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Population dynamics of corallivores (*Drupella* and *Acanthaster*) on coral reefs of Koh Tao, a diving destination in the Gulf of Thailand

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Abstract. Diving-related tourism is known to contribute both directly and indirectly to reef degradation around the globe, including Koh Tao, a popular diving destination in the Gulf of Thailand. Of the known publications on reef threats at Koh Tao, only three mention the effects of highly abundant coral predators. The present study combines results of a nine-year long period (2006–2014) of reef surveys to evaluate the abundance and impact of corallivorous *Drupella* snails and *Acanthaster* sea stars in this area. It also provides the first record of their simultaneous outbreaks on Koh Tao's reefs. The results are compared to those of other studies in order to evaluate how coral predation has influenced declines in reef health. The findings suggest that the combined effect of these corallivores has contributed substantially to coral degradation over the last decade and indicate that future assessments of reef decline in areas impacted by heavy tourism also need to address the effect of coral predation.

Key words. corallivorous snails, crown-of-thorns sea star, diving tourism

INTRODUCTION

Over the last century, coral reefs around the globe have been deteriorating at an increasing rate due to a multitude of threats and stresses (Pandolfi et al., 2003; Bruno & Selig, 2007; Wilkinson, 2008). The types and impact of various disturbances to reef health include both natural and anthropogenic threats, which vary greatly across spatial and temporal scales. The leading threats to coral reef health include climate change, development/pollution, and overfishing/overuse (Hoegh-Guldberg, 1999; Walther et al., 2002; Pandolfi et al., 2003; Carpenter et al., 2008). Although individual threats to coral reefs are well studied and understood, it is usually difficult to quantify the impact of any single stress factor on a natural coral reef ecosystem independent of others (Brown & Howard, 1985). This lack of scientific understanding of interrelationships between various reefs stresses limits the success of efforts to effectively create policy and regulate conflicting uses to prevent reef decline (Sale et al., 2014).

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Widespread recreational use of coral reefs for snorkeling and self-contained underwater breathing apparatus (scuba) diving has also been found to contribute to reef degradation through both direct and indirect stresses, which is a growing topic of concern (Hawkins et al., 1999, 2005; Rouphael & Inglis, 2002; Zakai & Chadwick-Furman, 2002; Barker & Roberts, 2004; Guzner et al., 2010; Toyoshima & Nadaoka, 2015; Giglio et al., 2016; Webler & Jakubowski, 2016) also involving areas in Southeast Asia and Thailand in particular (Uy et al., 2005; Worachananant et al., 2008; Abidin & Mohamed, 2014; Lamb et al, 2014; Wongthong & Harvey, 2014; Roche et al., 2016; Zhang et al., 2016). Some of the impacted diving destinations are located in the Coral Triangle and are famous for their rich marine biodiversity, such as northeastern Borneo (Waheed & Hoeksema, 2013; Zhang et al., 2016). Direct impacts of snorkeling and scuba diving on reefs include contacting or breaking corals, pollution/nitrification, re-suspension of sediment, and changes to fish behaviour. Indirect effects include pollution from boats, damage from anchors, and the effects of reef tourism support industries on land.

Recent studies on the island of Koh Tao, Thailand, have indicated that stresses related to island tourism (Weterings, 2011; Szuster & Dietrich, 2014) and scuba diving (Strookman, 2012; Lamb et al., 2014; Wongthong & Harvey, 2014; Hein et al., 2015) are important contributors to local reef decline. In order to evaluate whether observed trends are caused by direct use and not by other factors, it is necessary to have accurate long-term information on other salient reef threats. Studies indicate that the main damage caused by divers to reefs is through the breaking and scarring of corals, which has been shown to reduce colony size and result in mortality in about 2–20% of cases involving corals less than 20 cm (Cumming, 2002). One factor affecting coral colonies after physical damage is that it attracts and creates a point of entry for corallivores, which may form aggregations inside or around the wounds (Morton et al., 2002; Kita et al., 2005; Potkamp et al., 2017). In addition, an increase of corallivore abundance has been linked to a range of other stress-inducing events (Knowlton et al., 1981, 1990; Moyer et al., 1982; Kobluk & Lysenko, 1993; McClanahan, 1994; Antonius & Riegl, 1998; Plass-Johnson et al., 2015) and some of these could also catalyse a secondary or indirect effect of over-use through scuba diving.

On Koh Tao, multiple contributing threats have affected reef health over the last several decades, with high spatial and temporal variability between impacts at different reef sites. Population imbalances or outbreaks of both *Drupella* and *Acanthaster* have played significant roles in the deterioration of many reef areas around the globe but of the over 15 current scientific publications that discuss reef threats to Koh Tao, to date, two discuss coral predation by *Drupella* snails (Hoeksema et al., 2013; Moerland et al., 2016), and only one illustrates coral predation by *Acanthaster* sea stars (Scott et al., 2015).

Drupella is a genus of small muricid gastropods found throughout the tropical Indo-Pacific, which feed on living coral tissue. They deposit egg capsules in clusters on their host corals, apparently with a preference for bare skeleton where soft tissue is gone (Sam et al., 2016). Six species are currently recognised on account of a recent phylogeny reconstruction (Claremont et al., 2011), two of which were identified on Koh Tao in recent surveys; *D. rugosa* and *D. margariticola* (Moerland et al., 2016). Although there is a lack of information on these snail species prior to a report from Japan (Moyer et al., 1982), they have subsequently been found in large aggregations or outbreak populations in areas such as Kenya (McClanahan, 1994), Western Australia (Ayling & Ayling, 1987), Hong Kong (Cumming, 1998; Morton & Blackmore, 2009), and the Red Sea (Antonius & Riegl, 1997). *Drupella* can consume living coral tissue at a rate of about 1.8 cm^2/day per individual with coral cover reduced by 75% in some outbreak cases (Cumming, 2009). These outbreaks or overpopulations have led to dramatic loss of living coral tissue (Turner, 1994), reduced reef resilience and recovery (Lam et al., 2007), resulting in population regime shifts, and increased disease incidence (Nicolet et al., 2013). Theories point to the loss of predators through fishing (McClanahan, 1994, 1997) and decreased water quality due to other anthropogenic activities (Moyer et al., 1982) as the cause of these outbreaks.

Crown-of-thorns sea stars (*Acanthaster* spp.) are corallivorous animals commonly found in the Indo-Pacific region. Morphological and molecular analyses have indicated the existence of more than one species of what has so far been considered as *Acanthaster planci* (Nishida & Lucas, 1988; Benzie, 1999; Vogler et al., 2008), two of which are formally described as the commonly known *A. planci* (Linnaeus, 1758) and the less well-known *A. brevispinus* Fisher, 1917 (see Mah, 2015). Therefore, the species complex is henceforth referred to as *Acanthaster*.

Acanthaster populations have reached outbreak proportions in numerous outbreak events since the first reports from Japan and the Great Barrier Reef in 1960s (e.g., Endean & Chesher, 1973; Moran, 1986, 1990; Yamaguchi, 1986; Birkeland & Lucas, 1990; Baird et al., 2013; Pratchett et al., 2014). There appears to be great variation in the extent of predation during outbreak periods, with limited to devastating declines in scleractinian corals during outbreaks in Hawaii (Branham et al., 1971), southern Japan (Yamaguchi, 1986; Sano, 2000), the Andaman Sea (Chansang et al., 1987), the Great Barrier Reef (De'ath & Moran, 1998; Pratchett et al., 2009; Wooldridge & Brodie, 2015), the Philippines (Bos, 2010), Brunei (Lane, 2012), French Polynesia (Kayal et al., 2012; Kayal & Kayal, 2017), the Maldives (Saponari et al., 2015), and Chagos (Roche et al., 2015). This variation in damage has largely been attributed to differences in abundance of *Acropora* corals, the primary preferred prey, followed by *Montipora* and *Pocillopora*, with *Porites* being the least preferred of the major prey genera (Pratchett, 2010; Kayal et al., 2012; Baird et al., 2013). *Acanthaster* can consume between 148–238 cm^2/day per individual (Cumming, 2009). Interestingly, recent findings indicate that scleractinian corals may be protected against predation when they occur in close proximity to macro-algae and fire corals (Clements & Hay, 2015; Kayal & Kayal, 2017). There are currently no published records for *Acanthaster* population densities for Koh Tao and there is limited information for the Gulf of Thailand.

Koh Tao is a small, 19 km^2 island located in the Western Gulf of Thailand, which is surrounded by dense fringing reefs and several submerged pinnacles. Tourism, almost non-existent on the island 20 years ago, has boomed in recent years with between 300,000–400,000 tourists visiting the island each year by 2010 (Larpnun et al., 2011) plus an unknown number of snorkeling or diving day trip boats from neighbouring islands on a daily basis. The island accounts for the highest number of diving certifications issued for any location in Asia, and second in the world; with >60,000 dive certifications being issued in 2011 alone (Wongthong & Harvey, 2014). Although the growth in tourism has brought economic wealth to the island, the terrestrial and marine ecosystems have been greatly stressed in the process (Yeemin et al., 2006; Weterings, 2011). There is little historical information on the reefs of Koh Tao to evaluate past levels of reef coral abundance and diversity, however, reef decline had already been recognised in the region as early as the early 1990s (Garces, 1992). A study by Yeemin et al. (2006) found that there was a 17% decline in coral cover on the island within a five-year period, largely due to the 1998 mass coral bleaching event. Since 2010, coral predation has been recognised as a threat to Koh Tao's coral reefs by the local dive tourism industry, leading to actions by volunteers to remove the snails (Scott, unpubl. data).

Differentiating and evaluating the interaction of the natural and human-caused influences on reefs is one of the major challenges for both theoretical and applied marine ecology (McClanahan, 1994; Ban et al., 2014). The present study combines nine years (2006–2014) of regular reef monitoring

Table 1. Live hard coral cover (%) at Koh Tao over the period 2006–2014 measured in transects (total n=327) at six selected locations.

Location	**n**	**2006**	**2007**	**2008**	**2009**	**2010**	**2011**	**2012**	**2013**	**2014**	**Mean± s.e.**
Hin Wong Bay	60	52.5	55.3	62.3	56.8	41.3	37.5	33.2	50.6	71.8	51.3±8.7
Sairee	18	50.1		62.5	72.5			40.6	34.8	43.1	50.6±5.8
Tanote Bay	52	44.6		22.3	47.0	42.3	28.8	23.8	31.1	33.6	34.2±3.3
Chalok Ban Kao	66	17.8	16.3	33.8	22.3	29.0	18.0	21.1	26.4	38.8	24.8±2.5
Ao Leuk	92	24.8		21.6	26.0	28.2	25.4	21.8	30.4	30.4	24.5±1.9
Sai Nuan	39	17.1		19.7	28.6	29.7	25.9	17.5	16.5	26.8	22.7±2.0
Means		36.2	27.8	37.0	32.0	33.1	27.1	27.1	32.6	39.1	
±s.e.		5.9	13.8	7.6	7.3	5.3	3.1	3.6	3.8	4.3	

surveys and data collection to evaluate the abundance and impact of coral eating *Drupella* and *Acanthaster* on the island of Koh Tao. It also provides the first record of coral predator levels on Koh Tao's reefs and compares those observed levels to the threat maps in other studies to evaluate the significance of coral predation and the interaction of predation with other local threats to reef health. By providing a review of the areas where coral predation-related damages will be difficult to differentiate, it is hoped that future studies on predation and diving damage to reefs will have higher levels of precision, which can be used to increase the effectiveness of reef-based tourism planning and management.

MATERIAL AND METHODS

Data collection. Data was collected according to the locally designed Save Koh Tao Ecological Monitoring Program (EMP) (Scott, 2012). The EMP surveys are based on methods of the Coastal Preservation and Development (CPAD) Foundation and Reef Check International (Phillips et al., 2010). At each site (Fig. 1), surveys were conducted along two transects laid between permanently marked locations, a 'Shallow' (3–5 m depth) and 'Deep' (6–9 m depth) line. Each survey line consisted of four 20 m long transects with 5 m intervals, yielding a total of eight replicate transects per site, per survey. Altogether, a total of 327 surveys from six (out of 15) EMP locations around the island conducted over a nine-year period (2006–2014) were analysed for hard coral cover (Table 1). These sites were chosen as each of them had a minimum of 15 surveys for data analysis.

The densities of *Drupella* and *Acanthaster* individuals were counted in 20 × 5 m^2 (=100 m^2) quadrats using the belt transect method in which invertebrate indicator species are scored within 2.5 m each side of the 20 m transect line. *Acanthaster* surveys were included from the start of the monitoring (2006) and *Drupella* was added in the survey protocol only from 2009 onwards. Because they are highly cryptic and have variable abundances, the snails were given an 'abundance score' on a scale of 0 to 3 as follows: 0 (none observed), 1 (<0.5 indiv. m^{-2}), 2 (0.5–1.5 indiv. m^{-2}), and 3 (>1.5 indiv. m^{-2}). *Acanthaster* counts were multiplied by 100 to allow comparisons with other studies that express densities as numbers per hectare (ha^{-1}). The percent cover of hard corals, macro-algae and other substrata were estimated using the point intercept method, in which divers record the substrate category directly under the transect line every segment of 0.5 m in a full 20 m transect.

Data analysis. Only sites at which more than 15 surveys were completed in the nine-year period were included in the analysis. All univariate analyses were performed using Microsoft Excel (V14.3.8) and XLSTAT (203.5.03).

Hard coral cover. The percent hard coral cover of each transect was extrapolated from the database and compiled according to site and year. Differences in mean hard coral cover per year were compared among sites, and years over the period 2006–2014, using 1-way analysis of variance (ANOVA). Assumptions of normality were checked using the Shapiro-Wilks test (Royston, 1982).

Predator densities. *Drupella* abundances at eight sites (Fig. 1) were compiled six times for the period 2009–2014 and compared among years, depth, sites, and months. As the data did not meet the assumption of normality after transformation, the significance of each difference was tested using the non-parametric Kruskal-Wallis test (Hollander and Wolfe, 1973). The same procedure was performed eight times to compare differences in the *Acanthaster* abundance among years (2006–2014, 2007 excluded), depth, sites, and months. In addition, focused surveys for *Drupella* snails were completed on two occasions, in October 2010 and February 2011. The snails were counted in 1 m^2 quadrats at 5 m intervals along a 200 m long transect line laid haphazardly at 4 m depth on the reef in Chalok Ban Kao.

Coral predators and their substrata. Linear regressions were performed to investigate the relationship between the abundance of *Drupella* and *Acanthaster* with hard coral cover and macro-algae cover respectively.

***Drupella* and *Acanthaster* abundance relative to reef threats.** Abundances of *Drupella* and *Acanthaster* individuals were then plotted against published descriptions of diving pressure, level of use, and degree of reef protection on Koh Tao (Weterings, 2011; Lamb et al., 2014; Hein et al., 2015). The study by Weterings (2011) used dive school questionnaires to quantify the number of dives being conducted at any single site and used weighted equations to create a relative scale

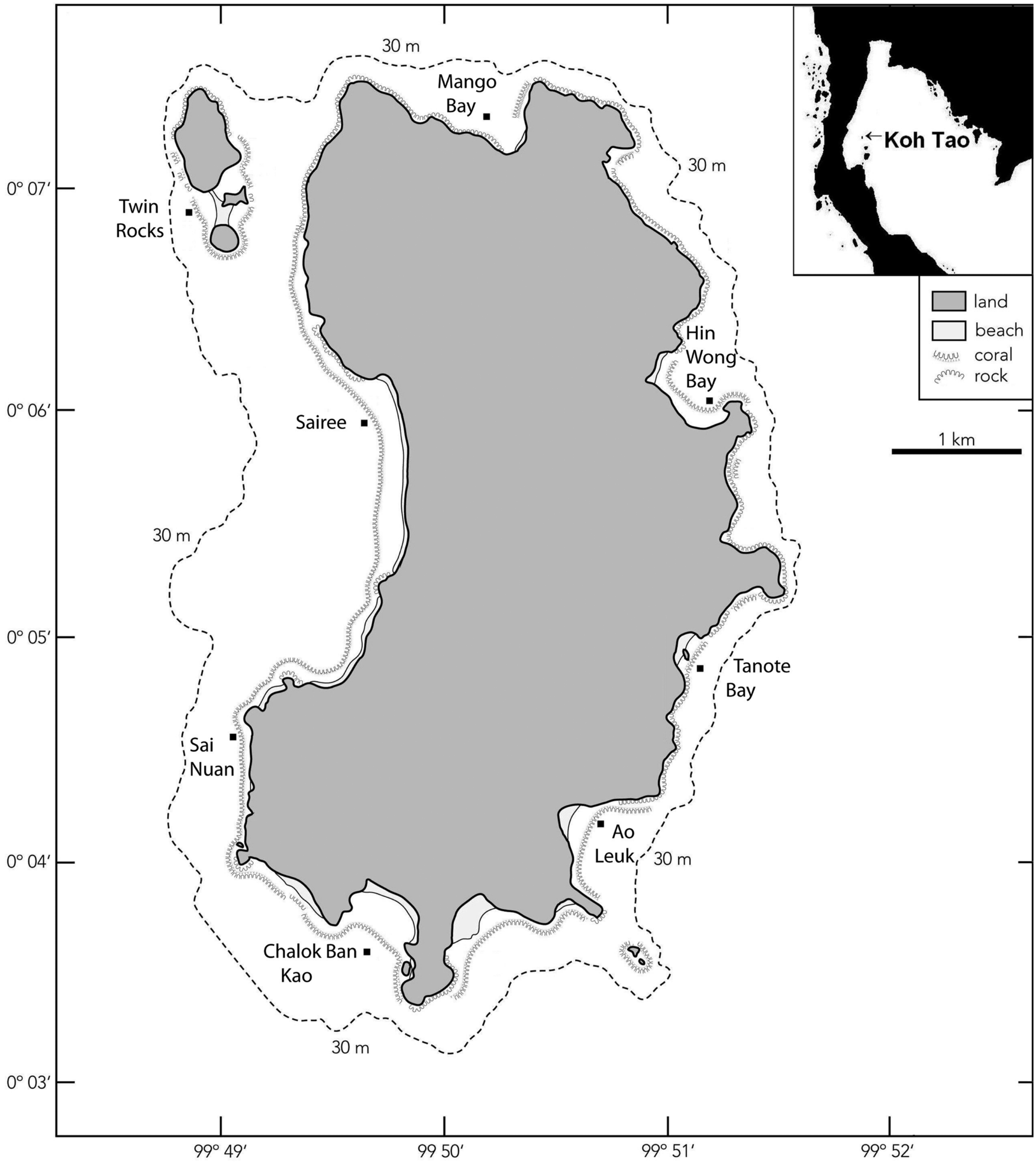

Fig. 1. Map of survey sites used in this study (after Hoeksema et al., 2012). Six of them were monitored for hard coral cover: Hin Wong Bay, Sairee, Sai Nuan, Chalok Ban Kao, Ao Leuk, and Tanote Bay. These sites and two additional ones (Mango Bay and Twin Rocks=Twins) were also used for predator studies.

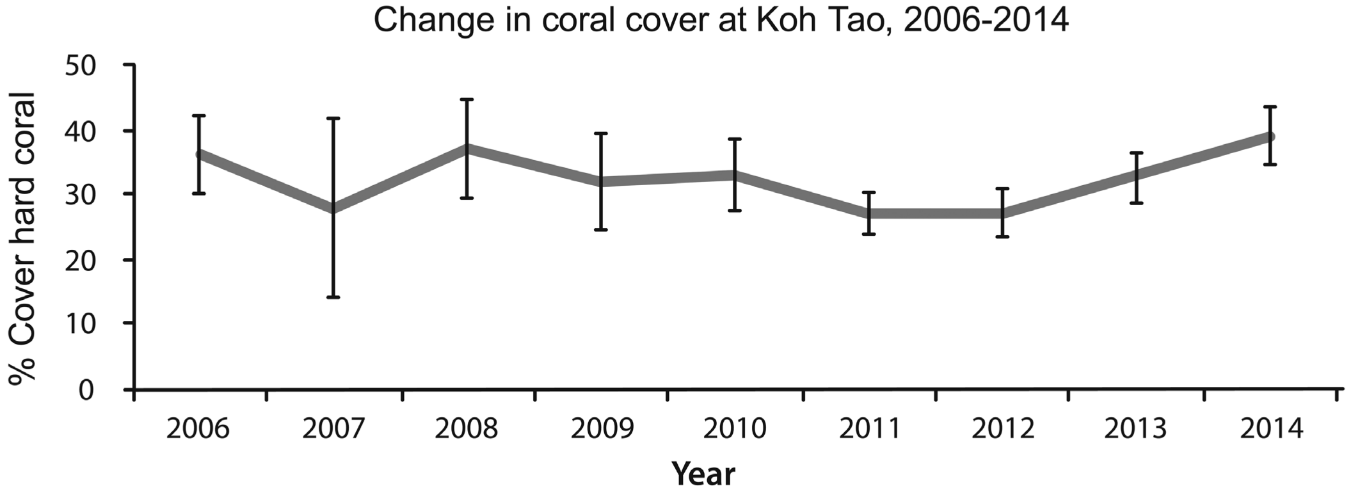

Fig. 2. Variation in mean hard coral cover at Koh Tao over the period 2006–2014 for the six selected sites indicated in Table 1.

of dive site use, with the maximum value (i.e., most dived site) set to 20. The values for dive site pressure were plotted against both *Drupella* and *Acanthaster* abundances at sites that overlapped with EMP monitoring, and linear regression analyses were performed to investigate the significance of these relationships. A study by Lamb et al. (2014) used the data by Weterings (2011) and local knowledge of reef sites to identify five 'high-use' and five 'low-use' sites around the island. They looked at 10,499 coral colonies at those sites to identify the percent of corals as 'Healthy', 'Diseased', 'Compromised Health', or 'Physically Damaged,' in order to assess the impact of diving on these reef areas. The total percent of corals coded as non-healthy between both high- and low-use sites overlapping with this study was plotted against both *Drupella* and *Acanthaster* abundances. Again, linear regression analyses were performed to test the significance of the relationships between coral health categories and *Drupella* and *Acanthaster* abundances, respectively. A 1-way analysis of variance was also used to compare differences in abundances between both taxa found in overlapping high-use and low-use sites respectively. Finally, the study by Hein et al. (2015) categorised sites based on their protection through the local zoning and coastal regulations implemented in 2012 (Platong, 2012). Abundances of *Drupella* and *Acanthaster* were plotted against overlapping sites in MPA and non-MPA respectively and 1-way analyses of variances were used to determine the significance of these relationships.

RESULTS

Variation in coral cover. Over the period 2006–2014, mean coral cover ranged from 27.1 ± 3.1% in 2011 to 39.1 ± 4.3% in 2014 (Table 1, Fig. 2), but variation over the years was not significant (ANOVA Df=8, p=0.859). Coral cover varied significantly between sites (ANOVA Df=8, p <0.001), with Hin Wong Bay having the highest mean coral cover (51.3 ± 8.7%), showing an increase of 27% over the period. Had Sai Nuan had the lowest mean coral cover (22.7 ± 2.0%), but showed an increase of about 36% over the nine-year period. Two sites decreased in coral cover over the study, losing 16–33% of hard coral cover (Sairee and Tanote Bay).

***Drupella* abundance.** The mean relative abundance of *Drupella* varied significantly by year (Kruskal-Wallis test Df=5, p=0.013), more than doubling from 0.41 ± 0.12 in 2009 to 0.87 ± 0.12 in 2014 (Fig. 3a). No significant variation between months or seasons was observed (Kruskal-Wallis test Df=11, p=0.541). Abundance varied significantly over sites (Kruskal-Wallis test Df=15, p <0.001) with the highest mean *Drupella* abundance for the period 2009–2014 recorded at Sairee (1.4 ± 3.4), and the lowest in Tanote Bay (0.22 ± 0.07) (Fig. 3e). It was also more than three-fold higher in shallow surveys than in deep ones (1.0 ± 0.8 and 0.31 ± 0.05 respectively, Kruskal-Wallis test Df=1 p <0.001; Fig. 3c).

***Acanthaster* abundance.** The mean density of *Acanthaster* sea stars for the period 2006–2014 was 7.1 ± 1.9 individuals ha^{-1}, and ranged from 4.5 ± 2.2 ha^{-1} (2009) to 9.7 ± 4.7 ha^{-1} (2012), but did not vary significantly by year (Kruskal-Wallis test Df=8, p=0.189; Fig. 3b). *Acanthaster* abundance varied significantly by site (Kruskal-Wallis Test Df=5, p <0.001), the location with the highest mean density was Mango Bay (18.8 ± 6.7 ha^{-1}; Fig. 3f), and the site with lowest density was Chalok Ban Kao (3.2 ± 1.2 ha^{-1}). *Acanthaster* density did not vary significantly by depth (Kruskal-Wallis test Df=1, p=0.142; Fig. 3d), or by month (Kruskal-Wallis test Df=11, p=0.641; Fig. 3g).

Coral predators and hard coral cover. The abundance of *Drupella* snails was positively correlated with live hard coral cover (R^2=0.572, p <0.001; Fig. 4), but there was no correlation for *Acanthaster* (R^2=0.043, p=0.409). There was also no correlation between *Drupella* or *Acanthaster* abundance and cover by macro-algae, respectively (R^2=0.177, p=0.082; R^2=0.001, p=0.893), and between the abundance of *Drupella* snails and *Acanthaster* abundance (R^2=0.009, p=0.806).

***Drupella* and *Acanthaster* abundance relative to reef threats.** *Drupella* abundance showed no correlation with diving pressure (R^2=0.001, p=0.943) according to the results of Weterings (2011) and there was also no significant correlation between *Acanthaster* populations and diving pressure (R^2=0.071, p=0.402). When coral predator

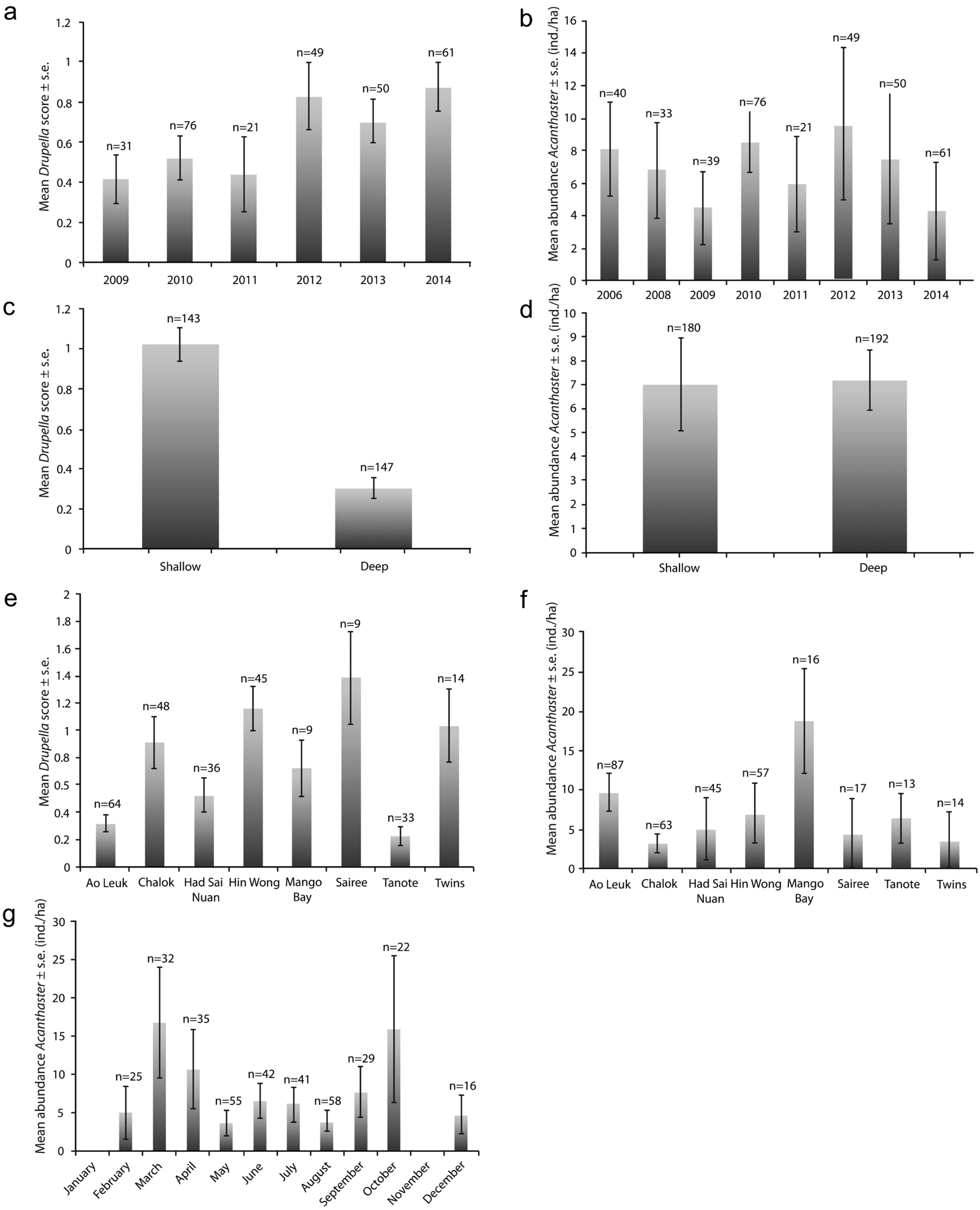

Fig. 3. Population dynamics of coral predators around Koh Tao in 2006–2014. a, Relative *Drupella* abundance showing significant variation over time (p=0.013). b, Mean *Acanthaster* abundance not varying significantly over time (p=0.189). c, Mean *Drupella* abundance is significantly higher in shallow quadrats as compared to deeper ones (p <0.001). d, Mean *Acanthaster* abundance shows no difference by depth (p=0.142). e, Mean *Drupella* abundance by site varied significantly (p <0.001). f, Mean *Acanthaster* abundance by site varied significantly p <0.001). g, Seasonal variability in *Acanthaster* abundance at EMP sites was not significant (p=0.641).

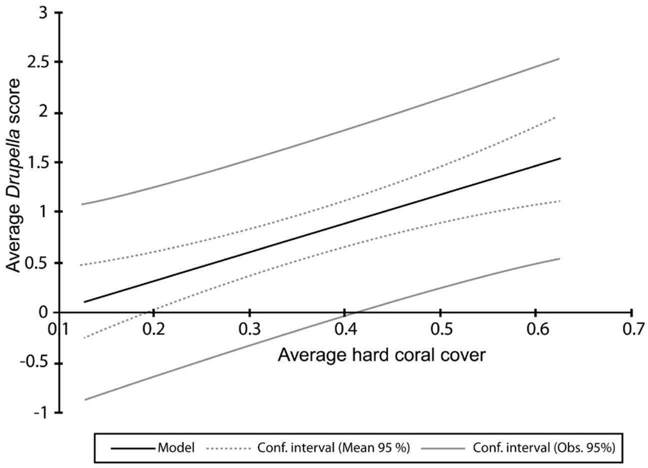

Fig. 4. Positive linear correlation between *Drupella* abundance and live hard coral cover (R^2=0.572, p <0.001).

abundance was compared to the combined stress model of Weterings (2011) there was no significant correlation for both *Drupella* (R^2=0.123, p=0.355) and *Acanthaster* (R^2=0.123, p=0.355). *Drupella* populations also showed no significant (R^2=0.404, p=0.175) correlation with lower reef health as recorded by Lamb et al. (2014) and neither did *Acanthaster* abundance (R^2=0.258, p=0.304).

When compared by site use categories developed by Lamb et al. (2014), no significant differences were found. *Drupella* snails showed scores of 0.95 ± 0.34 in high-use sites and 0.81 ± 0.19 in low-use sites, respectively (Fig. 5a; ANOVA Df=1, p=0.723). Mean *Acanthaster* abundance was 10.3 ± 4.2 indiv. ha^{-1} at low-use sites and 5.8 ± 1.9 indiv. ha^{-1} at high-use sites (Fig. 5b; ANOVA Df=1, p=0.406). Similarly, when compared with sites' protective status developed by Hein et al. (2015), *Drupella* snails seemed to be more abundant in MPA sites (0.95 ± 0.34 compared with 0.67 ± 0.26 at non-MPA sites) (Fig. 5c; ANOVA Df=1, p=0.549), and *Acanthaster* more abundant in non-MPA sites (7.2 ± 1.4 indiv. ha^{-1} compared with 3.0 ± 1.0 indiv. ha^{-1} at MPA sites) (Fig. 5d; ANOVA Df=1, p=0.087). Nevertheless, none of these differences were statistically significant.

DISCUSSION

Change in coral cover. Of the six sites with more than 15 total surveys for the period 2006–2014, two were in good condition. Coral cover increased in four of the six sites surveyed and decreased in the other two sites, Tanote Bay and Sairee. The decline in coral cover in Tanote Bay is mostly related to burial and sedimentation caused between 2006–2007 by the reservoir and road construction in the overlaying watershed (Larpnun et al., 2011). Human-induced sedimentation has been recognised as a serious threat to many corals worldwide (Erftemeijer et al., 2012). Many of the reefs on the southern part of the island suffered heavily during the bleaching event of 1998 (Sutthacheep et al., 2013) and were still in various stages of recovery over the period. Sairee was less impacted by the bleaching event and its decline in coral cover can probably be attributed largely to chronic pollution, disease, and overgrowth by macro-algae (Weterings, 2011; Lamb et al., 2014), whereas it also had the highest relative *Drupella* abundance of all sites surveyed.

The observed increase in coral cover at all other sites can probably be attributed to recovery from low initial coral cover following the large-scale mass bleaching event of 1998 (Yeemin et al., 2006), but it is not suggested that anthropogenic or natural disturbances have been alleviated over the last decade. Decline in coral cover from 2010–2011 can largely be attributed to the 2010 coral bleaching event (Hoeksema & Matthews, 2011; Chavanich et al., 2012; Hoeksema et al., 2012, 2013; Yeemin et al., 2012). Bleaching in surviving corals was not over in early 2011 for some coral species (Hoeksema & Matthews, 2015). Current recovery has been set back by the coral bleaching event of 2014, and the rise in *Drupella* snail abundance could have large implications to the survival and growth of future coral recruits (Turner, 1994).

EMP monitoring data for the period was also consistent with the finding by Lamb et al. (2014) that coral cover did not vary significantly between high and low use sites. This implies that diving pressure, at least in the short term, may not be a strong factor in controlling total coral cover. However, further investigation is needed to understand how diving affects the biodiversity and population dynamics of local reefs, as the study by Hein et al. (2015) found that there was a significantly higher proportion of resilient coral (e.g., Agariciidae) than less resilient corals (e.g., Acroporidae) between high- and low-use sites. Furthermore, it was found that damage to coral species at Koh Tao varied, depending on contact by divers (Strookman, 2012). Scuba diving and related coral reef tourism on Koh Tao is currently being conducted at an unsustainably high rate, as much as 15 times greater than the carrying capacity recommended by Hawkins & Roberts (1997) of 5–6 × 10^3 divers/year (Nichols, 2013; Hein et al., 2015).

Abundance of *Drupella*. The population levels and fluctuations of *Drupella* snails are relatively homogeneous around the island. The largest increase in *Drupella* snails (34%) occurred between 2013 and 2014. There was little seasonal variation in *Drupella* numbers, but increases were observed during the coral bleaching events of 2010 and 2014, as has been observed following bleaching events elsewhere (Baird, 1999).

Surveys involved in this project also covered the first recorded outbreak of *Drupella* for the Gulf of Thailand over subsequent years (Hoeksema et al., 2013; Moerland et al. 2016). According to Cumming (2009), an outbreak of *Drupella* starts over 1.4 indiv. m^{-2}. Generally, a *Drupella* density of 0–2 indiv. m^{-2} occurs in non-outbreak situations and densities of 2–3 indiv. m^{-2} may be worth monitoring. The focused quadrat surveys (1 m^2) conducted in October of 2010 in Chalok Ban Kao found the abundance to be 7.9 indiv. m^{-2} (± 3.1, n=24), which had declined to 5.6 indiv. m^{-2} (± 2.0, n=20) by February of 2011, partially due to the collection of over 14,000 individuals from the area by volunteer divers between August 2010 and February 2011.

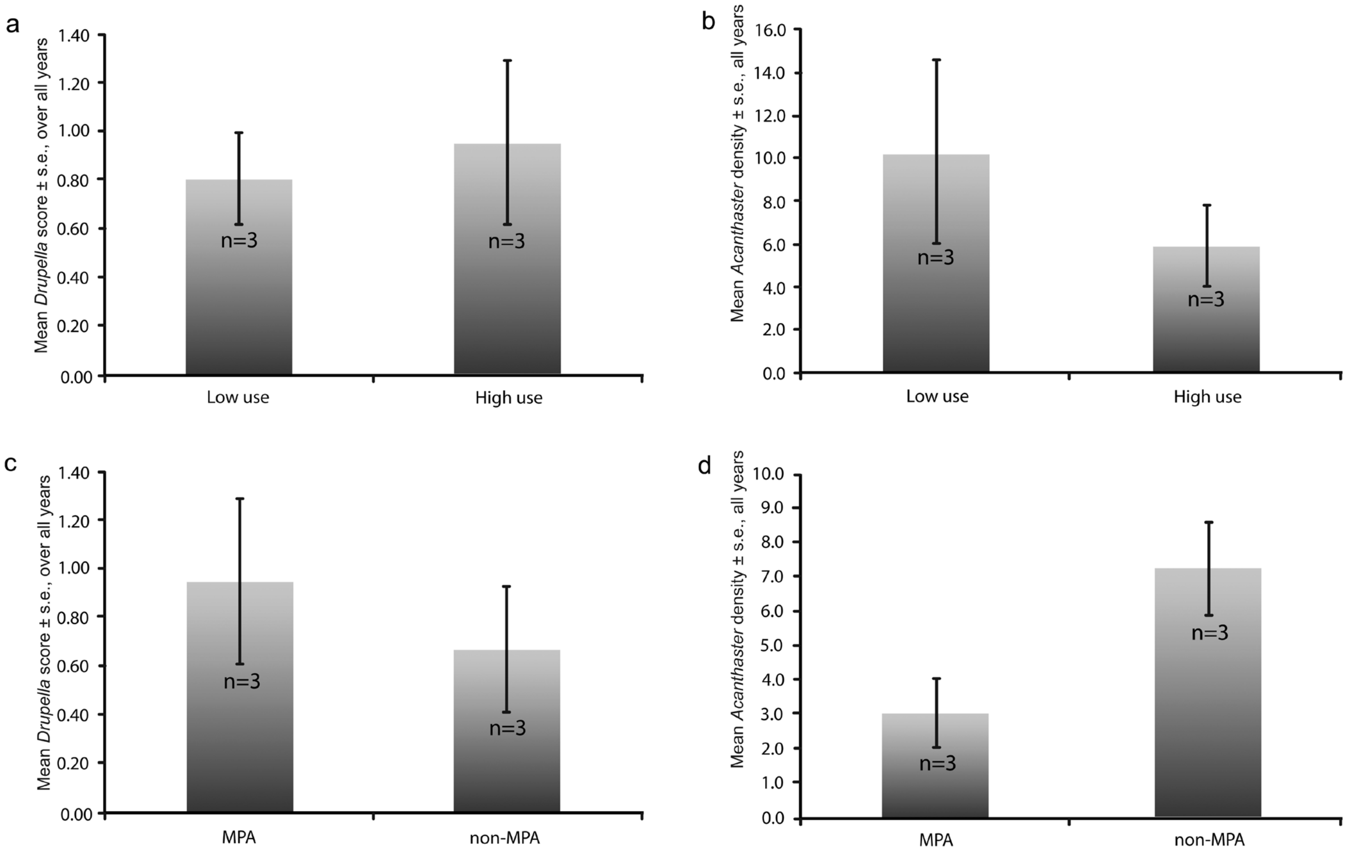

Fig. 5. Coral predator abundance compared to previously published results on Koh Tao's reefs; differences are not significant. *Drupella* (a) and *Acanthaster* (b) abundance in low- and high-use sites as designated by Lamb et al. (2014). Similar for the designations as MPA or non-MPA sites used by Hein et al. (2014) concerning *Drupella* (c) and *Acanthaster* (d).

In subsequent surveys performed in the same area in 2014, 1,205 snails were collected with a large majority (>95%) consisting of *Drupella rugosa*, while only 60 out were identified as *D. margariticola* (Moerland et al., 2016).

During 2010–2011, *Drupella* snails were observed feeding on corals of 20 genera, primarily *Acropora*, *Montipora* and *Pavona*, similar to *D. rugosa* in other areas; (see Boucher, 1986; Baird, 1999; Morton et al., 2002; Tsang & Ang, 2015). Prey preference shifted locally in those years following a major coral bleaching event (Hoeksema et al., 2013), which has been observed on other reefs following changes in coral community and *Drupella* density (Shafir et al., 2008). Although the vast increase in relative abundance over multiple years indicates the progression of a *Drupella* outbreak, the absolute counts show that the resulting densities are in line with typical outbreak densities above 3 indiv. m^{-2} (Moerland et al. 2016).

Drupella abundance was found to be highest in shallow reef areas, which is congruent with several other studies (reviewed by Cumming, 2009). Shallow reefs are also under greater threat by reef-based tourism, as they are accessible to both divers and snorkelers, adding difficulty to separating diving related causes of reef decline from predation by *Drupella* snails. The shallow reef (1–5 m depth) of Chalok Ban Kao Bay for example has experienced multiple large disturbances, including coral bleaching, sedimentation, and anchor damage. The site also has some of the highest concentrations of *Drupella*, with volunteers removing over 43,900 snails between 2010 and May of 2015 from a reef area of only about 0.2 km^2 (Scott, unpubl. data).

Abundance of *Acanthaster*. Overall *Acanthaster* numbers per hectare over the survey period showed no significant changes, primarily due to relatively large annual variation in numbers. However, the results may show two aggregations peaks, in March and October, which may be spawning events (Fig. 3g). A study by Bos et al. (2013) identified March to April as the spawning season for *Acanthaster*, which was confirmed in 2015 when spawning was serendipitously observed by the authors in Laem Tien Bay on April 21 at 1502 hours Indochina Time (ICT), and again in Ao Leuk Bay on May 1 at 1204 hours ICT. *Acanthaster* spawning was also observed on Koh Tao in 2014 (Scott et al., 2015), occurring on September 12, a month before the observed increase in seasonal abundance (Fig. 3g).

Observations on the island have been made of individuals feeding on corals belonging to typical prey genera such as *Acropora*, *Montipora*, *and Pocillopora*, and less typical genera such as *Platygyra* and *Porites*. An *Acanthaster* outbreak has been defined as >15 indiv. ha^{-1} (Cumming, 2009), meaning that both the mean value for the island as a whole, and most sites individually were not at outbreak levels. However, the mean abundance at some sites during some years had exceeded this limit (Hin Wong Bay and Sai Nuan in 2011; Ao Leuk and Tanote Bay in 2013; and

Sai Nuan in 2014). Furthermore, it is relevant to note that *Acanthaster* sea stars are very motile (Mueller et al., 2011), and that their migration may cause short-term variability in density measurements.

***Drupella* and *Acanthaster* abundance relative to previous local studies.** *Drupella* and *Acanthaster* abundances showed no significant correlation to diver impact levels of reefs around Koh Tao as compared to those determined in 2010 by Weterings (2011), which is in contrast with results on *Drupella* in the northern Red Sea (Guzner et al., 2010). When coral predator abundance was compared to the combined stress model of Weterings (2011), there were no significant correlations. It should be noted however that the location lacks effective control sites as in the study by Guzner et al. (2010), and even those sites not listed by Weterings (2011) as 'highly impacted' by divers are still dived on.

The relative abundance of *Drupella* showed no significant correlation to the observations of coral health and disease by Lamb et al. (2014). Little is understood about the causes and implications of *Drupella* snail population increases, except that multiple factors interact to create the conditions for outbreaks (McClanahan, 1994), and more robust data and studies are needed to fully understand these interactions. *Drupella* snails have been shown to be a highly effective transmission vector for Brown Band Disease, as well as white syndromes and SEB and Black Band Disease (Antonius & Riegl, 1998; Nicolet et al., 2013). It is currently unclear whether *Drupella* snails promote coral disease outbreaks or are merely attracted to them.

When the abundance of *Drupella* snails was plotted against the descriptions of high- and low-use sites as designated by Hein et al. (2015), the abundance of *Drupella* snails did not show significant differences, which does not agree with results from Eilat, Gulf of Aqaba, where higher abundances were found in high-use than in low-use areas (Guzner et al., 2010). A study by Turner (1994) found higher abundances of *Drupella* snails in non-protected reef sites than in protected ones, but when *Drupella* abundance on Koh Tao was averaged according to MPA vs. non-MPA status, no significant difference was found. As the MPAs were only designated in 2012, more long-term monitoring is needed to evaluate their effectiveness (Hein et al., 2015). *Acanthaster* abundance also did not show significant differences between low- and high-use sites, despite the regular collection of the sea star by concerned local divers.

CONCLUSION

Although there is no question that the local dive industry is negatively impacting reef health and resilience, to date the direct impacts of scuba diving on Koh Tao has not been adequately quantified or evaluated independent of other contributing threats. Several recent studies (e.g., Weterings, 2011; Strookman, 2012; Szuster & Dietrich, 2014; Lamb et al., 2014; Wongthong & Harvey, 2014; Hein et al., 2015) have greatly contributed to the understanding of reef decline on Koh Tao, and have highlighted the problems associated with diving tourism and the need to better manage areas for recreational use. However, none of those studies included the role of *Drupella* or *Acanthaster* in explaining their findings.

Present findings suggest that although there is no significant correlation between corallivore population densities and diving pressure, those of *Acanthaster* have remained unchanged and those of *Drupella* have significantly increased throughout the study period. Few studies and no management reports for Koh Tao have addressed the issue of coral predation, however, the ongoing outbreak of *Drupella* snails and the occurrence of some significantly high local densities of *Acanthaster* found in this study warrant inclusion in all future assessments of reef threats, decline, or management on the island, and elsewhere. More accurate global data on the population trends and dynamics of corallivores which potentially contribute significantly to reef decline can further improve understanding and management of coral reefs in the face of human population growth, development, and climate change.

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