate can be 10,000× lower than in the air (Chung-Davidson et al., 2011), aggregation attractants need to be long-range, robust, and highly potent molecules that attract conspecifics from a great distance, or short-range, weak molecules designed to maintain conspecifics in a particular area once there. The use of attractants to lure aggregations to a point source for effective culling is often termed 'attract and kill'; and is a widely utilised method across pest insect management (Witzgall et al., 2010; El-Ghany, 2019; Gregg et al., 2018). CoTS are often found in large aggregations, driven by factors such as spawning (Babcock and Mundy, 1992) and availability of prey (Ling et al., 1938), therefore identifying the conspecific and allospecific semiochemicals that initiate these aggregations could allow for implementing a similar 'attract and kill' regime for adult and juvenile CoTS.

Behavioural Y-maze assays have shown adult CoTS are particularly attracted to seawater conditioned with aggregating CoTS (Hall et al., 2017). Sequencing of the CoTS genome, along with proteomic analyses of CoTS-conditioned seawater, revealed a suite of 108 potential species-specific exoproteins (secreted proteins) (Hall et al., 2017): 71 from aggregating CoTS, 14 from alarmed CoTS (following exposure to their predator, the Giant triton snail; *Charonia tritonis*), and 23 from both conditions. Of these exoproteins, the detection of 15 ependymin-related proteins (EPDRs) from aggregating CoTS suggested that they might function as conspecific communication molecules. The unique expansion of EPDR genes across asteroids, which seemingly share little sequence similarity, implies that these genes have evolved rapidly into species-specific groups of putative communication factors (Hall et al., 2017). Although EPDRs have been suggested as possible candidates for conspecific aggregating semiochemicals, there were also 21 uncharacterised exoproteins detected (Hall et al., 2017), all of which could be novel communication/aggregation cues. Further investigations into CoTS EPDRs and uncharacterised proteins are needed to better understand their role in communication, particularly considering the sex-specific differential expression of EPDR genes in the radial nerve cord of male and female CoTS (Hall et al., 2017).

The same CoTS genome study (Hall et al., 2017) also revealed 950 G-protein-coupled receptor (GPCR) genes, 750 of which are rhodopsin-class GPCRs associated with olfactory receptors (Hall et al., 2017; Rosenbaum et al., 2009). These are organised in a species-specific tandem array of single exon genes, with some showing high gene expression in external and sensory tissues such as spines, body wall and the radial nerve, respectively, suggestive of their role in the detection of water-borne chemicals. Subsequent studies have found CoTS-specific GPCR olfactory chemoreceptors (*ApORs*) are localised in the tube feet and sensory tentacles, as well as differentially expressed in males and females (Roberts et al., 2018; Roberts et al., 2017). As has already been implied in some early studies (Beach et al., 1975), the identification of these differentially expressed *ApORs* is evidence enough that sex-specific

pheromones play a role in conspecific communication.

In the aquatic environment there are sufficient examples of how sex-specific pheromones function as aggregation attractants (Cummins et al., 2006; Cummins et al., 2005; Painter et al., 1998) and mate attractants (Hall et al., 2016; Kikuyama et al., 1998). Based on knowledge of the CoTS EPDRs and ApORs, this idea warrants further investigation for CoTS control. Investigations should focus specifically on the identification and characterisation of those conspecific and sex-specific pheromones capable of attracting one or both sexes for the purpose of motivating aggregation for synchronised spawning events, thus allowing these pheromones to be deployed in a mass trapping scenario to allow easier manual removal (Witzgall et al., 2010) or to induce out-of-season or early spawning of a single sex thereby limiting reproductive output.

Adult CoTS are corallivores and are often seen feeding on Scleractinian corals in large aggregations (Caballes and Pratchett, 2017; Caballes et al., 2021), with observations of adult CoTS migrations toward areas of CoTS feeding (Ormond et al., 1973; Keesing, 1990). It remains unclear whether feeding CoTS produce pheromones that signal to conspecifics of a healthy coral feeding area (e.g., as do ants (Jackson and Ratnieks, 2006)), or if there are specific kairomones emitted by partially eaten coral that alert CoTS to a profitable foraging area. The ecological benefit for CoTS in attracting conspecifics to a viable feeding area would be to altruistically ensure the future reproductive fitness of conspecifics (Cheney, 1972). However, sufficiently large aggregations would induce intense intraspecific competition; thus, it is more probable that a kairomone from damaged coral tissue is the most likely candidate, particularly as CoTS are also strongly attracted to the coral feeding activity of other starfish (Ormond et al., 1973). There is some evidence to indicate that such compounds, for example betaine, released from corals are kairomone candidates (Moore and Huxley, 1976; Schupp and Bruckner, 2008; Teruya et al., 2001; Sikorskaya, 2023), however, as these are also known to attract other aquatic species, i.e., the shrimp *Palaemonetes pugio* (Carr et al., 1984), common carp *C. carpio* (Murthy et al., 2016), and northern Pacific seastar *Asterias amurensis* (Yusup, 2009), these are unlikely to be CoTS-specific and consequently could attract other organisms to the area.

The challenge for CoTS control programs is to improve detectability of individuals for culling. Although CoTS can reach high densities, their cryptic nature means they can hide and camouflage deep in the reef matrix; even the larger (and more fecund) CoTS - which do the most damage to coral - are difficult to detect and cull (Plagányi et al., 2020). One study investigating the detectability of CoTS found that individuals <15 cm were virtually undetectable (MacNeil et al., 2016) and therefore rarely, if ever, culled. As a result, a differential pattern of culling generally occurs based on the ease of locating and culling CoTS of larger body size (Westcott et al., 2020); this biased culling is further exacerbated by smaller CoTS being primarily nocturnal (Burn et al., 2020). Since rates of coral consumption are correlated with body size (Keesing and Lucas, 1992), a failure to eliminate the larger and at least some of these smaller individuals means multiple reef revisitations and repeated culling efforts are required to access previously undetected CoTS, i.e., those smaller CoTS that subsequently emerge from the reef matrix in the absence of larger adults and thrive without competition (Westcott et al., 2020; Birkeland, 1989b). Luring adult CoTS out from the reef matrix and into shallower waters prior to culling using attractants could potentially improve culling efficiency and cost-effectiveness – increasing the number of individuals culled in the first visit to a target reef and reducing the number of revisitations required to achieve ecologically sustainable adult densities. However, it is imperative that the efficacy of any attractant be assessed for its capacity to also lure juveniles, as sex-specific and reproductive pheromones may only affect sexually mature larger individuals.

Negative phototaxis has been observed in juvenile CoTS; they are able to visually locate their habitat, albeit at lower spatial resolution than adults (Korsvig-Nielsen et al., 2019), suggesting that they may rely

more so on chemical cues. Several studies have documented the preferential dietary selection of CoTS juveniles for CCA and their transition to Scleractinian coral (Neil et al., 2022; Johansson et al., 2016; Deaker et al., 2020b). This preferential diet selection in these early life stages is unlikely to be visual, but chemically modulated since there is an ontogenetic change in diet. Only one study has attempted to understand attraction chemical cues in juvenile CoTS (Webb et al., 2023). In this study it was found that juvenile CoTS (in the transitional feeding stage between CCA and coral) showed positive chemotaxis to both CCA and coral cues, individually and combined, but had a greater preference to coral. Interestingly, cues from adult CoTS caused negative chemotaxis which is suggestive of negative density-dependant feedback as juveniles would be outcompeted by the presence of high-density adult CoTS formations in their transitional stage toward coral feeding. However, more evidence is needed to determine the utility of food related chemical cues in controlling juvenile populations. Regardless, current culling of juveniles is impractical using the lethal injection method, therefore, combining a juvenile attractant with a trap device, with cues such as CCA and coral, has the potential to easily remove larger numbers of juveniles from a reef, leaving fewer juveniles to reach the destructive adult life stage.

Inspired by the Gypsy moth ‘Slow-the-spread’ program (Coleman et al., 2023; Tobin and Blackburn, 2007), attractants (either alone or combined with traps) could be used to better support management decisions by improving monitoring through increased detection of juvenile and/or adult CoTS densities on reefs. For adults in particular, attractants could be deployed to a reef ahead of time to complement current surveillance strategies e.g., to improve density estimates from scooter assisted large area diver-based (SALAD) surveys (Chandler et al., 2023) by luring out the majority of individuals. This information could then guide the strategic planning and tactical deployment of control efforts to reefs that are deemed higher priority for predicted/ emerging outbreaks. However, as for the mountain pine beetle (*Dendroctonus ponderosae*) (Progar et al., 2014), application of a CoTS attractant may be more effective when densities are beginning to increase, rather than when densities are already too high (Babcock et al., 2020).

Recent studies have highlighted that large culling efforts might themselves have a detrimental effect on the reef ecosystem as decomposition of large CoTS numbers scattered across vast reef systems may cause a disturbance in reef biochemistry, resulting in localised acidification, eutrophication, and hypoxia, which in turn decreases the productivity of reef-building coral, coralline algae, and turf algae (Li et al., 2024). However, these data arise from laboratory studies only, and the implications of CoTS decomposition across vast kilometres of reef space, although currently lacking data, is unlikely to have drastic negative consequences given the spatial distance between culled CoTS individuals. However, if an attractant is used in a ‘lure-and-kill’ strategy, whereby a large number of CoTS are culled in a smaller area, then this may artificially exacerbate the concentrated decomposition effects in that area. Therefore, further research and amended management and culling strategies will have to be investigated for any potential attractant candidates used in a lure-and-kill strategy.

5.4. Natural predator semiochemicals

Natural repellent cues usually initiate an intrinsic survival response to potential life-threatening dangers such as predators, parasites, or dead/dying organisms. In the reef environment, repellents could potentially be deployed to disperse CoTS populations, deter CoTS from entering an area or suppress basic physiological processes such as reproduction and growth.

The Giant triton snail (*Charonia tritonis*) is a prominent natural predator of adult CoTS, being one of the few that can consume entire CoTS. Unlike fish predators, *C. tritonis* co-habits with CoTS on the reef substrate and are seemingly immune to the physical and chemical defences of the starfish (Bose et al., 2017). CoTS rely on chemosensation to

sense the presence of *C. tritonis*, and this predator-prey interaction provides an avenue for investigating 'push' control strategies. There are two main types of predator detection cues: *direct* detection of semi-chemicals from a present predator, or *indirect* detection of semi-chemicals emitted by conspecifics or other organisms reacting to the presence of a natural predator (Grostal and Dicke, 1999; Dicke and Sabelis, 1992; Jędrzejewski et al., 1993; Chivers and Smith, 1998).

Behavioural observations and Y-maze assays have shown that isolated CoTS are significantly adverse to the physical presence of *C. tritonis* or *C. tritonis*-conditioned water (Hall et al., 2017; Bose et al., 2017). However, owing to a lack of ecological information, it is unclear how CoTS react to these chemical cues in their natural environment. For example, do *C. tritonis* chemical cues trigger full dispersal of CoTS from the reef, or does their dispersal eventually elicit an aggregating response (safety in numbers) of CoTS? Such behaviours have been seen in other organisms in response to a predator presence (Kullmann et al., 2008; Pitcher, 1993; Jermacz et al., 2017; Rubenstein, 1978). Furthermore, does the detection of *C. tritonis* kairomones induce an alarm pheromone from CoTS to warn other CoTS of a predator presence? If this chemical cascade holds true, identifying both chemical signals might provide an amplified dispersal effect when deployed in tandem, i.e., faster dispersal.

Chemically induced dispersal of CoTS raises the question, where would they disperse to? Currently there is a significant lack of ecological data regarding where CoTS reside when not found on the reef. CoTS have been reported at depths ranging from 15 m (Beaman, 2018) to 48 m (Moran, 1986), so it is possible they would simply disperse into deeper waters to find refuge, thereby evading any manual control effort. Alternatively, they may relocate to the nearest available reef. Unless CoTS are severely depleted of food sources or starved, they tend to be reluctant to move between reefs (Sigl and Laforsch, 2016; Bos et al., 2013), particularly if the closest reef is at a significant distance (Pratchett et al., 2017a). Yet, CoTS have been observed traversing interstitial reef habitats (Suzuki et al., 2012), in some instances rolling between reefs, and this mode of locomotion may play a vital role in how they travel and disperse across reef systems. Data on this locomotion phenomenon is limited and more needs to be understood (Cranenburgh and Cranenburgh, 2020). Both scenarios (refuge and relocation) are not ideal for culling efforts. Therefore, repellents would likely be best integrated into a push-pull strategy, luring them away from one area to attract them to another area for easy removal.

Conspecific necromones might be an effective repellent for CoTS. Typically, cues from deceased organisms cause dispersal and aversive behavioural responses (Rollo et al., 1994; Stroud et al., 2014). Necromones usually have an adverse effect because the presence of dying organisms can indicate a dangerous environment (e.g., toxicity), the presence of a predator, or that the dead organism might harbour deadly viruses or bacteria. Field observations by culling teams have noted that CoTS tend to disperse from an area of dead/dying CoTS during extended periods of culling by injection (*Blue Planet Marine, pers. comms*). However, under aquarium conditions, CoTS have been observed feeding on dead conspecifics (*pers. obs.*). It is possible this is because of limited food availability within the aquarium environment as homogenised CoTS tissue did not elicit any change in movement rates of conspecifics (Pratchett et al., 2017b) suggesting putrefying chemistries are not acting as a deterrent or repellent. How this translates to the real-world behaviour observed on the reef remains to be established. Another problem with necromones is that they might not be CoTS-specific, and thus repelling non-target beneficial organisms from the reef might have implications (both short- and long-term) for the ecosystem (Drynan and Baker, 2023). Alternatively, CoTS necromones might enhance the presence of some predators (mainly fishes) that are known to feed on dead/dying CoTS (Cowan et al., 2017) and may have unintended consequences on other prey species.

The attraction (or lure) of natural predators to an outbreak area, referred to as the predator enhancement strategy, has been shown to

increase predation rates on pest species (El-Sayed et al., 2009). CoTS-conditioned water attracts *C. tritonis* and induces predatory behaviours eventuating in attack and consumption (Bose et al., 2017). However, currently, very little is known of *C. tritonis* ecology, or the predator-prey interactions with CoTS, and with their population numbers severely declining (Motti et al., 2022b), it remains uncertain whether this would be a successful strategy. Research to better understand these aspects of *C. tritonis* ecology and to accurately assess their distribution is urgently needed, not only to allow for better conservation efforts but also to understand the critical role they play within reef habitats, and whether their population decline is a confounding factor in the increase in CoTS outbreaks.

Predators such as *C. tritonis* are efficient at killing CoTS, specifically adults. Reducing the number of CoTS that reach maturity, i.e., having high fecundity and large size concomitant with coral-consuming capacity (Pratchett et al., 2017a; Babcock and Mundy, 1992), would make a considerable contribution toward long-term management strategies. Therefore, natural predators that feed on CoTS at different life stages may be vital to controlling population outbreaks. One key study identified 26 predatory species of juvenile CoTS, 10 of which consumed CoTS in their entirety (Desbiens et al., 2023). The red decorator crab (*Schizophrys aspera*) has been identified as a voracious predator of juvenile CoTS in the benthic communities, where it consumed whole juveniles in 89 % of the feeding trials (Desbiens et al., 2023; Wolfe et al., 2023). Other studies have gained traction in understanding predators of CoTS at their larval stages, whereby key fish species such as damselfishes and butterflyfishes (notably *Chaetodon auripres*) have been shown to consume CoTS larvae effectively (Cowan et al., 2016b; Yang et al., 2023). *Chaetodon auripres* was shown to consume larvae at a rate that was directly proportional to increasing larval density, highlighting its potential effectiveness as a CoTS larval biocontrol agent (Yang et al., 2023). To date, none of these early life-stage predators have been examined to better understand how CoTS semiochemical cues affect them or vice versa. Therefore, understanding how we can utilise them as natural predators with semiochemical cues is another promising avenue for a natural long-term control strategy.

It remains unclear how a semiochemical-mediated increase in natural predator populations would impact biodiversity and ecosystem structure. It is pertinent to consider that a localised increase in predator species density would presumably, (i) decrease predator density in surrounding areas, and (ii) result in increased predation of other non-target but potentially beneficial species. Further research is required to elucidate the ecological and environmental impacts of semiochemical-based CoTS predator enhancement before deployment as a pest management strategy. However, it is imperative that any such deployed tools be easily immobilised should any adverse impacts be observed.

6. Conclusions and moving forward

Culling of CoTS, to release the pressure on coral trying to recover from and adapt to a changing climate, has provided adequate preservation of targeted reefs, however, the sustainability, both economically and logistically, of CoTS manual culling programs might not be a feasible long-term solution. Globally, the supplemental use of semiochemicals, as natural and ecologically friendly alternatives to conventional pesticides, in pest control programs has been growing, and, as presented here, has real potential to provide solutions to control future CoTS outbreaks (Fig. 4.). This preliminary assessment of CoTS semiochemicals and their potential as control agents provides the foundational knowledge upon which avenues for field application are highly feasible and could yield enormous success. With this research still ongoing (with governmental and stakeholder support), and suitable and effective semiochemical candidates still being identified, the following future avenues of this research need to be considered and strategised:

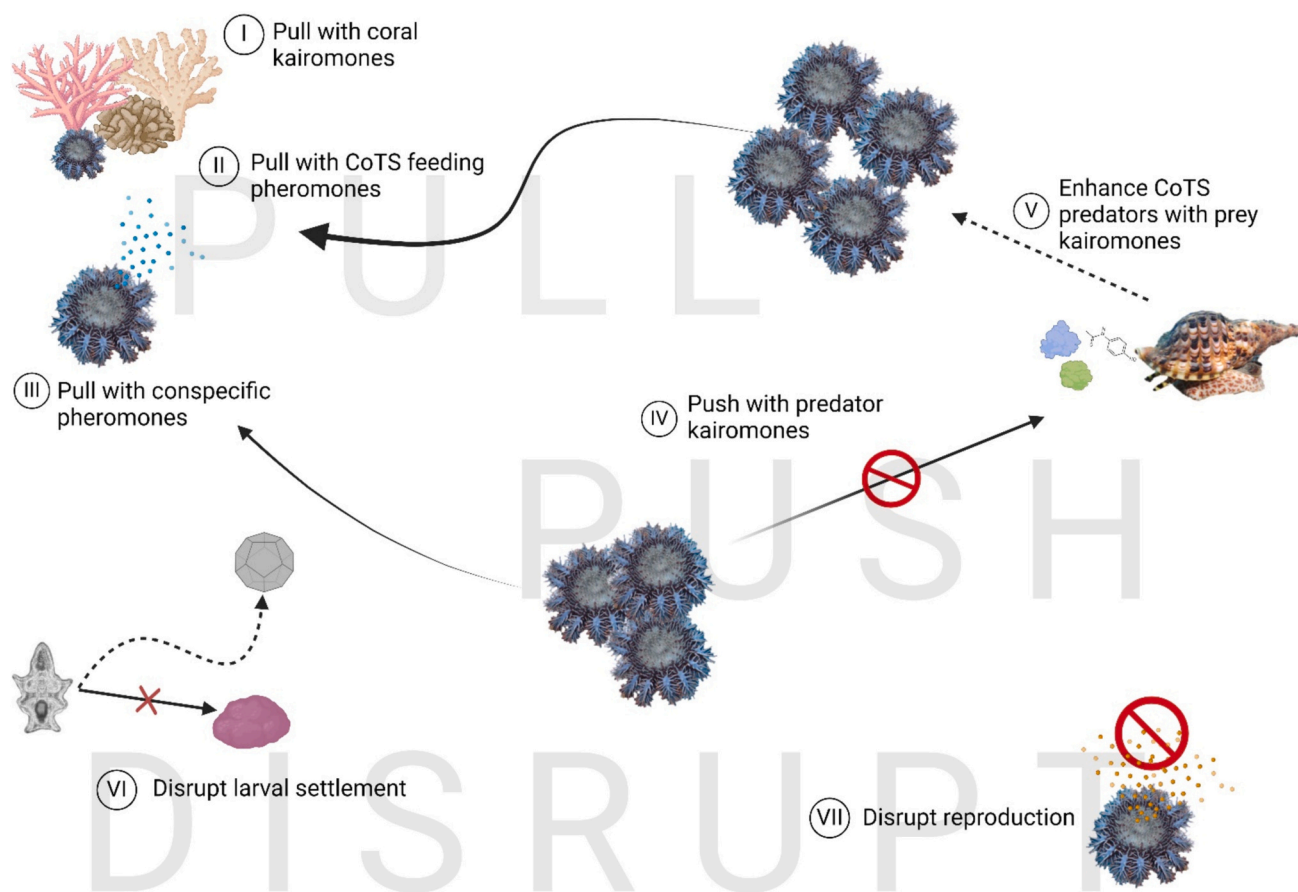


Fig. 4. A diagram of the possible uses of semiochemicals in controlling CoTS. Image created in [Biorender.com](https://www.biorender.com).

(i) *Identification of promising semiochemical candidates, followed by the engineering and development of a chemical emitter device.* The most promising of the semiochemical candidates are attractants, which are versatile and able to act across different life stages, whilst also being elucidated from different sources, e.g., conspecific vs. allospecific semiochemicals. The identification of a single molecule that can act as an effective attractant is likely quixotic, rather, the most promising chemical candidates are mixtures of a specific suite of chemicals. However, it is evident that further research is sorely needed regarding the chemical ecology of CoTS and the functional characterisation of candidate semiochemicals.

We propose that controlling CoTS at multiple life-stages, in particular early settled juveniles and adults, will provide the best solution for both short- and long-term management (Motti et al., 2022a). Short-term solutions could include deploying semiochemical attractants to lure CoTS (from larval stages to adults) to specific areas to expediate easier removal by culling teams; long-term solutions could involve controlling reproduction and spawning stages as to significantly reduce the total numbers of CoTS in later generations. Determining how best to implement these strategies, e.g., by targeting low density populations thereby preventing or containing the initiation of population irruptions, will be key to any success. Further, by identifying and understanding the mode of action of the most effective semiochemical candidates we can then begin to implement a rational engineering design of semiochemical release (or chemoemitting) devices as well as develop and integrate workable control strategies into the CoTS Integrated Management Program.

(ii) *Regulatory approvals for use.* Semiochemical control products are significantly safer for human and environmental health than

other chemicals such as pesticides. However, the deployment of novel semiochemical control agents, particularly in protected zones such as the GBR, will have to undergo strict policy and regulatory assessment before any in-field testing can be utilised.

Semiochemicals currently fall within the Australian Government's Australian Pesticides and Veterinary Medicines Authority (APVMA) Agricultural and Veterinary Chemicals Code Act 1994 (APVMA, 2019; APVMA, 2022). They must be evaluated and registered by the APVMA with the National Registration Scheme for Agricultural and Veterinary Chemicals. However, the criteria for assessment have relevance only for terrestrial semiochemical products, and the regulatory decision pathway for the marine environment remains unclear. Hence, a roadmap to translate semiochemical innovation to product needs to be created to provide assurance of safety and sustainability of the product and articulate benefits to the reef and ensure readiness for implementation.

(iii) *Engaging communities and publics about semiochemicals and their use as marine biocontrol agents.* The GBR is a globally recognised and World Heritage listed marine ecosystem that holds significant value for local communities, the Australian public and the broader international community. It also has profound significance for around 70 Traditional Owner groups whose ongoing custodial rights over the Great Barrier Reef and potential to co-deliver pest control and other management activities are recognized in the Australian and Queensland Governments' Reef 2050 Long-Term Sustainability Plan (Australian Government, 2023).

Alongside regulatory approvals, the successful design and implementation of semiochemical technologies in the GBR will require the development of effective partnerships with Reef Traditional Owners,

engagement with other affected Reef communities and the support of the broader Australian public.

It has been suggested that semiochemical control methods may offer advantages when it comes to public acceptability compared to the use of synthetic pesticides that attract concerns due to perceived health and environmental risks (Faleiro et al., 2016; Ivaskovic et al., 2021). However, empirical research exploring the factors influencing perceptions of semiochemical pest control methods in agriculture and conservation context are limited. One study has shown a preference toward pheromones over pesticides in relation to German agriculture (Lehberger and Becker, 2021), while another has indicated some preference toward pheromone attractants amongst available (non-pesticide) options in the management of mountain pine beetles in Canada (McFarlane et al., 2006). Other studies indicate that community perceptions of biotechnologies and other novel pest control methods are highly contextual, and can involve the consideration of many factors including concerns regarding side-effects and impacts to non-target animals, as well as levels of trust in the managing bodies implementing them (Palmer and Mercier, 2021; Thresher et al., 2019).

How affected communities respond to the prospect of semiochemicals in CoTS management is an important consideration for the development of this technology, alongside its technical feasibility, and environmental benefits.

Exploration of community perceptions of the use of semiochemicals in CoTS management has revealed that GBR managers can recognize the potential for more efficient manual removal of CoTS through the use of semiochemicals (Paxton et al., 2023), and quantitative research with the Australian public suggests a moderate level of support for research into the use of semiochemicals in CoTS management (Lockie et al., 2024). However, as the details about the potential applications of semiochemicals in CoTS management become clearer, more targeted engagement with communities, stakeholders and the Australian public will enable valuable dialogue around the acceptable implementation of semiochemicals in CoTS management, and how to enhance the potential social and environmental benefits of this technology.

In providing these perspectives on the potential for semiochemical intervention in CoTS control, we have drawn together preliminary knowledge across multiple disciplines, and it has become clear that innovative strategies to manage CoTS must focus on limiting their predatory pressures and supporting the natural adaptation of coral reefs to climate change. This approach will depend heavily on successful interdisciplinary collaboration. Gaining the benefits of semiochemicals not only requires us to understand the semiochemical repertoire that might be utilised to modify CoTS behaviour, but to work with engineers to develop innovative chemical emitting devices, ecologists and modelling statisticians to understand and better predict the potential large-scale ecosystem impacts of using specific semiochemicals, and social scientists to enhance regulatory frameworks and engagement strategies within a globally recognised and nationally important marine protected area. Successful collaboration will not only underpin the implementation of semiochemicals in CoTS management, but it might also lead the way to the better control of other asteroid pest species such as the ochre seastar (*Pisaster ochraceus*), the northern Pacific seastar (*Asterias amurensis*) and Forbes seastar (*A. forbesi*) as well as other marine pests.

List of Abbreviations

APVMA	Australian Pesticides and Veterinary Medicines Authority.
ApORs	<i>Acanthaster planci</i> Olfactory Receptors.
CoTS	Crown-of-Thorns starfish.
EPDR	Ependymin-related proteins.
GPCR	G-protein-coupled receptor.
NEB	Natural enemy biocontrol.

CRedit authorship contribution statement

Richard J. Harris: Writing – review & editing, Writing – original draft, Resources, Investigation, Data curation, Conceptualization. **d’Artagnan L. Barnard:** Writing – review & editing, Resources, Investigation. **Gillian Paxton:** Writing – review & editing. **Stewart Lockie:** Writing – review & editing. **David J. Craik:** Writing – review & editing. **Scott F. Cummins:** Writing – review & editing. **Conan K. Wang:** Writing – review & editing. **Cherie A. Motti:** Writing – review & editing.

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Declaration of competing interest

We declare no competing interests.

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Data availability

No data was used for the research described in the article.

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