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ORIGINAL PAPER

Association of *Waminoa* sp. (Acoela) with corals in the Wakatobi Marine Park, South-East Sulawesi, Indonesia

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Abstract This is the first quantitative study on the prevalence of epizoic *Waminoa* sp. acoel worms and their association with corals in the Wakatobi Marine National Park (WMNP), South-East Sulawesi, Indonesia. Three replicate transects were laid on the reef crest, flat and slope at six sites in 2006 and eight sites in 2007. Four of the sites were common in both years. In total 69 transects were surveyed in 2006, and 87 transects in 2007. A total of 4.8% of all observed hard corals were associated with acoel worms in 2006 and 2.6% of hard and soft corals in 2007. Acoels were present on 16 and 21 of the coral taxa studied in 2006 and 2007 respectively. The worms were strongly associated with the azooxanthellate coral *Tubastrea* spp. and were rare or absent on the most abundant coral genera *Montipora* and *Porites*. The mean number of corals having acoels was highest on reef slopes, whereas acoels were virtually absent on reef flats. Corals that had a high and a medium cover of worms were more common in 2007 than in 2006. No significant trend in the adaptation of the zooxanthellae of *Waminoa* sp. to different depths at different sites was revealed. The impact of the worm on the coral is unknown, but high numbers may have a shading effect and a negative impact on the coral's photophysiology. This acoel merits more study of its life cycle, its photophysiology, and its impact on its host corals.

Introduction

The Acoela comprises small, 0.5–10 mm long, soft-bodied worms (Hooge et al. 2002), which typically have a central syncytium instead of an epithelia-lined gut (Tyler 2003). Molecular systematists suggest that the Acoela is the most basal group of the bilaterian triploblasts (Ruiz-Trillo et al. 1999, 2004) and have raised the group containing the Acoela plus the Nemertodermatida, that is the Acoelomorpha, to phylum level (Baguñá and Riutort 2004). To date, over 340 species of acoels have been described, and these are divided into 21 families (Tyler et al. 2005). Three of these families comprise species with symbiotic unicellular algae, namely Convolutidae, Sagittiferidae, and Haploposthiidae (see Hooge et al. 2002; McCoy and Balzer 2002). We studied an undescribed species of such symbiotic acoels, a species that would be classified in the genus *Waminoa*, which Ogunlana et al. (2005) recently assigned to the family Convolutidae.

Acoels are common in littoral, sublittoral and pelagic environments and can be found in temperate as well as tropical habitats (McCoy and Balzer 2002). Five species have been identified to be associated with corals. *Waminoa*

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litus Winsor, 1990, was found in Australia and in Micronesia. *Convolutriloba hastifera* Winsor, 1990, was found on an unnamed coral from the vicinity of Townsville, Australia. *Waminoa brickneri* (Ogunlana et al. 2005) was found to be associated with at least 14 species of corals in the Red Sea (Barneah et al. 2004). Three species of *Convolutriloba* have been discovered in aquaria: *C. retrogemma* (Hendelberg and Åkesson 1988), *C. longifissura* (Bartolomaeus and Balzer 1997) and *C. macropyga* (Shannon and Achatz 2007). Coral-associated acoels can cover corals in relatively large numbers and are often sufficiently conspicuous to make the coral appear spotted (Ogunlana et al. 2005). Trench and Winsor (1987) suggested that the coral-associated acoels could be a benthic phase in a life cycle involving pelagic individuals that have been identified as species of *Haplodiscus*.

Environmental factors are probably important in determining the reproductive state of the worms: it is known that the development and maintenance of the female reproductive system in turbellarians can be affected by exogenous factors, among which seasonal factors and particularly temperature may cause the alternation between sexual and asexual states (Ax 1977). Asexual reproduction has been documented for *Waminoa* (O. Barneah, personal observation). Sexual reproduction may be seasonal (Barneah et al. 2007a). Sexual reproduction was observed in *Convolutriloba macropyga* but copulation is yet to be described (Shannon and Achatz 2007).

The abundance, distribution, and physiology of coral-associated acoels remain poorly known, and their effects on the host corals have not been determined. *Waminoa* spp. worms may reduce the host coral's photosynthesis by shading (Barneah et al. 2007b) particularly when the coral's surface is more than 50% covered by worms. Evidence of the mucus acting as a possible food source was found when the soft coral *Stereonephthya cundabiluensis* lacked a mucus layer when it harboured flatworms, while colonies without acoel worms possessed a layer of mucus (Barneah et al. 2007b). Worms do not appear to consume coral tissue, since no nematocysts were found in their digestive system (Ogunlana et al. 2005).

Haapkylä et al. (2007) documented the occurrence of acoels on corals in the WMNP in Indonesia for the first time during a coral-health survey conducted in 2005. In the present study we investigated what we believe to be a single species of *Waminoa* in the WMNP. We have studied the prevalence of acoels on corals through 2006 and 2007, determined specific associations of the worms with different coral taxa, investigated their habitat preference and percentage area of host corals covered by them as well as their photophysiology. To the best of our knowledge, this is the first study on *Waminoa* sp. and their specific interaction with corals from Indonesia.

Materials and methods

Study site

The WMNP is the second largest marine national park in Indonesia and covers an area of 1.39 million hectares. It is situated in the Tukangbesi Island region between the Banda and Flores Seas, South-East Sulawesi (3°–6°S and 120°45′–124°06′E) (Fig. 1). Indonesian coral reefs are among the most diverse in the world (Allen 2007). The WMNP is situated in the Global Biodiversity Hotspot with 396 species of hermatypic scleractinian corals belonging to 68 genera and 15 families recorded (Turak 2003). In addition, 10 species of non-scleractinian or ahermatypic hard coral species and 28 soft coral genera were added to this list (Pet-Soede and Erdmann 2004).

Prevalence of acoels, their distribution and association with corals and the percentage of surface area covered by the worms were determined in two consecutive years. In 2006, six sites located around the islands of Hoga and Kaledupa were surveyed, and in 2007, eight sites (Fig. 1). The fringing reefs at these sites range in depth from <1 m to approximately 35 m and are situated between 500 m and 1 km offshore. Sampling was conducted between 3 July and 28 August 2006 and between 30 June and 2 September 2007.

Survey method

Surveys were conducted using belt transects (English et al. 1997) covering an area of 20 m × 1 m (0.5 m on each side of the transect line) in 2006 and 20 m × 2 m (1 m on each side of the transect line) in 2007. Three replicate transects were laid on the reef crest (3–7 m depth), flat (1–3 m depth) and slope (8–12 m depth). A total of 69 transects were surveyed in 2006 and 87 transects in 2007. Transects followed the depth contour of the reef. The first transect was located randomly to satisfy assumptions about the independence of data for statistical analysis. The additional transects were located at randomly derived distances from the first transect but always >20 m to ensure independence and to detect site specific trends and variances.

Each coral colony within the belt was counted and recorded to the genus level. A distinction between corals without flatworms and corals with flatworms was noted. The percentage of flatworms covering the coral's surface was estimated as low ($\leq$30%), medium (30–70%) and heavy ($\geq$70%). Data were expressed both as incidence (number of flatworm-associated colonies per site) and prevalence (proportion, or percentage, of flatworm-associated colonies per site). Prevalence of flatworms was calculated by dividing the number of colonies associated with flatworms by the total number of coral colonies. Means and

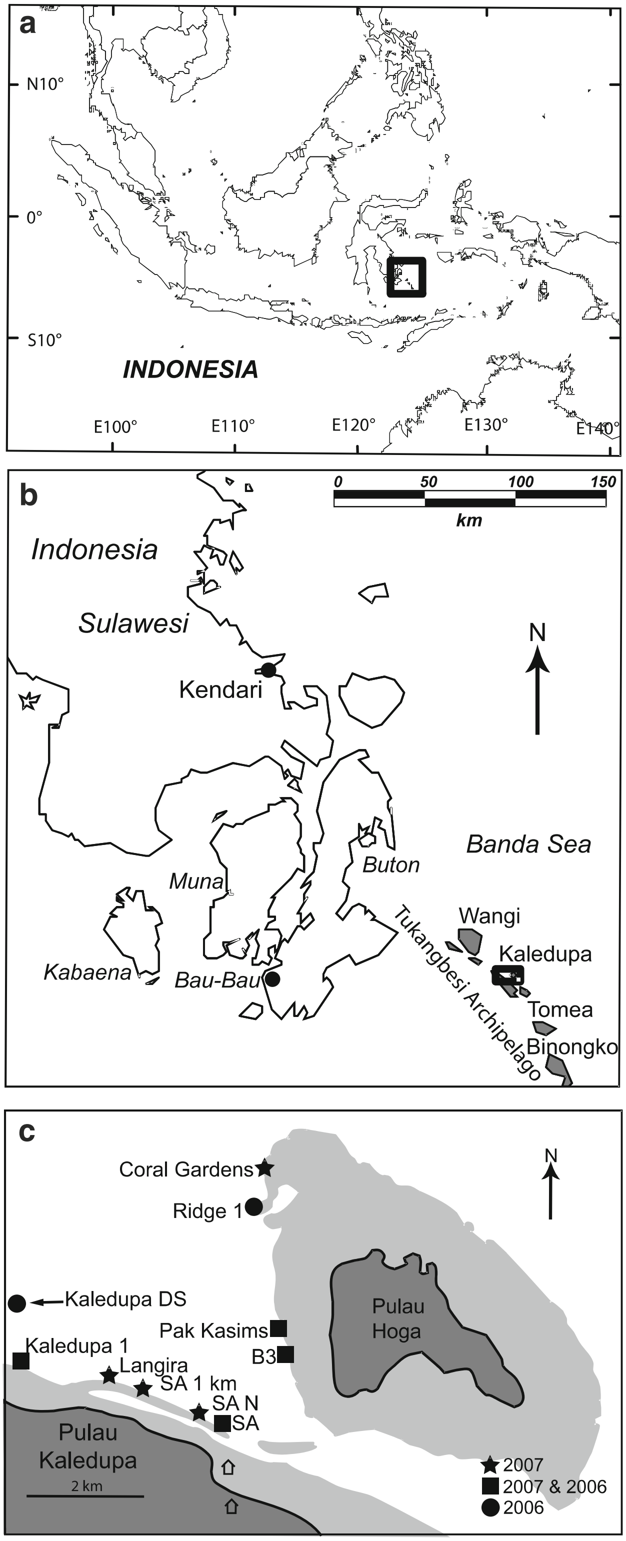

Fig. 1 Map of survey sites. **a** southeast Sulawesi marked with a rectangle; **b** WMNP includes Tukangbesi Archipelago: Wangi, Kaledupa, Hoga (*rectangle* near Kaledupa), Tomea and Binongko Islands; **c** survey sites used in 2006 and 2007 around Hoga Island. Areas with *light shading* represent reef flats around Hoga and Kaledupa Islands. Symbols show sites sampled in 2006, 2007, or both years

standard errors were calculated from all three transects at each depth at each site. All percentage data were arcsine transformed before analysis. For all statistical tests, any assumptions were tested prior to analysis. The significance level used was 0.05 except in cases where more than one analysis was conducted on the same data set, in which case the significance level was Bonferroni corrected to $\alpha' = \alpha/n$ where n was the number of tests performed.

Flatworm identification

Worms were collected from three sites (Buoy 3, Kaledupa Double Spur and Ridge 1) and observed in a laboratory under a light microscope at up to 400× magnification and photographed in situ. Photographs were compared to worms that had been found in the Red Sea. A further histological investigation was carried out. Worms were preserved in 4% formaldehyde in seawater and put into 2% liquid agarose gel. After the gel solidified it was dehydrated in a graded series of ethanol and butanol and embedded in paraffin. Serial sections 8 μm thick were cut using an MIR microtome. Sections were stained with Delafield Hematoxylin–Eosin. Zooxanthellae could clearly be seen on the pictures taken of the histological sections. The size of the worms ranged between 3 and 5 mm in diameter and did not depend on the habitat. None of the sectioned worms were mature, so identification to species was not possible; nonetheless, the features observed in live and sectioned worms were consistent with their being a single species of *Waminoa*. Several formalin-preserved specimens have been saved by O. Barneah.

Flatworm photophysiology: FIRe fluorometry

A total of 33 acoel worms were collected from different host corals between depths of 4 and 18 m at six sites (Ridge 1, Buoy 3, Kaledupa 1, Pak Kasims, Langira and Sampela). An ANOVA was performed to test for any photophysiological differences between acoels. Forty-one worms from the same six sites and same depth range were tested to see if their photophysiology differed with site and depth. Worms were detached by squirting water from a plastic pipette onto the host coral. A Fluorescence Induction and Relaxation (FIRe) fluorometer (SATLANTIC) was used to assess chlorophyll a fluorescence as described by Suggett et al. (2008). Flatworms were dark-adapted for 45 min at 26°C prior to experimentation. A fibre optic attachment was used to assay sample photophysiology, by placing the fibre optic tip on flatworms held in petri dishes over matt black cloth. Headspace between the cable tip and the worms was constant (1 mm). Reference excitation files were made specifically for fibre optic use at gains ranging from 0 to 1,200 at 100 unit increments.

Table 1 Observed and expected frequency of *Waminoa* sp. on coral colonies assuming no association with coral genus

Taxonomic group	2006			2007		
	Observed	Expected	χ^2	Observed	Expected	χ^2
Soft corals				25	77.0	35.1[b]
Porites massive	0	41.2	41.2[b]	0	51.3	51.3[b]
Montipora	11	49.5	30.0[b]	7	45.8	32.9[b]
Porites branching	0	28.4	28.4[b]	1	39.1	37.2[b]
Favia/Montastrea	2	17.6	13.9[b]	3	18.1	12.6[b]
Tubastrea	231	27.8	1483.8[a]	272	18.0	3589.3[a]
Fungia	0	3.8	3.8	3	14.0	8.6[b]
Pavona	9	15.2	2.5	5	13.2	5.1[b]
Platygyra/Goniastrea	3	8.4	3.5	4	9.8	3.4
Favites/Echinopora	1	9.2	7.3[b]	2	7.3	3.9[b]
Acropora bushy	0	5.9	5.9[b]	0	7.1	7.1[b]
Cyphastrea/Diploastrea	3	9.2	4.2[b]	6	6.3	0.0
Pachyseris/Gardinoseris	4	7.5	1.6	2	5.5	2.2
Goniopora/Alveopora	21	4.6	58.4[a]	12	5.4	8.0[a]
Others	19	75.6	42.4[b]	25	49.1	11.8[b]
Total			1726.8			3808.5

[a] Significant positive relationship

[b] Significant negative relationship

Results

Histological results confirmed that the subject of our study was a single species of acoel from the genus *Waminoa* with clearly distinguishable zooxanthellae. The worms had two algal symbionts like the *Waminoa* in the Red Sea. Of the 6,272 coral colonies examined in 2006, 304 (4.8%) had *Waminoa* sp. living on their surface, and all of these acoels on all of the coral hosts had a morphology consistent with an identification of *Waminoa* sp. In the following year, a larger sample of 14,147 different coral colonies were examined, and 367 (2.6%) of these were associated with the same *Waminoa* sp. (S1a and S1b).

Waminoa sp. were found on 16 and 21 of the 41 coral taxa recorded in the 2006 and 2007 samples respectively (S1b). In both years acoels were not distributed independently of coral taxa (2006: $\chi^2 = 1726.8$, $df = 13$, $P < 0.001$; 2007: $\chi^2 = 3808.5$, $df = 14$, $P < 0.001$). *Waminoa* sp. were strongly associated with *Tubastrea* spp. colonies, and rare or absent on the most abundant coral taxa (Table 1). In 2006 and 2007, 74 and 76% respectively of all flatworm-associated coral colonies encountered were *Tubastrea* spp. colonies. Similarly, 40% and 39% of all *Tubastrea* colonies encountered in 2006 and 2007 respectively were associated with *Waminoa* sp. In addition there was a weaker positive association between flatworms and *Goniopora*/*Alveopora* colonies (Table 1).

The reef crests and slopes of Buoy 3 were the most distinctive coral communities of all the study sites as they had an unusually high abundance of *Tubastrea* spp. colonies compared with other sites (Fig. 2). Buoy 3 included 78.4% ($n = 574$) of all *Tubastrea* spp. colonies encountered in the 2006 sample and 87.9% ($n = 693$) in the 2007 sample. Not surprisingly, the mean proportion of colonies associated with flatworms varied significantly with site in both 2006 and 2007 samples, with by far the highest percent associations occurring at Buoy 3 (S2, Fig. 2). Tukey post-hoc tests revealed that the only significant inter-site differences in coral-associated flatworms in both years were between Buoy 3 and the other sites. Flatworms were virtually absent from reef flats (only five flatworm-associated colonies were ever encountered on reef flats in both years). The mean proportion of colonies associated with flatworms on reef slopes was significantly greater than that on reef crests in both 2006 and 2007 samples (S2, Fig. 3).

At the four sites where surveys were repeated in both years (Buoy 3, Kaledupa 1, Pak Kasim's and Sampela) there was no consistent or significant change in the percentage of *Tubastrea* and *Goniopora*/*Alveopora* colonies associated with flatworms between 2006 and 2007 (Wilcoxon signed ranks test: $z = -1.15$, $P = 0.25$).

Corals with heavy flatworm cover (flatworms covered $\geq$70% of the 'host' coral colonies' surface area) were comparatively rare, accounting for less than 12% of associated colonies (S3). However, the level of association did appear to differ between years, and may have been expected to differ between favoured coral taxa (i.e. *Tubastrea* and *Goniopora*/*Alveopora*) and non-favoured taxa (i.e. all other taxonomic groups). To test for association between level of flatworm cover (heavy, medium and light; S3), year and favourability of 'host' taxa, we fitted a loglinear model to the frequency data from Buoy 3, Kaledupa 1, Pak Kasim's and Sampela using a backward elimination method. The best model only included one interaction term

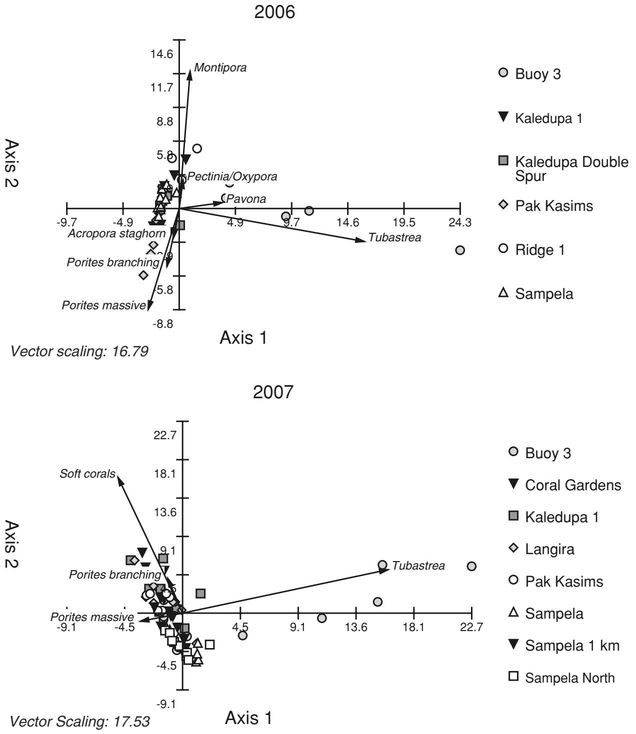

Fig. 2 PCA biplots of coral community data for each transect in 2006 and 2007. Axes 1 and 2 accounted for 68.1 and 59.5% of the variation in community composition in 2006 and 2007 respectively. Vectors labeled with coral genera show genera most influential in determining the variation. Five transects furthest down the *Tubastrea* spp. vector are transects from the crest and slope of Buoy 3 (*shaded circles*)

year × flatworm cover level (Model $\chi^2 = 4.1$, $df = 5$, $P = 0.54$; change in χ^2 if term removed = 10.0, $df = 2$, $P = 0.007$) showing that there was a significant association between cover level and year, but none between host favourability and cover level. Heavy and medium flatworm cover was more common in 2007 than in 2006 (S3).

The photophysiology of the acoel worms was tested between sites, depths and coral species. No significant results were found between the sites and depths (photochemical efficiency $F_{5,35} = 2.07$, $P = 0.09$, effective absorption $F_{5,35} = 0.88$, $P = 0.51$, electron turnover $F_{5,35} = 1.35$, $P = 0.27$) or host coral (photochemical efficiency $F_{4,28} = 1.56$, $P = 0.21$, effective absorption $F_{4,28} = 2.63$, $P = 0.06$, electron turnover $F_{4,28} = 1.18$, $P = 0.34$).

Discussion

The data suggest that the distribution of coral-covering flatworms among sites and positions was strongly determined by the distribution of the favoured 'host' corals, namely the azooxanthellate *Tubastrea* spp. This is the first time the worm has been recorded on an azooxanthellate coral. The occurrence of these flatworms on an azooxanthellate coral further strengthens the assumption that the worms do not utilize the coral's symbiotic algae or acquire their algal symbionts from the host coral (Barneah et al. 2007a, b).

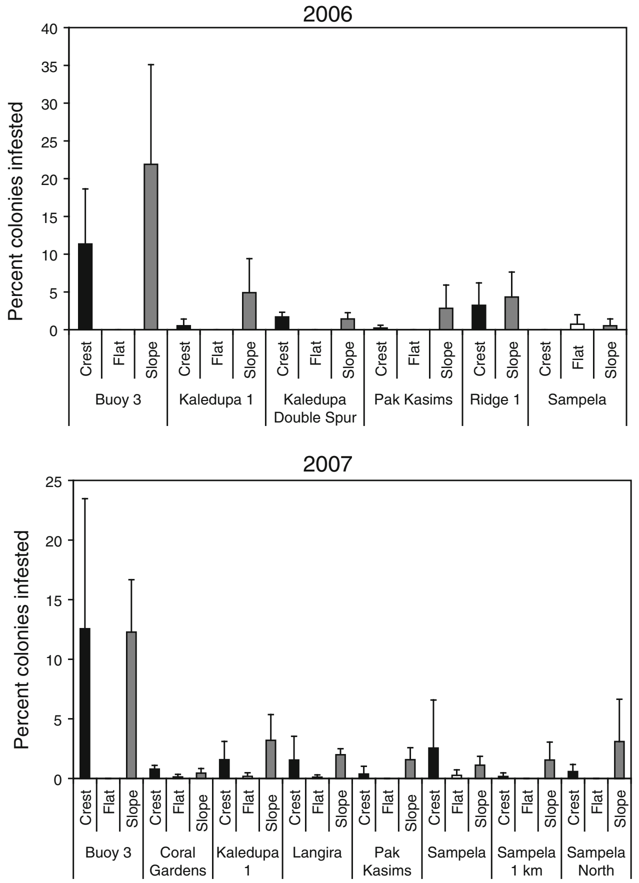

Fig. 3 Mean percentage + SD of all coral colonies associated with *Waminoa* sp. in 2006 and 2007 samples. Reef crest = *filled bars*, flat = *open bars*, slope = *shaded bars*

Tubastrea thrives on reef slopes subject to strong currents (Veron 2000) and under overhangs. This genus is very rare on reef flats and only five colonies of *Tubastrea* were encountered along sample transects on the reef flats in this study. No acoels were associated with these colonies. Microclimate may be important when considering the worm's choice of different host corals (Smith pers. obs. 2007). Reef flats are often habitats with high water movement, high temperature and UV radiation and may not be a suitable environment for the delicate acoel worm.

Photographs taken daily on the reef slope showed that the worms moved on the coral's surface (Haapkylä et al. 2007, unpublished data). Possible physiological and environmental settlement cues for acoels on corals remain to be investigated. The results from the present study show that acoel prevalence varied between 2 years being 4.8% in 2006 and 2.6% in 2007. In an earlier study on coral health from 2005 in the WMNP, the prevalence of acoels was only

0.8% (Haapkylä et al. 2007). The overall prevalence can be compared to the later studies but not the host coral preference since some coral genera were combined at the family level.

We found that acoels were associated with 16 and 21 coral taxa out of the 41 coral taxa studied in 2006 and 2007 respectively. The results of the only previous study investigating associations of acoels with corals showed that the acoel *Waminoa brickneri* was associated with 14 species of stony and soft corals in the Red Sea and the strongest association was found with *Turbinaria* and *Echinophyllia* (Barneah et al. 2004). Prevalence of both of these genera was 20%, but the number of observed colonies was only 10 for *Turbinaria* and 5 for *Echinophyllia*, versus 574 colonies of *Tubastrea* in 2006 and 693 colonies in 2007 in the present study. Therefore it may be unwise to compare the level of *W. brickneri* prevalence on corals in the Red Sea to the present study. In this study acoels were rare or absent on the most common genera *Montipora* and *Porites* (Table 1). We sampled for association of acoels with soft corals (*Sarcophyton* spp., *Sinularia* spp. and *Xenia* spp.) in 2007 and found a negative association (Table 1). We observed acoels a few times on the corallimorpharian *Discosoma* spp. There may also have been positive associations between flatworms and *Turbinaria* and *Psammorca*/*Coscinarea* colonies, but the low expected frequencies of association reduce the reliability of conclusions drawn from chi-squared tests.

Our observations on the photophysiology of the acoels show that the worms have a constant photophysiological signal regardless of where they were taken from. This is an interesting finding and suggests that the worm photophysiology does not change with depth. This study was limited to shallow surface waters (max depth 18 m); however Barneah et al. (2007b) found *Waminoa* spp. worms associated with corals as deep as 50 m in the Red Sea. The worms are likely to move among corals at various depths, hence they may not need to adapt their photophysiology to different light conditions. The density of zooxanthellae may change with depth as has been observed in many corals (e.g. McCloskey and Muscatine 1984). Decreased density of algal symbionts was observed in the acoel *Convolutriloba retrogemma* as a result of starvation and progeny release (Åkesson and Hendelberg 1989). Shannon and Achatz (2007) found decreased densities of algal symbionts in all *Convolutriloba* species as a result of being kept in the dark.

In this study the photophysiology of the worms was only measured in laboratory conditions, a fact that may have influenced the results. We did not measure photophysiological responses of the host corals themselves and therefore are not able to compare physiological adaptation of the zooxanthellae directly.

The mucus layer of coral surfaces is believed to constitute a major source of nutrients on a reef (Ducklow 1990; Wild et al. 2004) and may provide a potential food source for the flatworms. Ogunlana et al. (2005) concluded that worms had not consumed coral tissue since no nematocysts were found in *Waminoa brickneri*'s digestive system. Evidence of mucus acting as a possible food source was found in the case of the soft coral *Stereonephthya cundabiluensis* lacked a mucus layer when it harboured flatworms (Barneah et al. 2007b). Several authors (e.g. Brown and Bythell 2005) have discussed the importance of the mucus layer to coral defence and the topic has received further attention as research on coral diseases has increased. By feeding on coral mucus, the worm may make the coral more susceptible to various biotic and abiotic disturbances (Barneah et al. 2007b). It is possible that mucus sloughing could increase on corals that harbour numerous acoels. However, there was no evidence of increased host coral mortality on a flatworm-associated coral in the present study.

Waminoa spp. worms may reduce the host coral's photosynthesis by shading (Barneah et al. 2007b). It should be emphasized that in the present study <12% of the corals with acoels had high acoel cover (≥70%) and there were more corals that had medium and heavy cover of flatworms in 2007 than in 2006. Measurements of the photosynthesis of the host coral itself should be undertaken and compared to corals without acoels to understand how the coverage of worms may reduce the photosynthetic activity of the host coral.

Major questions remain unanswered regarding coral-associated acoels and their role in the complex coral reef environment. Studies on acoel life cycle, dispersion, dynamics and photophysiology should be conducted in order to better understand the association between acoels and their coral hosts.

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