Mass mortality event of the giant barrel sponge *Xestospongia* sp.: Population dynamics and size distribution in Koh Phangan, Gulf of Thailand

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Marine sponges are prominent organisms of the benthic coral reef fauna, provide important ecosystem services, but can be threatened by changing environmental conditions. This study presents the first documentation of a mass mortality event of the barrel sponge *Xestospongia* sp. in the lower Gulf of Thailand and its consequences on population dynamics and size distribution. Two anthropogenic impacted reefs (Haad Khom and Mae Haad) of the island Koh Phangan and two anthropogenic non-impacted reefs of the islands Koh Yippon and Hin Yippon within the Mu Ko Ang Thong Marine National Park were surveyed in the years 2015 and 2016. The results showed a strong shift in population densities at Koh Phangan. Fatal “bleaching” ending up in mass mortality was observed for these reefs in 2015. *Xestospongia* sp. abundance decreased from 2015 to 2016 by 80.6% at Haad Khom and by 98.4% at Mae Haad. Sponges of all sizes were affected, and mortality occurred regardless of the survey depth (4 m and 6 m). However, *Xestospongia* population densities in the Marine Park were at a constant level during the surveys. The abundances in 2015 were 65% higher at the Marine Park than at Koh Phangan and 92% higher in 2016.

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Abstract

Marine sponges are prominent organisms of the benthic coral reef fauna, provide important ecosystem services, but can be threatened by changing environmental conditions. This study presents the first documentation of a mass mortality event of the barrel sponge *Xestospongia* sp. in the lower Gulf of Thailand and its consequences on population dynamics and size distribution. Two anthropogenic impacted reefs (Haad Khom and Mae Haad) of the island Koh Phangan and two anthropogenic non-impacted reefs of the islands Koh Yippon and Hin Yippon within the Mu Ko Ang Thong Marine National Park were surveyed in the years 2015 and 2016. The results showed a strong shift in population densities at Koh Phangan. Fatal "bleaching" ending up in mass mortality was observed for these reefs in 2015. *Xestospongia* sp. abundance decreased from 2015 to 2016 by 80.6% at Haad Khom and by 98.4% at Mae Haad. Sponges of all sizes were affected, and mortality occurred regardless of the survey depth (4 m and 6 m). However, *Xestospongia* population densities in the Marine Park were at a constant level during the surveys. The abundances in 2015 were 65% higher at the Marine Park than at Koh Phangan and 92% higher in 2016.

Introduction

Various marine sponges play an important role as coral reef ecosystem engineers (Bell, 2008; Rix et al., 2016). Sponges have a positive impact on the complexity of the habitat structure and the local biodiversity (Maldonado et al., 2016), provide a home for invertebrate taxa (Wulff, 2006), and function as a food source (Engel and Pawlik, 2005). Due to their ability to filter large amounts of seawater (Reiswig, 1974), they have been recognized as an important component of benthic-pelagic coupling. In recent years there has been increasing evidence that sponges play an important role in biochemical cycles, in particular the uptake and transformation of dissolved organic matter (DOM) to particular organic matter (POM) via the so-called sponge-loop (Goeij et al., 2013; Rix et al., 2016; Schläppy et al., 2010).
The barrel sponge *Xestospongia* spp., a genus of the class Demospongiae, is a key species in tropical, shallow coral reefs (McMurray et al., 2015). This sponge is an ecological important member of the reef community, caused by its large size, its importance as a habitat engineer, and its function as a big seawater filterer (McMurray et al., 2014, 2010). Populations of the species *Xestospongia muta* occupy more than 9% of the coral reefs in some areas in the Caribbean (Zea, 1993, p. 83). Some individuals of the Caribbean reefs may be older than 2,300 years and can grow several meters in height and diameter (Gammill, 1997; Humann and Deloach, 1992; McMurray et al., 2008). Thus they are one of the oldest living organisms in the world (McMurray et al., 2008). However, McGrath and colleagues (2018) found contrary to McMurray twice as high growth rates for *Xestospongia* spp. from Wakatobi National Marine Park, Indonesia, compared to the Caribbean counterparts. This emphasizes that our knowledge of

Xestospongia spp. demography and size distribution in other tropical regions like the Indo-Pacific is still limited. Further research is needed to fill this gap, especially since sponges generally could play an increasing role for tropical reefs in the future. The main habitat-forming organisms, scleractinian corals, are threatened worldwide by multiple stressors such as rising water temperatures, ocean acidification, and pollution (Mollica et al., 2018; Mueller et al., 2022; Prada et al., 2017). With the decline of hard coral cover in shallow waters, coral reefs can undergo phase shifts from coral-dominated states to reefs dominated by algae or other invertebrates, including sponges (Bell et al., 2013; de Bakker et al., 2017; Dinsdale and Rohwer, 2011; Maliao et al., 2008). Reefs dominated by sponges have mainly been reported from the Caribbean but also from certain locations in the Indo-Pacific (Abigail L, 2011; Bell et al., 2013; Maliao et al., 2008; Reverter et al., 2021).

However, with increasing sponge research and benthic monitoring in the last decades, also more bleaching events, diseases, and mortality events were reported for sponges (Angermeier et al., 2011; Belikov et al., 2018; McMurray et al., 2011). *Xestospongia* spp. undergo cyclic bleaching like reef-building corals (McMurray et al., 2011). During this time, the sponges lose their reddish-brown coloration due to the loss of their photosynthetic symbionts and appear creamy-white (Erwin and Thacker, 2007; Vicente, 1990). The elicitors for a bleaching event are supposed to be multiple environmental factors like changes in light intensity and water temperature (McMurray et al., 2011). Unlike corals, the affected *Xestospongia* spp. can survive long-term bleaching without mortality. According to McMurray et al. (2011), this fact leads to the assumption that the host benefits just a little or not from its photosynthetic symbionts.

Sponge mortality is often caused by fatal bleaching with massive tissue loss due to diseases (Cowart et al., 2006). But not only diseases can trigger sponge mortality. Other environmental stressors such as changing environmental conditions and harmful algal blooms (HABs) can threaten sponge fitness (Bauman et al., 2010; Cebrian et al., 2011). Several bleaching, diseases, and mortality events have been documented for sponge species around the world (Angermeier et al., 2011; Luter et al., 2010; Stevely et al., 2011; Webster et al., 2008), although the causative agent has only been identified in one case (Webster et al., 2002). This is the first study from the lower Gulf of Thailand that investigated the population dynamics, the health status, and the size distribution of *Xestospongia* sp. before, during, and after a massive die-off.

Materials & Methods

The surveys were conducted under a Memorandum of Understanding with the Department of Marine and Coastal Resources Thailand and the Phuket Marine Biological Center, and with a research permit with permit number B8425313.

This study deals with a sponge species of the *Xestospongia* species complex (Swierts et al., 2017) and for simplicity, the sponges are further referred to as *Xestospongia* sp. Surveys were performed at different time points in March and April of the years 2015 and 2016. To determine the size and age structure of the *Xestospongia* populations at the study sites, surveys were carried out in March 2015 before the mortality event took place (2015.1), once the mass mortality was recognized during the ongoing mortality event in April 2015 (2015.2), and during the next field season in March and April 2016. All data were collected by snorkeling.

Study sites. Four coral reefs were chosen in the shallow waters of the lower Gulf of Thailand. Two of them were located on the island of Koh Phangan, and the other two were in the Mu Ko Ang Thong Marine National Park (*Fig. 1*). By choosing these study sites, the observed reefs were divided into reefs with different human impact levels: anthropogenic impacted (Koh Phangan) and anthropogenic non-impacted (Marine National Park).

The investigated reefs of Koh Phangan were located in the northern and northwestern part of the island at the beaches Haad Khom (9°47'54"N, 100°00'53"E) and Mae Haad (9°47'30.9"N, 99°58'35.3"E) (*Fig. 1b*). Both were impacted by tourism. Several bungalows and bars were located at Mae Haad, snorkelers got easily to the reef on foot, and fishing was recognized in front of the reef during our surveys. Haad Khom was less touristic, and snorkelers just got to the reef by boat. The reef of Mae Haad was during the surveys less degraded than the reef of Haad Khom, which showed lower live coral cover and higher cover of dead coral overgrown by filamentous algae (JS Mueller, P-J Grammel and E Schoenig, 2015, 2016, pers. comm.). In contrast to this were the reefs around the small, bordering islands Koh Yippon and Hin Yippon (9°47'54"N, 99°42'50"E) (*Fig. 1a*). The two islands are in the northern part of the Mu Ko Ang Thong Marine National Park and are approximately 35 km to the west of Koh Phangan. The coral reefs here are located in protected areas and exposed to little human influence due to the Marine National Park, founded in 1980 (White, 1991, p. 348). Tourism at the Marine National Park is limited, and diving activities are just permitted for a few parts of the park.

Field survey methods. All reefs were surveyed in water depths of 4 m and 6 m with the belt transect method or with timed-swim surveys. Surveyed reef areas covered between 2,500 to 6,000 m² for each location. The geographic positions of the survey areas were marked with GPS coordinates, but no permanent transects were installed. This means, that the same area was observed between the years and the study hereby provides an overview of the Xestospongia population dynamics at all four locations, but there are no statements about the temporal development of single sponge individuals during the survey years.

The belt transect method is commonly used for surveying impacts on benthic communities (Hill and Wilkinson, 2004). In our study, the transects were set parallel to the coastline holding the same water depth of 4 and 6 m. One transect always was 50 m in length and 5 m in width to each side resulting in a 500 m². In both observation depths, three to six transects were rolled out with a distance of approximately 5 m to each other. In more detail, during all three surveys in Haad Khom (2015.1, 2015.2, 2016), six transects were conducted at each depth (4 m and 6 m) covering in total 6,000 m². Both locations in the Marine Park were observed respectively with three transects at each depth (4 m and 6 m) during the 2015.1 surveys covering 3,000m³. A second survey in the Marine Park during 2015.2 was not initiated, because there were no signs of bleaching. During the 2016 surveys in the Marine Park three transects were accomplished at 4 m depth but only two transects at 6 m in each location (due to bad weather), covering 2,500 m².

Timed-swim surveys were conducted at Mae Haad in 2015.1 and 2016 because *Xestospongia* individuals were only found in small, clustered areas during preliminary surveys. The belt transect method was not suitable for this situation, and with timed-swim surveys, it was able to monitor a larger area (Hill and Wilkinson, 2004). The surveys were conducted by one observer snorkeling, in zig-zag and without gaps, from the shallow (4 m) to the deep (6 m). The observation time was 60 minutes, resulting in an observed area of approximately 6,000 m² per year. Due to time constraints during the 2015.2 surveys, the belt transect method was used with three transects per depth (50 m x 5 m width to each side in 4 m and 6 m) at Mae Haad, covering an area of 3,000 m².

All *Xestospongia* individuals within the transects or observed during the timed-swims were counted and measured to the nearest cm to determine the abundances and sizes. During all surveys, the observer tried their best to document all *Xestospongia* individuals, also with very small sizes.

Population densities & health status of *Xestospongia* sp.. *Xestospongia* abundance was determined by counting all observed individuals. The health status of every individual was documented and assigned to different states: “healthy” and “bleached”. “Healthy” means no signs of bleaching or other diseases, and “bleached” characterized individuals with first signs of bleaching up to fully bleached and disintegrated sponges.

Size distribution of *Xestospongia* sp.. The calculation of the *Xestospongia* biomass was based on different size measurements and corresponding volume concentrations. In detail, the height (h), the osculum diameter (od), and the base diameter (bd) of the sponges were measured in the field. The volume was afterwards calculated following McMurray et al. (2008). In this study, sponges were classified into six volume classes to simplify further presentations of the results. Size classes were determined based on noticeable changes in the volume distribution of all investigated sponges in 2015.1. The following six volume classes were chosen for this purpose: (I) 0-300 cm³, (II) 301-1,300 cm³, (III) 1,301-10,000 cm³, (IV) 10,001-30,000 cm³, (V) 30,001-100,000 cm³, and (VI) 100,001-300,000 cm³. To extrapolate *Xestospongia* size-at-age, the measured size (volume) data were analyzed using the averaged model from McGrath et al. 2018 (2018), who analyzed the growth of Indonesian *Xestospongia* sp.

Statistics. To compare sponge abundances and the ratio of healthy to bleached sponges between survey depths (4 m and 6 m), data from all sites were analyzed separately using Welch`s t-test to account for the potential lack of homogeneity (Rasch et al., 2011). Since depth had no effect on abundance and sponge health, data from both depths were pooled for further analyses. To analyze the effect of the bleaching event on sponge abundances, data from 2015.1 and 2016 were compared using a one-way repeated measures ANOVA. Abundance data from Mae Haad could not be statistically analyzed due to using the timed-swim method with no replication, but with a large observation area in 2015.1 and 2016. Statistical analyses were performed with the program SPSS (version 25).

Results

Population densities & health status of *Xestospongia* sp.. The study was initiated in 2015 to assess the abundance and the size distribution of *Xestospongia* sp. in the lower Gulf of Thailand. During the surveys, a mass mortality event of benthic organisms and fish was recognized at the study sites Mae Haad and Haad Khom, including *Xestospongia* species, the sea snail *Tectus* sp., and bleached scleractinian corals (e.g., *Pocillopora* and *Acropora*). At the beginning of the observations on 31 March, several healthy-looking *Xestospongia* individuals with a white mucus-like covering were recognized (*Fig. 2a*). During the next days, *Xestospongia* sp. showed visual bleaching signs (*Fig. 2b*), and numbers of other affected reef fauna seemed to increase.

During all surveys, mean *Xestospongia* abundances showed no significant differences (all $p>0.05$, see *Table S1*) between the survey depths of 4 m and 6 m, except during the 2015.1 surveys at Koh Yippon, where abundance was higher at 4 m ($p=0.009$) (see *Table S1*). Abundance data from Mae Haad could not be analyzed for differences in depth, due to the adjusted survey method (timed-swim) in 2015.1 and 2016. However, bleaching in 2015.2 occurred regardless of the depth in Mae Haad ($p=0.179$) and Haad Khom ($p=0.150$) (*Table S1*).

0.02 healthy *Xestospongia* individuals per m² and no bleached ones were found at Mae Haad in the 2015.1 surveys before the mass mortality event started (*Fig. 3a*). During the second survey (2015.2), 75% of all observed *Xestospongia* sp. were bleached. One year later, only 0.0003 individuals per m², both healthy-looking, were found. The number of individuals decreased by 98.4% in one year (from 2015.1 to 2016).

A similar situation was documented at the other anthropogenic impacted study site Haad Khom (*Fig. 3b*). During the first survey in 2015.1, on average 0.02 healthy-looking *Xestospongia* individuals per m² and no bleached sponges were counted per transect. During the second survey four weeks later (2015.2), the number of healthy sponges decreased with 83.6% of all observed *Xestospongia* sp. being bleached. In 2016, on average only 0.004 individuals per m² were documented, all looking healthy. The abundance of *Xestospongia* sp. had significantly ($p=0.000007$) dropped by 80.6% from 2015.1 to 2016.

The investigations on the anthropogenic non-impacted study sites in the Marine Park showed no decrease in sponge abundance at Hin Yippon (p=0.3871), but a decrease from surveys in 2015.1 to 2016 at Koh Yippon (p=0.0563) (*Fig. 3c*). The second survey (2015.2) was not conducted at these locations, because there were no signs of bleaching. At Koh Yippon, the survey in 2015.1 showed on average 0.09 *Xestospongia* sp. per m², while sponge counts in 2016 were about 1/3 lower compared to 2015.1 (on average 0.05 sponges per m²). All sponges appeared healthy during both surveys. At Hin Yippon, on average 0.060 *Xestospongia* sp. individuals per m² were documented in 2015.1, while 0.056 healthy individuals per m² were documented on average in 2016 (*Fig. 3d*).

Size distribution of *Xestospongia* sp.. At Mae Haad, the observed *Xestospongia* individuals were represented in all volume classes during 2015.1 (*Fig. 4a*). The class 1,301-10,000 cm³ was thereby most common (40 individuals). The fewest sponge numbers were found in class 100,001-300,000 cm³ (4 individuals). In the 2016 surveys, only 2 sponges in total were documented, both in class 1,301-10,000 cm³.

At Haad Khom, *Xestospongia* individuals were observed in all volume classes during 2015.1 (*Fig. 4b*). With 44 individuals, most sponges had a volume of 1,301-10,000 cm³, followed by 28 individuals in volume class 301-1,300 cm³. The highest volume class (100,001-300,000 cm³) was represented by a single sponge. In 2016, sponges were just observed in the four first volume classes, the last two classes were not found anymore. Most of the surviving sponges were in the classes 301-1,300 cm³ and 1,301-10,000 cm³ (6 and 11 sponges in total). The volume classes 0-300 cm³ and 10,001-30,000 cm³ included 2 sponges each.

The sponges at the Koh Yippon reef were present in all volume classes, and volume distribution was similar in both survey years (*Fig. 5a*). The volume class 1,301-10,000 cm³ had the highest individuals with 102 sponges in 2015.1 and 48 sponges in 2016. Volume classes 301-1,300 cm³ and 10,001-30,000 cm³ contained 54 and 51 individuals, respectively in 2015.1. The other classes had lower sponge numbers, while the class with volume 100,001-300,000 cm³ had the lowest individual count with 6 *Xestospongia* sp. in 2015.1 and a single sponge in 2016.

In Hin Yippon, every volume class was also represented in both survey years (*Fig. 5b*). In the 2015.1 surveys, the highest number was observed in volume class 1,301-10,000 cm³ with 67 individuals, followed by 42 individuals in volume class 301-1,300 cm³. With 4 individuals, class 100,001-300,000 cm³ was the one with the lowest *Xestospongia* number. In 2016, this class included 2 individuals and was therefore also the class with the lowest individual count. Volume class 1,301-10,000 cm³ was with 64 *Xestospongia* individuals the class with the highest count in 2016, followed by volume class 301-1,300 cm³ with 34 sponges.

Further, the weighted average of different growth models was applied to extrapolate the age of the observed sponges (McGrath et al., 2018). Sponges of the highest volume class (100,001-

300,000 cm³) represent ages of 17-26 years (*Fig. S1*). The smallest volume class (0-300 cm³) covers the ages 0 up to 1 year. The oldest sponge was estimated to be 24 years old and was found during the 2015.1 surveys in Haad Khom. This sponge had a volume of 236,544 cm³.

Discussion

At Mae Haad and Haad Khom, 75.6% and 83.6% of all *Xestospongia* were bleached during the 2015.2 surveys, and subsequently most of them died and did not exist anymore in 2016. The number of individuals decreased by 98.4% at Mae Haad from 2015.1 to 2016 and by 80.6% at Haad Khom (*Fig. 3*). During the survey in 2016, no remains of dead sponges were observed. Generally, bare skeletal fibers of dead sponges disintegrate within a short period of time making dead sponges difficult to detect during surveys (Webster, 2007). The massive bleaching and mortality occurred regardless of the survey depth (*Table S1*). After visible bleaching, there was a rapid decline in sponge abundances due to a dramatic mass die-off of *Xestospongia* species. Based on McMurray et al. (2011) fatal bleaching of *Xestospongia* sp. in the Caribbean usually does not result from cyclic bleaching, but can be caused by e.g. diseases and other pathogens. According to our observations, the mortality event in 2015.2 was not a specific sponge disease as numerous *Xestospongia* individuals and other sponge species started to bleach. During the surveys, the mortality of further marine fauna was documented, including numerous individuals of the sea snail *Tectus* sp., fish, crustaceans, and as well as bleached scleractinian corals and other sponges (P-J Grammel and E Schoenig, 2015, pers. comm.). Taken these observations into account, the mass mortality event could have had various reasons. Having numerous other species from different phyla affected, could most likely indicate two possible scenarios for this mortality event: a heatwave or a local harmful algal bloom (HAB). Mass mortality events affecting species from various phyla have been reported from the Mediterranean Sea as a result of marine heatwaves with increased sea water temperatures (Garrabou et al., 2022, 2009; Rubio-Portillo et al., 2016). Studies from other locations have reported increased water temperatures due to El Nino Southern Oscillation in 2015/2016, which affected marine organisms and resulted likewise in bleaching and mortality (Head et al., 2019; Rubio-Portillo et al., 2016). The Gulf of Thailand also recorded higher water temperatures in 2015 (NOAA National Centers for Environmental Information, 2016). Nevertheless, the mass mortality event was only a local phenomenon. Only sponges at the two monitored reefs of Koh Phangan were impacted, while no affected sponges were found at the same water depths at the monitored reefs of Koh Yippon and Hin Yippon. Considering these circumstances, it becomes most likely that the mass mortality event may have been triggered by a local HAB. In general, HAB events are increasing rapidly in density, distribution, and intensity, and most coasts worldwide are nowadays threatened (Bauman et al., 2010; Gobler et al., 2017; Xiao et al., 2019). This is caused amongst others by climate change and increasing nutrient pollution (Gobler, 2020; Heisler et al., 2008). HABs are caused by toxic microalgae or cyanobacteria, which can lead during outbreaks to illness and death of fish, other marine invertebrates, seabirds, and even humans (Starr et al., 2017; Young et al., 2020). Sponges are important for benthic-pelagic coupling as they filter large amounts of water (up to 1,000 $L*h^{-1}*kg^{-1}$ body mass, (Vogel, 1977)). This in turn could make them also very susceptible to HABs, by retaining the microalgae and thereby accumulating the produced toxins, leading ultimately to the death of the affected sponges (Anderson, 2007). In 2015, HAB events were reported for other regions around the world, including the U.S. West Coast, coastal areas in Northern Europe, and Canada (Karlson et al., 2021; McCabe et al., 2016; McKenzie et al., 2021). For example, the HAB at the U.S. West Coast was a coastwide event, negatively impacting fisheries and initiated by anomalously warm water conditions (McCabe et al., 2016; Moore et al., 2020). At our study site in Mae Haad, Stuhldreier et al. (2015) reported run-off by a small river in the bay with sewage water discharges from bungalows. Subsequent analyses of the river water showed high phosphate concentrations. This could indicate that the river is a possible land-based source of increased nutrient input. Both, increased nutrient pollution and increased water temperatures due to El Nino Southern Oscillation, could be possible triggers for a HAB outbreak resulting in the observed mass mortality of *Xestospongia* sponges. But it is difficult to determine the reason for the sponge mortality event because environmental parameters such as nutrients, pH, salinity were not taken, due to a lack of analytical capabilities in 2015. Therefor we can only speculate on the cause of this mortality event. Rosenfeld (2021, unpublished data) compared different environmental parameters around five sites on Koh Phangan in 2019, including reefs in Mae Haad and Haad Khom. Differences in environmental parameters (pH, NOx, and PO_4^{3-}) were rather small between the bays ranging in pH from 7.95 to 8.12, in NOx from 2.44 to 2.91 µmol L^{-1}, and for PO_4^{3-} from 1.52 to 1.73 µmol L^{-1}. However, analysis of Mae Haad river, which discharges into Mae Haad bay showed very high nutrient levels with 7.24 µmol L^{-1} for NOx and 6.06 µmol L^{-1} for phosphate. Such high nutrient levels could certainly promote algae blooms at Mae Haad, although we do not know if such high nutrient levels were also present in 2015 during the mass mortality event. Monitoring programs and management actions in Koh Phangan are needed in the future to detect possible (human) impacts and to reduce negative consequences on ecosystem health. Sponge mortality events have also been reported by Stevely and colleagues (2011) from the Florida Keys. They observed widespread sponge mortality of various sponge species which occurred together with cyanobacterial blooms, the likely cause of the observed mortality. They also documented long-lasting ecological consequences for the recovery of sponge communities for more than one decade.

However, the anthropogenic non-impacted reefs of Koh Yippon and Hin Yippon showed just little changes in the abundance of *Xestospongia* sp. between the years 2015 and 2016. The variances could be caused by possible differences in the position of the transect tapes between the two surveys, as permanent transects could not be installed in the marine park. The missing of one transect at a depth of 6 m during the survey in 2016 could also have a possible impact. However, the anthropogenic non-impacted study sites represented in both study years populations with a higher number of observed *Xestospongia* sp. than at the anthropogenically impacted locations. A decline in sponge health was not detected during the surveys at both

Marine Park locations. These facts lead to the assumption that anthropogenic impacted coral reefs were more in change than non-impacted coral reefs. This underlines the importance to establish and enforce protected Marine Parks for maintaining healthy ecosystems.

Regarding the size distribution of *Xestospongia* sp., sponge sizes (according to volume classes) showed a similar Gaussian distribution at all study sites in both survey years. The total number of *Xestospongia* sp. increased from the class with the smallest volume (0-300 cm^3) to a class of the middle (always the class 1,301-10,000 cm^3) and then decreased again when it comes to higher volumes. In other words, the highest counts of *Xestospongia* sp. were found for all study sites at the middle class 1,301-10,000 cm^3. The lower number of small individuals could be, for example, caused by a higher risk of being eaten by predators. Larger individuals are probably more often affected by environmental factors over time due to their higher age (Smith and Smith, 2009). The mass mortality event also showed its effects on the size distribution. Only two sponges of the previously dominant middle volume class were still alive at Mae Haad in 2016. At Haad Khom, *Xestospongia* individuals within the small and middle classes survived after the massive bleaching. The results show that sponges of all sizes were affected by the mass mortality event. This means that an extraordinary event took place for the region in northern Koh Phangan, because large sponges, which are robust organisms and should have the ability to survive cyclic bleaching, were gone in 2016.

To estimate the age of sponge individuals, size-at-age models have been used in earlier studies. Reports from Caribbean *Xestospongia muta* revealed ages of 127 years, and estimated the largest sponges on these reefs to be more than 2,300 years old, reflecting *Xestospongia* spp. as a long-lived and slow-growing sponge species (McMurray et al., 2008). Contrary and more recently, McGrath et al. (2018) found Indo-Pacific *Xestospongia* spp. from Sulawesi, Indonesia, to be faster growing than their Caribbean relatives. We used the parameter from the growth model from McGrath et al. (2018) to estimate the age of our sponges, since they are both Pacific populations and represent more likely the same species. The largest measured individuals of the investigated *Xestospongia* sp. in our study (2015.1 at Haad Khom) were up to 24 years old (*Fig. S1*). One year later, the oldest sponge at the same location was only 9 years old. Sponges of the middle volume classes, which were most abundant and survived the bleaching, were around 3-7 years old. Demographic studies on *Xestospongia* spp. are complicated since molecular studies have recently shown that the three different *Xestospongia* species described in the Atlantic and Indo-Pacific are part of a more complicated species complex (Evans et al., 2021; Swierts et al., 2017). Morphologically similar species occur apparently sympatrically and might feature differences in growth performance.

Conclusions

This study documented an extraordinary massive mortality event of *Xestospongia* populations from two reefs of Koh Phangan, Thailand. *Xestospongia* sp. mortality ranged from 98.4% at Mae Haad to 80.6% at Haad Khom (between monitoring events in 2015 and 2016). Study sites at the Mu Ko Ang Thong Marine National Park were not affected. This localized mortality event was probably triggered by a local HAB or undetected local higher water temperatures. *Xestospongia* sp. of all sizes were affected. Due to their large size they add complexity to the 3D reef structure and provide several ecological services, such as water filtration (McMurray et al., 2014, 2010). The lack of *Xestospongia* sp. following the mass mortality event in the two surveyed bays, could lead to a decrease in biodiversity, a weaker filter efficiency and loss of 3D complexity and function (e.g., habitat and shelter) of the reefs. The enormous loss of *Xestospongia* sp. in Mae Haad and Haad Khom could also have serious long-term consequences for the sponge populations and for the coral reefs in these locations, as reproduction and recruitment patterns for this species are unknown. Therefore, it will be important to determine and reduce triggers of such mass mortality events, especially for essential habitat-forming organisms such as *Xestospongia* spp.

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In memory of our colleague Eike Schoenig, who passed away during the writing of this manuscript. As founder of CORE sea, he was a role model of dedication and commitment to the protection of coral reefs. As an adviser and teacher for students, he left a legacy for many to follow his lead. He was a pioneer in marine research of Koh Phangan and essential in conducting this research project and supporting the students working on it. We are very grateful to him for all his support on this study.

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Figure 1

Map of the study sites.

The study sites within the Mu Ko Ang Thong Marine National Park are shown in a), and b) shows the two study sites on the island of Koh Phangan.

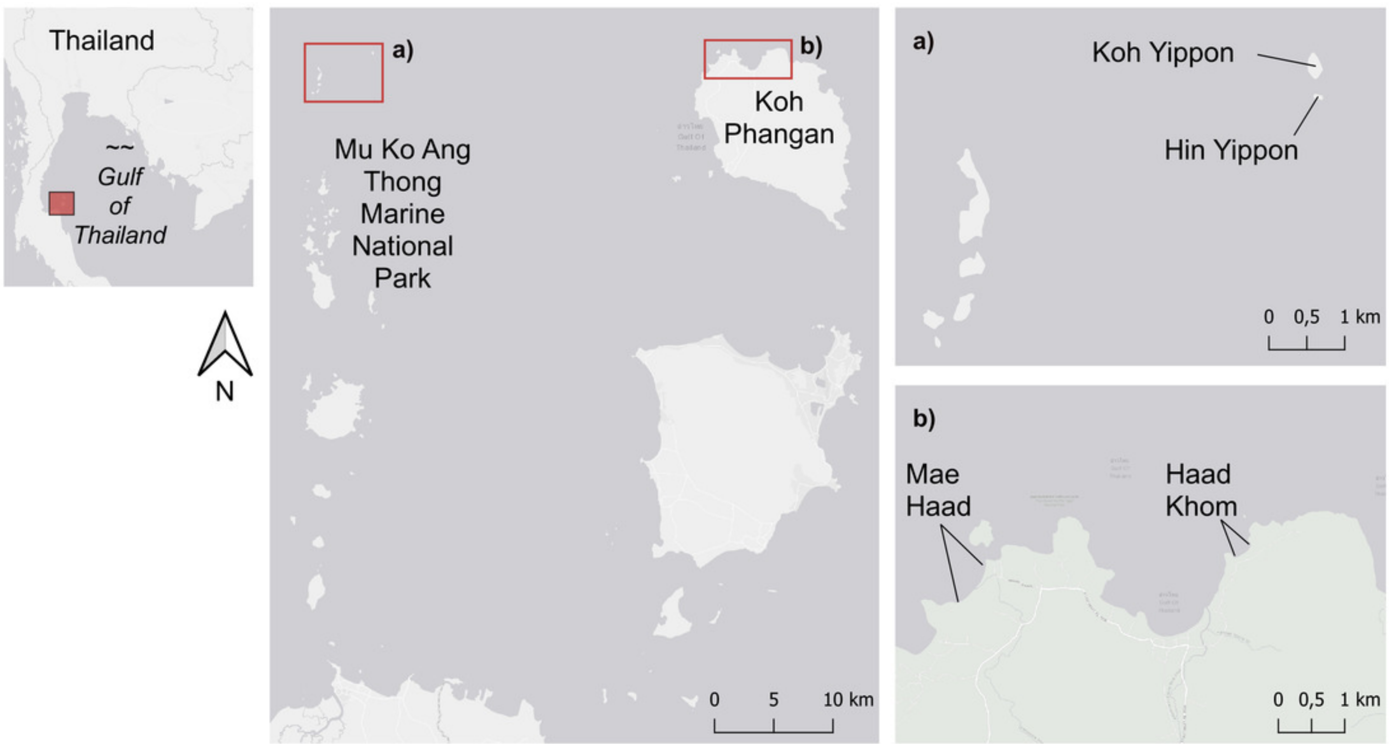


Figure 2

Impacted *Xestospongia* sp.

Examples of observed *Xestospongia* individuals with a) mucus-like covering and b) bleaching signs during the studies in 2015.2 at Haad Khom and Mae Haad.

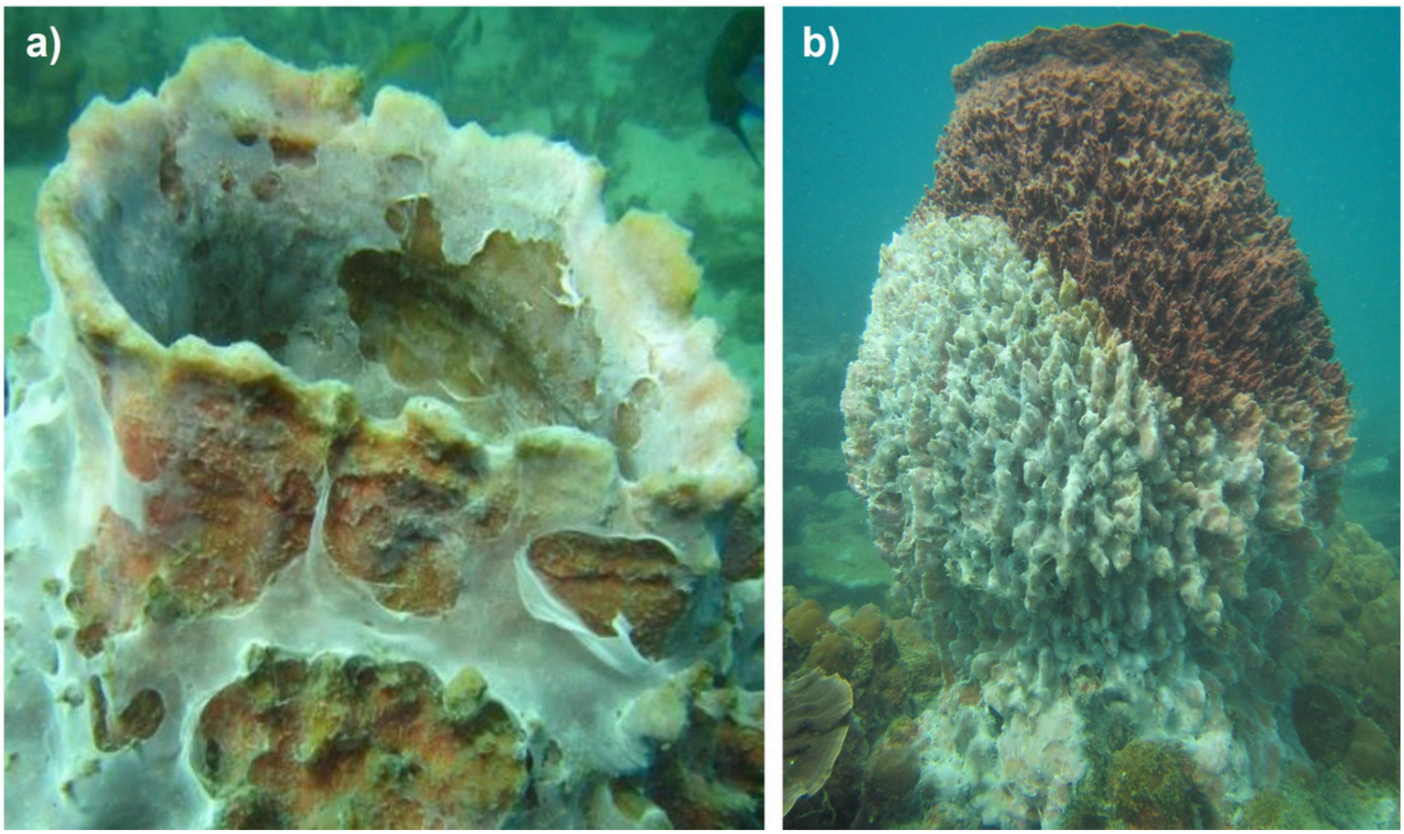


Figure 3

Xestospongia sp. numbers and fitness status from all locations in the years 2015 and 2016.

The x-axis shows the time of the surveys, separated in pre- (2015.1), peri- (2015.2), and post- mass mortality event (2016). For all locations, the sponge numbers per m^2 are shown. Different bar colors represent the fitness status: healthy (yellow) and bleached (grey). The standard error of the mean *Xestospongia* counts per transect is given with error bars. The asterisk (*) indicates a significant difference from 2015.1 to 2016 with $p<0.05$ (repeated measures ANOVA).

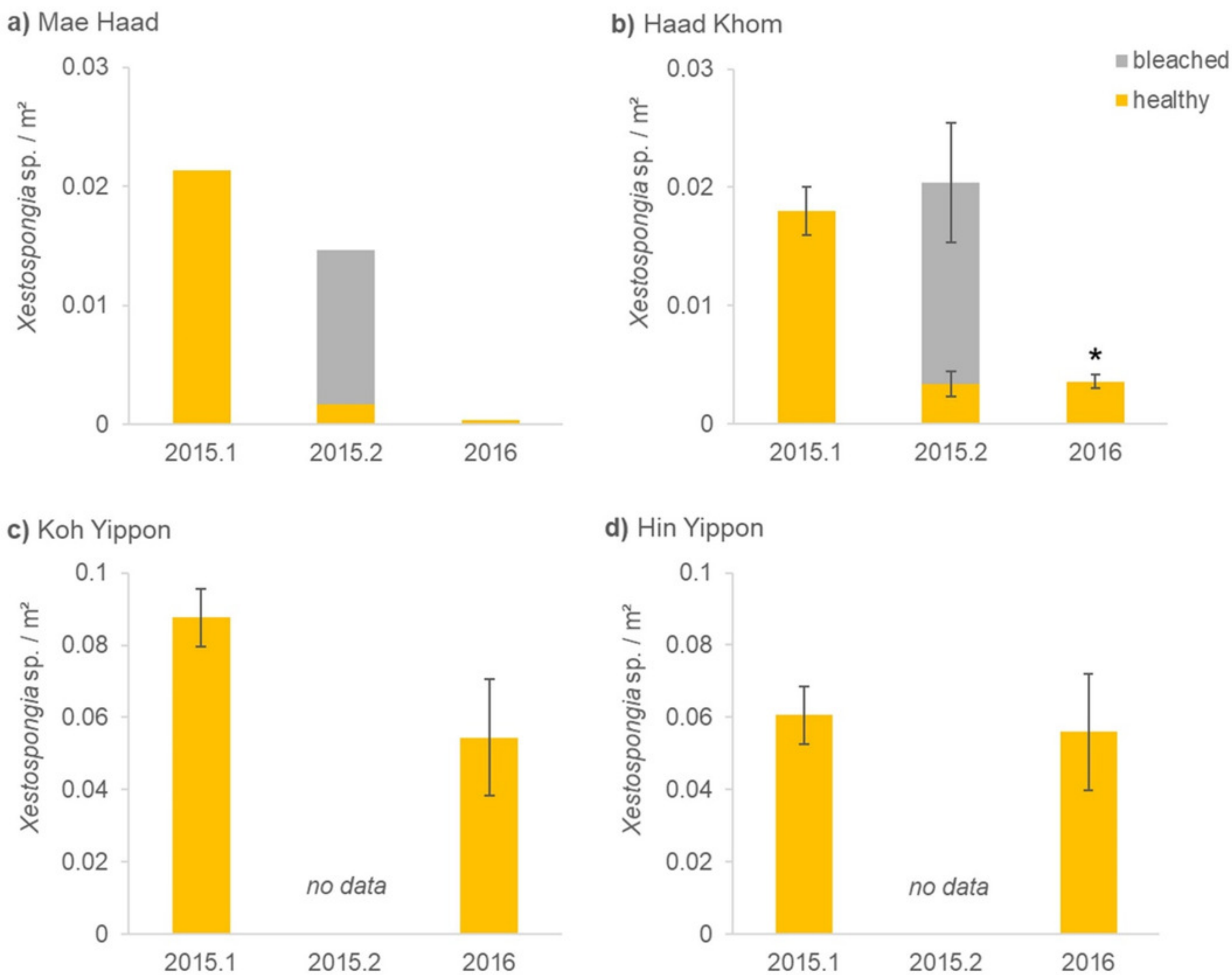

a) Mae Haad
b) Haad Khom
c) Koh Yippon
d) Hin Yippon
bleached
healthy
Xestospongia sp. / m²
0.03
0.02
0.01
0
0.1
0.08
0.06
0.04
0.02
2015.1
2015.2
2016
*
no data

Figure 4

Size distribution of *Xestospongia* sp. at Mae Haad and Haad Khom in the years 2015 and 2016.

The x-axis shows the sponge volume classes, and the y-axis shows the total number of sponges at an area of 6,000 m^2 in Mae Haad (a) and Haad Khom (b). Size distribution is shown for the surveys in 2015.1 (pre-mortality in dark grey) and 2016 (post- mortality in light grey).

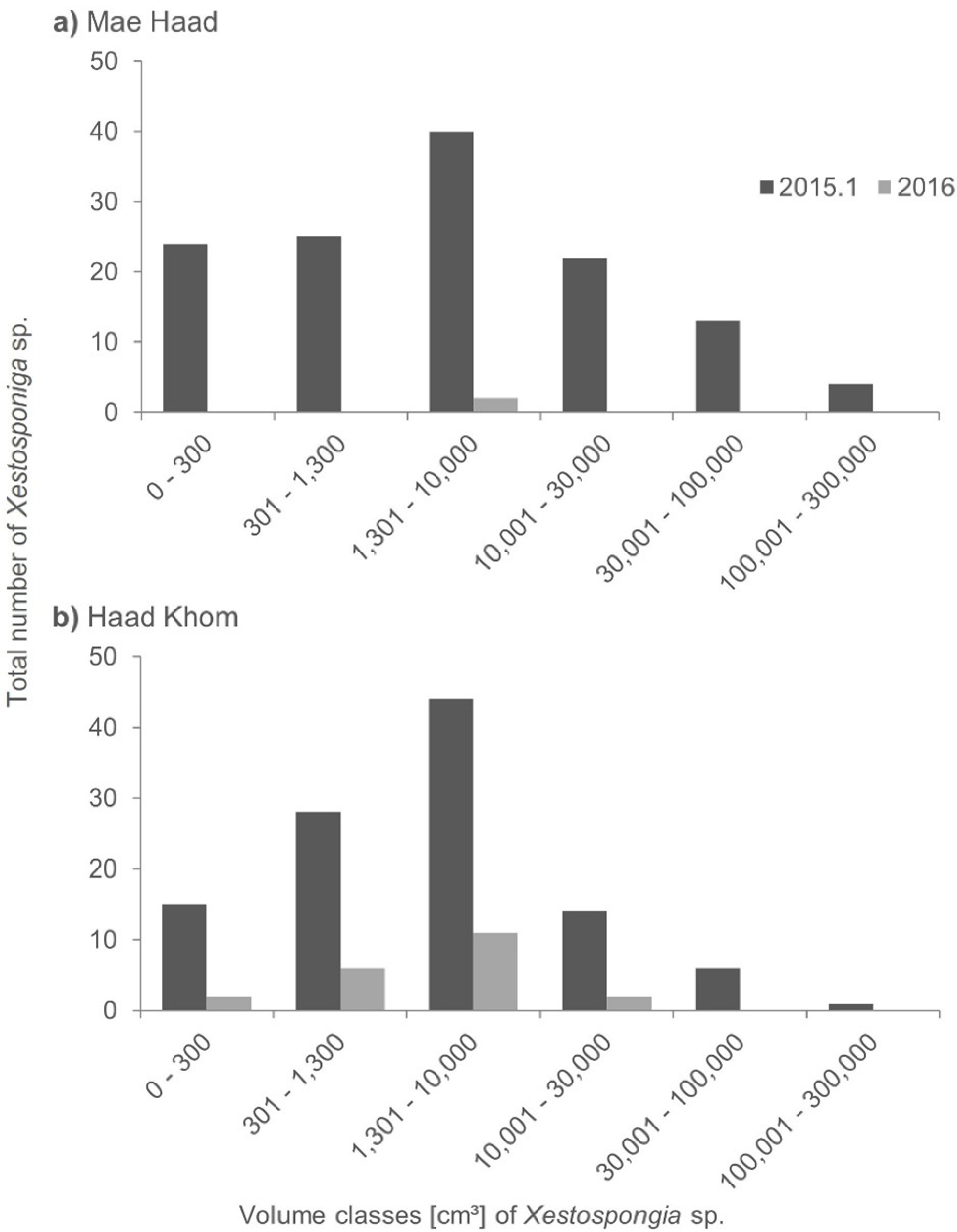
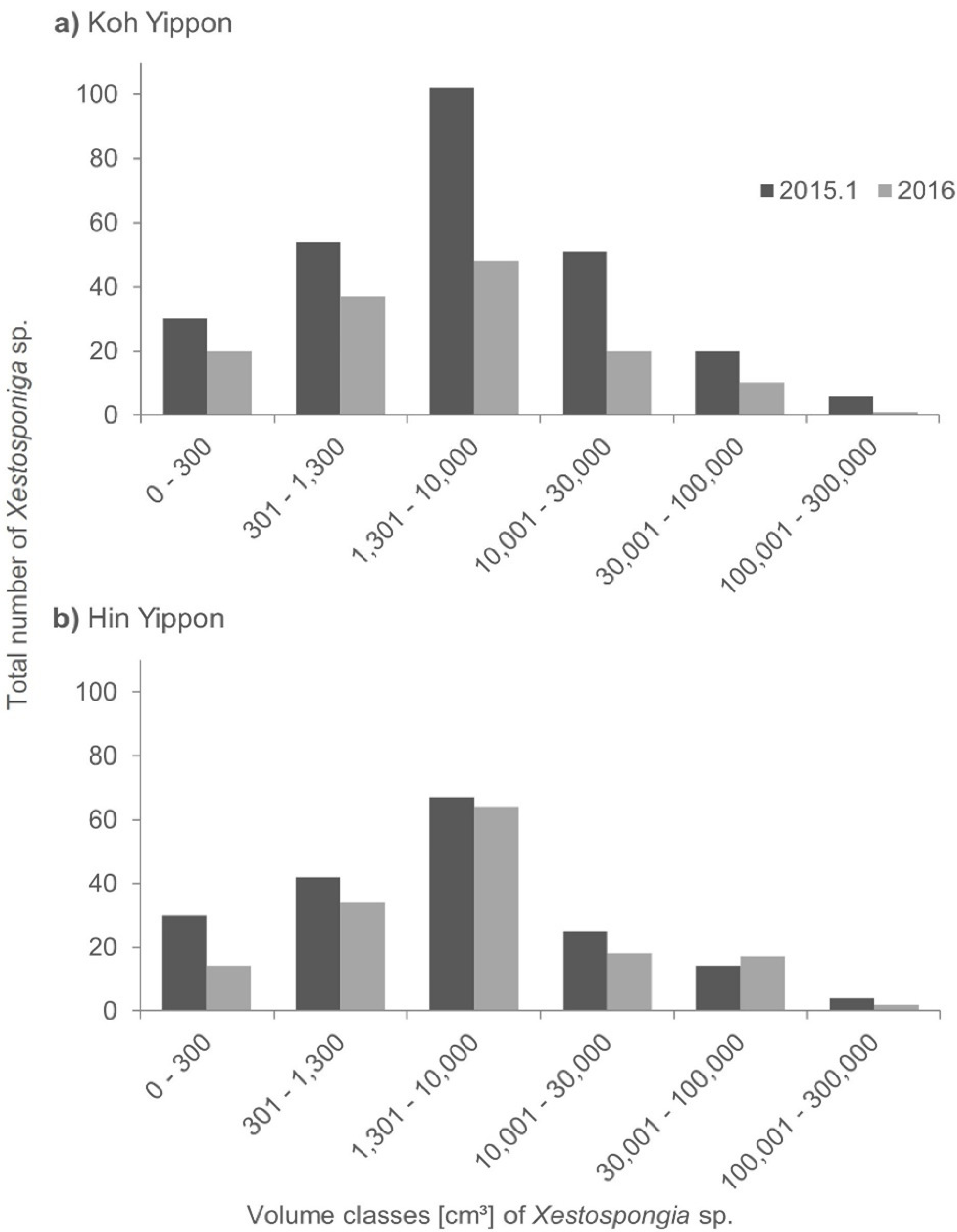

a) Mae Haad
b) Haad Khom
Total number of Xestosponiga sp.
2015.1
2016
50
40
30
20
10
0
0 - 300
301 - 1,300
1,301 - 10,000
10,001 - 30,000
30,001 - 100,000
100,001 - 300,000
Volume classes [cm³] of Xestospongia sp.

Figure 5

Size distribution of *Xestospongia* sp. at Koh Yippon and Hin Yippon in the years 2015 and 2016.

The x-axis shows the sponge volume classes, and the y-axis shows the total number of sponges in an area of 3,000 m^2 (2,500 m^2 in 2016) in Koh Yippon (a) and Hin Yippon (b). Size distribution is shown for the surveys in 2015.1 (pre-mortality in dark grey) and 2016 (post-mortality in light grey).


a) Koh Yippon
b) Hin Yippon
Total number of Xestosponiga sp.
2015.1
2016
100
80
60
40
20
0
0 - 300
301 - 1,300
1,301 - 10,000
10,001 - 30,000
30,001 - 100,000
100,001 - 300,000
Volume classes [cm³] of Xestospongia sp.