



Host specificity of coral-associated fauna and its relevance for coral reef biodiversity



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ARTICLE INFO

Article history:

Received 8 June 2023

Received in revised form 16 August 2023

Accepted 14 September 2023

Available online 12 October 2023

Keywords:

Coral-associated fauna

Coral reefs

Cryptic invertebrates

Host-parasite relationships

Host specificity index

Marine biodiversity

ABSTRACT

Coral-associated fauna predominantly consists of invertebrates and constitutes an important component of coral reef biodiversity. The symbionts depend on their hosts for food, shelter and substrate. They may act as parasites by feeding on their hosts, by overgrowing their polyps, or by excavating their skeletons. Because some of these species partly reside inside their hosts, they may be cryptic and can easily be overlooked in biodiversity surveys. Since no quantitative overview is available about these inter-specific relationships, this present study addresses variation in host ranges and specificity across four large coral-associated taxa and between the Atlantic and Indo-Pacific oceans. These taxa are: coral barnacles (Pyrgomatidae, $n = 95$), coral gall crabs (Cryptochiridae, $n = 54$), tubeworms (Serpulidae, $n = 31$), and date mussels (Lithophaginae, $n = 23$). A total of 335 host coral species was recorded. An index of host specificity (S_{TD}) was calculated per symbiont species, based on distinctness in taxonomic host range levels (species, genus, family, etc.). Mean indices were statistically compared among the four associated taxa and the two oceanic coral reef regions. Barnacles were the most host-specific, tubeworms the least. Indo-Pacific associates were approximately 10 times richer in species and two times more host-specific than their Atlantic counterparts. Coral families varied in the number of associates, with some hosting none. This variation could be linked to host traits (coral growth form, maximum host size) and is most probably also a result of the evolutionary history of the interspecific relationships.

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1. Introduction

Coral reefs are among the most species-rich ecosystems of the world. While covering only 0.2% of the total ocean surface, they are estimated to be inhabited by approximately 830,000 multicellular species (Reaka-Kudla, 1997; Fisher et al., 2015). Macro-invertebrate species play an important role in this biodiversity (Patton, 1976; Paulay, 1997; Glynn and Enochs, 2011), as they represent approximately 17% of all species occurring on coral reefs (Ray and Grassle, 1991; Reaka-Kudla, 1997). Many of these invertebrates show a symbiotic relationship with stony corals, which are the most dominant reef builders (Zann, 1980, 1987; Glynn and Enochs, 2011; Stella et al., 2011). Since coral reef ecosystems are currently under great pressure, and both coral cover and diversity are declining as a result of climate change (Pandolfi et al., 2003; Hoegh-Guldberg et al., 2007; Carpenter et al., 2008), the resulting habitat loss has an immediate effect on species that rely

on them for their existence (Bush and Kennedy, 1994; McKinney, 1997).

Many coral associates show an obligate relationship with their host, meaning that they are not able to survive on their own (Castro, 1976; Chan et al., 2020b). Therefore, the local extinction of a host species causes the immediate disappearance of its epibiont as well, increasing the loss of biodiversity unless the epibiont has alternative hosts on which it can rely for its survival. Hence, when requirements for coral conservation need to be considered, the uniqueness and vulnerability of their associated fauna should also be taken into account (Hoeksema, 2017; Montano, 2020, 2022). Other coral-associated invertebrates show a facultative symbiosis (Castro, 1976). These species can survive on alternative substrates and will therefore be less vulnerable to the globally observed decline in coral cover and diversity (Gardner et al., 2003; Bruno and Selig, 2007; Carpenter et al., 2008; De'ath et al., 2012; Eddy et al., 2021; Muir et al., 2022).

Another important aspect of coral-associated invertebrates is the impact they have on their host's health (Barton et al., 2020). A large proportion of coral-associated invertebrates (36%) feed on their host corals (Stella et al., 2011), which may facilitate the set-

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tlement of various epibionts (Hutchings, 1986). Another adverse effect for corals is bioerosion of the coral skeleton by macroboring symbionts such as date mussels (Lithophaginae) (Scott and Risk, 1988), excavating sponges (de Bakker et al., 2018), and annelid worms (Hutchings, 2008; Dee et al., 2023). Some encrusting ascidians, octocorals and sponges are generalist associates known to indiscriminately overgrow and kill large areas of coral surface (Rodríguez-Martínez et al., 2012; van der Ent et al., 2016; Madduppa et al., 2017; Wulff, 2017; Turicchia et al., 2018; Allchurch et al., 2022; Reimer et al., 2022), but not necessarily smother all endolithic coral symbionts that they encounter (Hoeksema et al., 2015, 2016, 2018c, 2020). Coral barnacles of the subclass Cirripedia (Benzoni et al., 2010), polychaete tube-worms (Hoeksema et al., 2019a, 2019b, 2022c), acoelomorph flat-worms (Hoeksema and Farenzena, 2012; Maggioni et al., 2022b), scallops (Chan et al., 2020a; Scaps, 2020), and worm snails (Adhavan et al., 2021; Hoeksema et al., 2022a; Bieler et al., 2023) have been shown to cause stress or damage to nearby coral polyps. On the other hand, beneficial effects for the hosts have also been reported, such as corallivore deterrence by serpulid fan worms and other symbiont species (DeVantier et al., 1986; Pratchett, 2001; Montano et al., 2017b). These animals are supposed to increase water circulation, thereby increasing the arrival of food particles to the coral polyps and removing waste products (Strathmann et al., 1984; Marsden et al., 1990; Dai and Yang, 1995; Floros et al., 2005). A classic example of mutualism consists of sipunculan worms of the genus *Aspidosiphon* that live protected inside the skeletons of free-living corals of the genera *Heterocyathus* and *Heteropsammia* and help them to move around on sandy substrates and to keep them in upright position (Goreau and Yonge, 1968; Rice, 1976; Igawa et al., 2017; Herrán et al., 2022).

Not all coral taxa are equally inhabited by coral-associated invertebrates. Corals of the genera *Pocillopora* and *Porites*, for example, have an exceptionally diverse symbiont fauna (Stella et al., 2011). This unequal hospitality is partly related to the host specificity of the associated species. Some gall crab species (Cryptochiridae) only occur on a very limited number of hosts, often restricted to a single genus (van der Meij, 2012). The mechanism behind this observation is presently unclear, but it possibly depends on the settlement behaviour of larvae, as observed in coral-dwelling tube worms and barnacles (Marsden, 1987; Hunte et al., 1990; Brickner and Høeg, 2010; Liu et al., 2016; Yap et al., 2023). The selection of a host species might be related to its protective potential, as epifaunal biodiversity is higher in tightly-branched species than in open-branched species (Vytopil and Willis, 2001). This, however, is species-dependent as *Spirobranchus* tubeworms favour massive host species (Montebon and Yap, 2009; Hoeksema et al., 2019b). Furthermore, there is bias in the information on host preferences because some studies are focused on the associated fauna of particular host coral taxa such as scleractinian families (Hoeksema et al., 2012; Montano et al., 2015; Ivanenko et al., 2018), genera (Pisapia et al., 2020; Nogueira et al., 2021), or single species (McCloskey, 1970; Oigman-Pszczol and Creed, 2006; Terrón-Sigler et al., 2014; Hoeksema et al., 2017), or on particular habitats such as artificial reefs (Lymperaki et al., 2022).

Many coral-associated species are cryptic and understudied due to their small size (Glynn et al., 2014; Maggioni et al., 2022a; Samimi-Namin et al., 2023), use of camouflage (Montano and Maggioni, 2018; Mehrotra et al., 2020; Yiu and Qiu, 2023), dwelling in coral cavities (Hoeksema and García-Hernández, 2020; Hoeksema et al., 2022b), hiding underneath corals (Hoeksema et al., 2013b) or between their tentacles (Hoeksema and Fransen, 2011; Bos and Hoeksema, 2015, 2017; Fransen et al., 2023). From a logistic perspective, deep distribution ranges of coral associates may be a limiting factor in their discovery, depending on the bathymetrical range of host species at depths of 25 m and bey-

ound, where time available for SCUBA diving is limited (Zibrowius, 1982; Manning, 1991; Zibrowius and Gili, 1990; García-Hernández et al., 2020; Vimercati et al., 2023). By the application of molecular techniques on such symbiotic groups, more information on obscure coral-associated fauna has become available recently and much more is expected in the near future (Malay and Michonneau, 2014; Kunihiro et al., 2019; Maggioni et al., 2022a; Wong et al., 2023). Also, it is unclear how host species differ in the diversity of their associated species assemblages and by what characteristics (e.g. morphological, chemical, behavioural) they are determined. For example, some coral species, such as the mushroom coral *Heliofungia actiniformis* (Quoy & Gaimard, 1833), have long tentacles and hiding space underneath their skeleton, which function as habitat for a large variety of associated species such as fishes, shrimps, copepods, bivalves, gastropods, acoel flat-worms, and brittle stars (Vagelli and Erdmann, 2002; Hoeksema and Fransen, 2011; Hoeksema et al., 2012; Gittenberger and Hoeksema, 2013; Bos and Hoeksema, 2015, 2017; Rauch et al., 2019). Besides their contribution to species diversity, they may impact coral communities by their high densities (Scaps and Denis, 2008).

Several studies have shed light on specific coral-symbiont relationships and a broader picture of their share in the total coral reef biodiversity becomes increasingly clear. However, quantitative information on associated fauna and their host ranges is only limited to a few focus taxa. There is no good overview of host specificity among coral-associated fauna, which is relevant if their vulnerability depends on changing host availability. In this study, four widely distributed species-rich groups of coral-associated invertebrates are examined (three families and one subfamily) to study the importance of stony coral species as their hosts and how much they score on a scale of host specificity. The four major taxa of reef coral symbionts are (i) the family Pyrgomatidae of the crustacean order Balanomorpha (Fig. 1), (ii) the family Serpulidae of the annelid class Polychaeta (Fig. 2), (iii) the family Cryptochiridae of the crustacean order Decapoda (Fig. 3), and (iv) the subfamily Lithophaginae (family Mytilidae) of the molluscan class Bivalvia (Fig. 4). They are commonly represented in the field (Scott, 1987; Lymperaki et al., 2022; van der Schoot and Hoeksema, 2022) and in the literature (this study). Pyrgomatidae is a family of coral barnacles within the subclass Cirripedia, most of which partly live inside live coral (Chan et al., 2020b; Fig. 1). Cryptochiridae is a family of crabs that act as obligate associates of live scleractinian corals (Fize and Serène, 1957; Kropp, 1990; van der Meij et al., 2015b; Fig. 2). Serpulid tube worms (Fig. 3) occur in both tropical and non-tropical waters, with a majority that is not coral-associated (ten Hove and Kupriyanova, 2009; Capa et al., 2021). Lithophaginae consists of boring mytilid bivalves (date mussels), which either excavate into live coral or limestone rock (Owada, 2007; Fig. 4). Pyrgomatidae and Cryptochiridae are comprised of species that have an obligate relationship with live host corals (Ross and Newman, 1973; van der Meij et al., 2015b). Serpulidae, however, is not limited to a specific host group, because many of its species live attached to abiotic substrates (ten Hove and Kupriyanova, 2009; Kupriyanova et al., 2023). The substrate generalists among them, such as *Spirobranchus triquetter* (Linnaeus, 1758) and *Spirobranchus polytrema* (Philippi, 1844), can also live on dead coral skeleton of, for example, *Cladocora caespitosa* (Linnaeus, 1767) in the Mediterranean (Arvanitidis and Koukouras, 1994; Pitacco et al., 2021). Similarly, Lithophaginae is distinguished by species that excavate hard substrate, although not exclusively live coral (Owada, 2007; Owada and Hoeksema, 2011) and a recent study has shown that this subfamily is polyphyletic (Taylor et al., 2023). Thus, the latter two groups also contain species that are not necessarily coral-associated, because they may also occur in dead coral and limestone rock, whereas the former two groups



Fig. 1. Coral barnacles (Pyrgomatidae) in host corals of the following species: (A) *Cantellius* sp. *Stylaster* sp., Stylasteridae (West Papua, Indonesia, 2007); (B) *Nobia grandis* in *Euphyllia glabrescens*, Euphylliidae (West Papua, Indonesia, 2007); (C) *Cionophorus soongi* in *Astreopora myriophthalma*, Acroporidae (West Papua, Indonesia, 2007); (D) *Cantellius* sp. in *Pavona bipartita*, Agariciidae (northeastern Sabah, Malaysia, 2010); (E) Unidentified pyrgomatid in a fragment of *Cycloseris distorta*, Fungiidae (Nha Trang, Vietnam, 2008); (F) Unidentified pyrgomatid on the lower side of *Cycloseris tenuis*, Fungiidae (Maldives, 2014). Arrows indicate barnacles. Photo credit: B.W. Hoeksema.

exclusively consist of coral symbionts. It is noteworthy, however, that obligate symbionts such as some gall crabs and date mussels may be able to survive in dead coral parts when the rest of the host colony is still alive (Hoeksema et al., 2022b; van der Meij, 2022).

To quantify host dependence of the coral-associated species in the present analysis, the hosts from which they have been observed are presented together with an index for host specificity (Poulin and Mouillot, 2003; Poulin, 2011). The taxonomic distinctness between the species in the host range of a coral associate is used to calculate an index of host specificity (S_{TD}) with the lowest values expressing the highest degrees of host specificity. This index is based on the taxonomic distinctness between the host coral spe-

cies of a symbiont, in which host species are considered more distinct when they belong to different higher order taxa such as genera, families and orders. It is hypothesized that coral-associated species of taxa that have been reported from other substrates than live coral, such as certain species of *Spirobranchus* and *Lithophaginae*, on average show less host specificity than those that have been recorded from live coral.

This index may depend on overall species richness of biogeographical regions and on the dominance among host-specific species or host-generalist species. Coral reefs in the Atlantic Ocean are less rich in species than those of the Indo-Pacific, which contains the global centre of maximum marine biodiversity

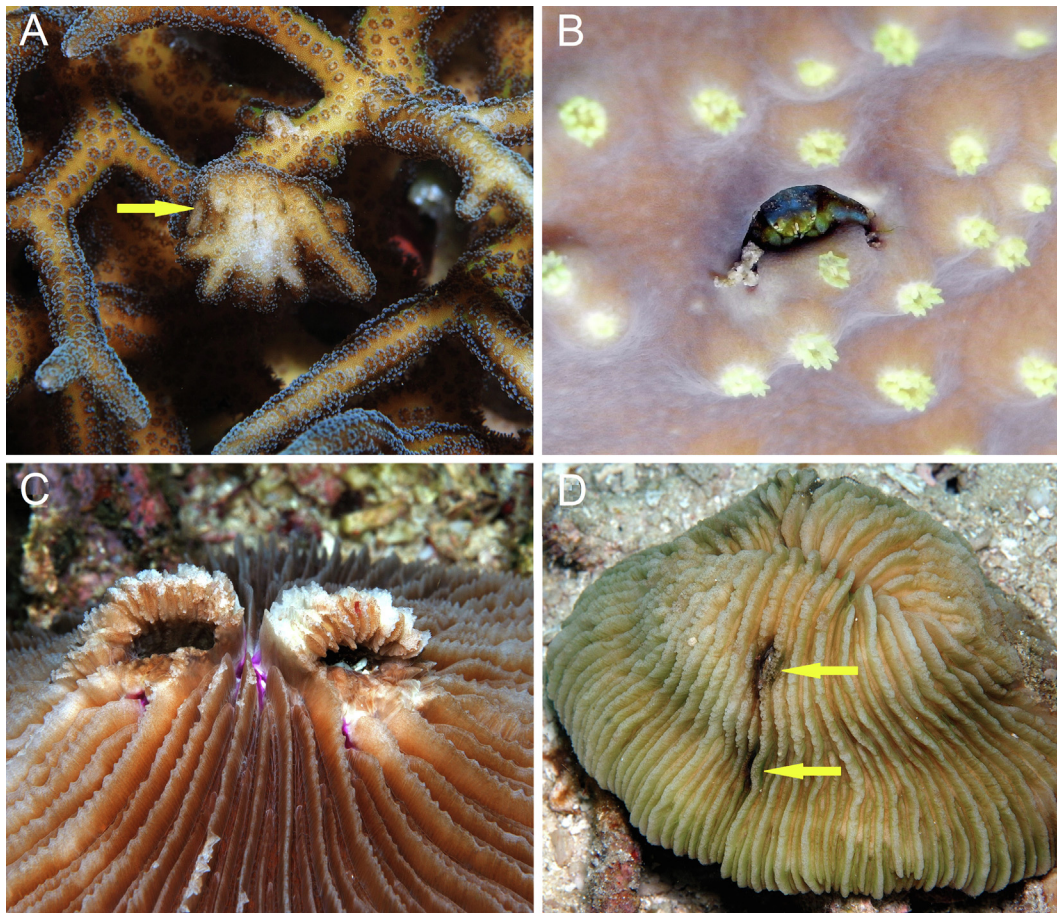


Fig. 2. Coral gall crabs (Cryptochiridae) in various scleractinian host corals: (A) gall of *Hapalocarcinus marsupialis* in *Seriatopora hystrix*, Pocilloporidae; (B) *Pseudocryptochirus viridis* in *Turbinaria reniformis*, Dendrophylliidae; (C) two galls of *Fungicola utinomi* in a mushroom coral, *Danafungia horrida*, Fungiidae; (D) two galls of *Fungicola syzygia* in a mushroom coral, *Pleuractis moluccensis*, Fungiidae. Localities: West Papua, Indonesia, 2007 (A, C, D) and northeastern Sabah, Malaysia, 2010 (B). Arrows indicate gall-crab dwellings. Photo credit: B.W. Hoeksema.

(Hoeksema, 2007; Huang et al., 2015; Veron et al., 2015). New coral species are still being discovered and their taxonomy is undergoing much change (Veron, 2000; Hoeksema and Cairns, 2023).

In the Atlantic, the present record of reef coral species ($n = 80$) divided over 32 genera and 15 families is much lower than in the Indo-Pacific, which contains 860 species, 107 genera, and 22 families (Veron, 2000; Hoeksema and Cairns, 2023). Hence, the ratio of scleractinian reef coral species per genus and per family in the Atlantic is 2.5 (80/32) and 5.3 (80/15), and in the Indo-Pacific 8.0 (860/107) and 39.0 (860/22), respectively. Generalist coral associates therefore have a pool of available host species that is divided over relatively more genera and families in the Atlantic than in the Indo-Pacific. Thus, their host specificity is expected to be lowest in the Atlantic. Assuming that host-specific symbiont species have the capacity to expand their host range mainly within the same host genus and less frequently within the same family, the potential number of closely related host species per symbiont is lowest in the Atlantic and therefore their host specificity is expected to be higher there. If new coral symbionts are able to evolve independently from their hosts, causing closely related symbionts to share the same host species (but in isolated populations), then this may not affect host specificity of the symbiont but instead increase the hospitality of the host. Other corals may have no associated species at all.

Thus, species diversity of coral-associated fauna in a region depends on which associated groups are most dominant (host-specific or generalist) and on host popularity. To understand the

importance of these associations, we need to know the numbers of hosts per symbiont and their taxonomic distinctness. The outcome not only depends on host-symbiont co-evolution in both regions but also on whether dominant host coral shapes per region are suitable for hosting symbionts (e.g., massive, branching, or free-living). In this way, we are also able to detect which coral families are poor in associated fauna, which may help to understand the way in which interspecific associations contribute to coral reef biodiversity.

The results can be applied to develop species-targeted conservation strategies that take the importance of host corals into account. Coral reef conservation studies usually emphasize the importance of coral cover instead of coral biodiversity (Mumby and Harborne, 2010; Selig and Bruno, 2010; Brodie and Waterhouse, 2012; Ortiz Cajica et al., 2020). While the former is primarily of local importance, the latter is relevant for the survival of reef coral communities as a whole.

2. Materials and methods

2.1. Selection of taxa and the search for records

The coral-associated species included in this study (Cryptochiridae, Lithophaginae, Pyrgomatidae, Serpulidae) were selected because they are species-rich, much studied, and represented in both the Atlantic and the Indo-Pacific oceans (ten Hove and

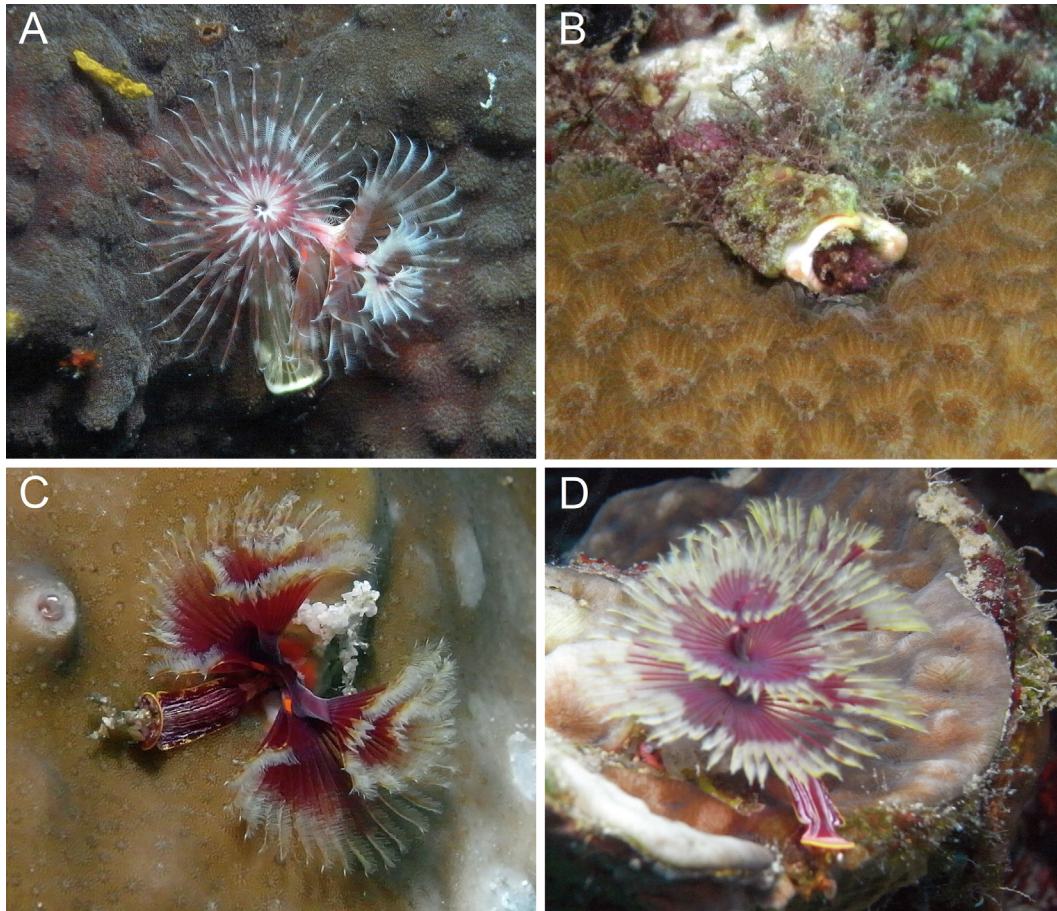


Fig. 3. New scleractinian host records for *Spirobranchus* (Serpulidae). (A) *Spirobranchus corniculatus* hosted by *Cyphastrea kausti*; (B) *Spirobranchus richardsmithi* (retracted) hosted by *Goniastrea retiformis*; (C) idem hosted by *Porites rus*; (D) idem hosted by *Coscinaraea monile*. Localities: Red Sea, Saudi Arabia, off Thuwal, 2014 (A) and Farasan Banks, 2017 (B–D). Photo credit: B.W. Hoeksema.

Kupriyanova, 2009; Stella et al., 2011; Molodtsova et al., 2016; Chan et al., 2020b). A prerequisite for inclusion of associated taxa is the presence of a life-lasting symbiotic host, either by living partly buried in it, e.g. coral barnacles and serpulid worms, or by being housed inside a permanent cavity with an opening on the host's surface, e.g. boring mussels and coral gall crabs. As a consequence, groups consisting of motile symbionts, and those that are understudied or species-poor, are excluded.

Records of symbiont species were retrieved from scientific literature that was published before 2023. Recent literature was searched through Google Scholar (<https://scholar.google.com/>) based on the genus names of associates as key words. Old cited works found in references were also consulted. Books and historical works were obtained as hard copies from the library of Naturalis Biodiversity Center (Leiden, Netherlands) or online from the Biodiversity Heritage Library (<https://www.biodiversitylibrary.org>). Data was obtained from 53 references on Pyrgomatidae, 39 on Cryptochiridae, 47 on Serpulidae, and 29 on Lithophaginae (Tables 1–4).

A record was included when both the host and the associated animal were identified to species level and the latter was clearly recorded as living in or on a live host coral. A host is here defined as a stony coral belonging to the Anthozoan order Scleractinia or family Corallidae (Octocorallia), or the hydrozoan families Milleporidae and Stylasteridae. Symbiont species without a host coral record were excluded from the analysis. Fossil records were also not included (e.g. Goreau et al., 1976; Klompmaker et al., 2016; Vinn et al., 2021; Karasawa and Kobayashi, 2022).

The classification and scientific names of symbiont and host species in the original source publications were verified for their current taxonomic status with the help of the World Register of Marine Species (WoRMS, 2023), and corrected if required. When only the genus name of the host coral was mentioned, this was recorded as a single species, '*genus* sp.'. When additional congeneric hosts were identified to species level, hosts only recorded at genus level were ignored to prevent the inclusion of duplicates. The total number of recorded specimens was counted, which in some cases was referred to as a minimum. If a number of records was not mentioned, the number of recorded host species was regarded as such.

Records from the Atlantic (At) concern tropical regions in the western Atlantic, the Caribbean Sea, the Gulf of Mexico, islands in the mid-Atlantic region, the eastern Atlantic and the Mediterranean Sea. Those from the Indo Pacific (IP) encompass tropical regions from the east coast of Africa, the Red Sea, and the Persian Gulf to the west coast of the Americas. Alternative substrates on which species were recorded were classified as: (i) dead coral skeletons; (ii) manmade materials; (iii) mollusc shells, either inhabited or uninhabited; (iv) limestone and non-biogenic rock; (v) mangrove roots; (vi) octocorals; (vii) sponges.

2.2. Host specificity index

For each associated species, a host specificity index (S_{TD}) was calculated, which is used to express the degree of host specificity of an associated organism. With the help of this index, symbiont

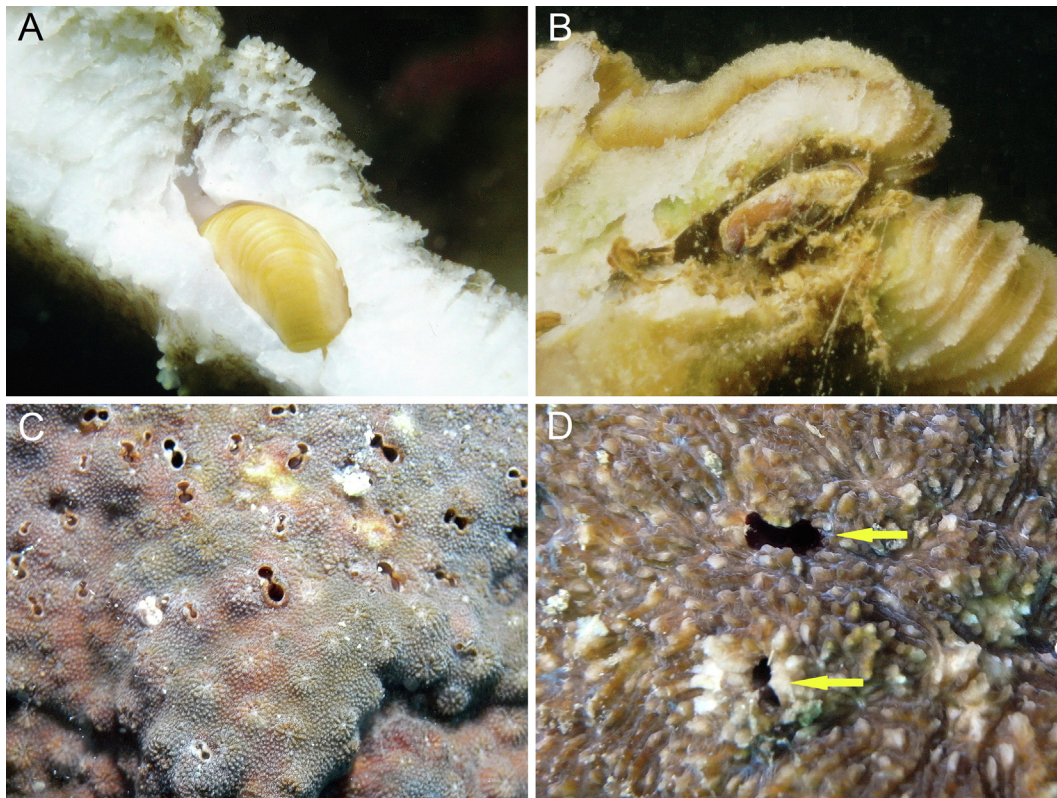


Fig. 4. Examples of date mussels (Lithophaginae) and their host corals. (A) *Fungiacava eilatensis* in a mushroom coral, *Podabacia motuporensis*, Fungiidae (South Sulawesi, Indonesia, 2001); (B) *Leiosolenus lima* in a mushroom coral, *Pleuractis molluccensis*, Fungiidae (South Sulawesi, Indonesia, 2001); (C) numerous boring orifices of *Leiosolenus* sp. in a colony of *Cyphastrea kausti*, Merulinidae (Red Sea, off Thuwal, Saudi Arabia, 2014); (D) two boring orifices (arrows) of *Leiosolenus* sp. in a mushroom coral, *Podabacia lankaensis*, Fungiidae (Strait of Malacca, Malaysia, 2013). Photo credit: B.W. Hoeksema.

taxa can be compared with regard to their host diversity. It can also be applied to compare taxonomic groups of symbiont taxa in different biogeographic regions. The index is based on the average taxonomic distinctness (TD) of all host species used by a symbiont species. The taxonomic distinctness between host species is defined as the number of steps that have to be taken to reach the same taxonomic level i.e., genus, family, order etc.

The index S_{TD} was calculated using the formula for taxonomic distinctness of Clarke and Warwick (1998, 1999).

$$S_{TD} = 2 \frac{\sum \sum_{i < j} \omega_{ij}}{s(s-1)}$$

in which s is the number of host species, the double summation is over the species set $\{i = 1, \dots, s; j = 1, \dots, s, \text{ such that } i < j\}$, and ω_{ij} is the taxonomic distinctness between host species i and j , or the number of taxonomic steps required to reach a node shared by both (Poulin and Mouillot, 2003; Poulin, 2011). Krasnov et al. (2004) excluded all single findings of a parasite host combination, however in this study the threshold was set at a minimum of two records for a symbiont species to be included. Therefore a S_{TD} value was only calculated when more than one host species and a minimum of three individuals were recorded. In case three or more individuals were recorded with only one host species, they were assigned a default $S_{TD} = 0$. This is more strict than the suggested default value of 1 (Poulin, 2011) to discriminate between symbionts with one host species and symbionts with multiple host species within one genus, as has been applied in an earlier study (Krasnov et al., 2005). To test for the dependence of the index S_{TD} regarding the number of records per symbiont species, a regression analysis between S_{TD} and the number of records was performed for all sym-

biont groups. To illustrate the effect on the inclusion versus exclusion of symbiont species with a low number of records, the regression analysis was performed in two ways: (i) with all symbiont species included, in which species with a single record were assigned a default $S_{TD} = 0$; (ii) including only symbiont species with at least three records (Fig. 5). For this reason the comparison analyses between geographic regions (Atlantic versus Indo-Pacific) and between symbiont groups were also performed in two ways: (i) all symbiont species included; (ii) only symbiont species with at least three or more records (Fig. 6). All *Hydroides* sp., except *H. lirs*, were excluded from the analysis as no records for these species were found.

2.3. Statistical analysis

S_{TD} was compared across the four symbiont groups and the two geographic regions. The statistical analysis for these comparisons was performed with the software program R (R Core Team, 2022: <https://www.R-project.org/>). A Generalized Linear Model (GLM), with Gaussian distribution was applied to fit the data (GLM, package: stats, version 4.3.0). The residuals of the GLM were visually assessed for normal distribution with a Q-Q plot and a density plot. When the GLM returned a significant result ($P < 0.05$), a pairwise comparison test was performed (GLHT, package multcomp, version 1.4-20) with a Tukey post-hoc test with adjusted P -values. The dependence of S_{TD} on the number of records was analysed with a linear regression (ggplot, package ggplot2, version 3.4.0) for which the P values and both the multiple R-squared and the adjusted R-squared were retrieved by the 'pearson' method (stat_cor, package: ggpubr, version 0.5.0).

Table 1
Range of host coral species of the coral barnacle family Pyrgomatidae (95 associates) based on published records.

Species	Nr. records	Region	S _{TD}	Nr. hosts	Substrate	References
Ceratoconchinae Newman & Ross, 1976						
Ceratoconcha Kramberger-Gorjanovic, 1889						
<i>C. domingensis</i> (Des Moulins, 1866)	92	At	2.33	3	L	46,50
<i>C. floridana</i> (Pilsbry, 1931)	>15	At	2.57	15	L	31
<i>C. paucicostata</i> Young, 1989	2	At	0.00	1	L	31
<i>C. quarta</i> (Kolosváry, 1947)	102	At	2.47	6	L	44
Megatrematinae Holthuis, 1982						
Adna Sowerby, 1823						
<i>A. anglica</i> Sowerby, 1823	>40	At, IP	2.79	40	L	17,23,43,46
Megatrema Sowerby, 1823						
<i>M. madreporarum</i> (Bosc, 1812)	>10	At	2.60	10	L	22
<i>M. youngi</i> Ross & Pitombo, 2002	1	At	-	1	L	43
Memagreta Ross & Pitombo, 2002						
<i>M. pandorae</i> Ross & Pitombo, 2002	5	IP	0.00	1	L	43
Pyrgomatinae Gray, 1825						
Ahoekia Ross & Newman, 1995						
<i>A. chuangi</i> Ross & Newman, 1995	3	IP	0.00	1	L	39
<i>A. microtrema</i> Ross, 2000	23	IP	0.00	1	L ^a	37
<i>A. tanabensis</i> Ross & Newman, 1995	12	IP	0.00	2	L	39
Arossella Anderson, 1993						
<i>A. lynnae</i> Ross, 2000	>1	IP	-	1	L ^b	36
<i>A. projectum</i> (Nilsson-Cantell, 1938)	1	IP	-	1	L ^b	45
Australhoekia Ross & Newman, 2000						
<i>A. cardenae</i> Ross & Newman, 2000	3	IP	1.00	2	L ^a	41
Cantellius Ross & Newman, 1973						
<i>C. acutum</i> (Hiro, 1938)	3	IP	1.00	3	L	14,31,38,49
<i>C. albus</i> Ren, 1986	3	IP	1.00	2	L	35
<i>C. alphonsei</i> Achituv, 2001	6	IP	2.14	1	L	1
<i>C. alveopora</i> Kim, 2021	>7	IP	0.00	1	L	26
<i>C. arcuatus</i> (Hiro, 1938)	>500	IP	2.78	10	L	17,31,52
<i>C. brevitergum</i> (Hiro, 1938)	1	IP	-	1	L	31,52
<i>C. cardenae</i> Achituv & Hoeksema, 2003	6	IP	0.00	1	L	3
<i>C. cornutergum</i> Achituv, 2020	1	IP	-	1	L	52
<i>C. euspinulosum</i> (Broch, 1931)	>14	IP	2.47	15	L	7,17,23,31,33,52
<i>C. gregarius</i> (Sowerby, 1823)	1	IP	-	1	L	38
<i>C. hiroi</i> Galkin, 1982	1	IP	-	1	L	21
<i>C. hoegi</i> Achituv et al., 2009	5	IP	3.00	2	L	9,14,52
<i>C. iwayama</i> (Hiro, 1983)	>24	IP	1.96	11	L	7,34,35,52
<i>C. madreporum</i> (Borradaile, 1903)	1	IP	-	1	L	38
<i>C. maldiviensis</i> Galkin, 1982	1	IP	-	1	L	20,31
<i>C. pallidus</i> (Broch, 1931)	>57	IP	2.81	57	L	7,12,14,23,29,31,33,35,46,52
<i>C. pseudopallidum</i> (Kolosváry, 1947)	1	IP	-	1	L	31,38
<i>C. secundus</i> (Broch, 1931)	>8	IP	1.71	8	L	14,31,49
<i>C. septimus</i> (Hiro, 1938)	>21	IP	2.09	21	L	2,14,33,52
<i>C. sextus</i> (Hiro, 1938)	3	IP	1.00	2	L	9,14,38
<i>C. sinensis</i> Ren, 1986	3	IP	2.33	3	L	31
<i>C. sumbawae</i> (Hoek, 1913)	7	IP	2.00	3	L	38,52
<i>C. transversalis</i> (Nilsson-Cantell, 1938)	>4	IP	2.33	4	L	14,38,52
<i>C. tredecimus</i> (Kolosváry, 1947)	>32	IP	2.14	32	L	7,23,38
Cionophorus Ross & Newman, 2001						
<i>C. guillaumae</i> (Achituv & Newman, 2002)	2	IP	0.00	1	L	7
<i>C. kushimotoensis</i> Ogawa & Nomura, 2010	22	IP	0.00	1	L	32
<i>C. soongi</i> (Ross & Newman, 1999)	5	IP	1.00	3	L	40, 53
Creusia Leach, 1817						
<i>C. spinulosa</i> Leach, 1818	>5	IP	2.80	6	L	10,31
Darwiniella Anderson, 1992						
<i>D. angularis</i> Chan et al., 2012	5	IP	1.80	5	L	14,18,25
<i>D. conjugatum</i> (Darwin, 1854)	>8	IP	2.93	8	L	14,19,23
Eohoekia Ross & Newman, 1995						
<i>E. chaos</i> Ross & Newman, 1995	12	IP	0.00	1	L	39
<i>E. nyx</i> Ross & Newman, 1995	4	IP	0.00	1	L	39
Galkinius Perreault, 2014						
<i>G. adamanteus</i> Chan et al., 2013	2	IP	0.00	1	L	14,15
<i>G. altiopiculus</i> Chan et al., 2013	8	IP	2.00	4	L	14,15
<i>G. angustiradiata</i> (Broch, 1931)	1	IP	-	1	L	27
<i>G. decima</i> (Ross & Newman, 1973)	>30	IP	2.81	7	L	34,38,47
<i>G. depressa</i> Chan et al., 2013	17	IP	2.33	4	L	14,15
<i>G. equus</i> Chan et al., 2013	13	IP	0.00	1	L	14,15,52
<i>G. indica</i> (Annandale, 1924)	>55	IP	2.64	56	L	14,23,31,46
<i>G. maculosus</i> Chan & Liu, 2017	14	IP	1.00	2	L	16,17
<i>G. supraspinulosa</i> Ogawa, 2000	1	IP	-	1	L	30
<i>G. tabulatus</i> Chan et al., 2013	1	IP	-	1	L	14,15
<i>G. trimegadonta</i> Chan et al., 2013	2	IP	2.00	2	L	14,15

(continued on next page)

Table 1 (continued)

Species	Nr. records	Region	S _{TD}	Nr. hosts	Substrate	References
Hiroa Ross & Newman, 1973						
<i>H. stubbingsi</i> Ross & Newman, 1973	>10	IP	1.40	10	L	7,14,46
Hoekia Ross & Newman, 1973						
<i>F. fornix</i> Ross & Newman, 1995	1	IP	-	1	L	39
<i>F. monticulariae</i> (Gray, 1831)	13	IP	0.00	1	L ^a	39
<i>F. mortenseni</i> Ross & Newman, 1995	3	IP	0.00	1	L	39
<i>F. philippinensis</i> Ross, 2000	4	IP	0.00	1	L ^a	39
Neopyrgoma Ross & Newman, 2002						
<i>N. lobata</i> (Gray, 1825)	1	At	-	1	L	42
Neotrevathana Ross, 1999						
<i>N. elongata</i> (Hiro, 1931)	>14	IP	2.75	14	L	14,28,29,33,46,48
Nobia Sowerby, 1839						
<i>N. conjugatum</i> (Darwin, 1854)	>9	IP	2.78	11	L	31,34,35
<i>N. grandis</i> Sowerby, 1839	>30	IP	2.64	9	L	10,30,46,51
<i>N. halomitrae</i> (Kolosváry, 1947)	1	IP	-	1	L	23
<i>N. orbicellae</i> (Hiro, 1934)	>5	IP	3.00	2	L	24
Parahoekia Ross & Newman, 1995						
<i>P. aster</i> Ross & Newman, 1995	2	IP	0.00	1	L	39
Pyrgoma Leach, 1817						
<i>P. cancellatum</i> Leach, 1818	>12	IP	1.92	12	L	14,46,52
<i>P. japonica</i> Weltner, 1897	2	IP	3.00	2	L	7,13,25
<i>P. kuri</i> Hoek, 1913	1	IP	-	1	L	31,42
<i>P. projectum</i> Nilsson-Cantell, 1938	1	IP	-	1	L	42
<i>P. sinica</i> (Ren, 1986)	2	IP	3.00	2	L	31,42
<i>P. spurtruncata</i> (Kim et al 2019)	4	IP	0.00	1	L	25
Pyrgopsella Zullo, 1967						
<i>P. annandalei</i> (Gruvel, 1906)	15	IP	0.00	1	L	8
Savignium Leach, 1825						
<i>S. crenatum</i> (Sowerby, 1823)	>30	IP	2.30	21	L	10,29,31,33,34,46
<i>S. tuamotum</i> Achituv & Langsam, 2005	1	IP	-	1	L	5
Trevathana Anderson, 1992						
<i>T. conica</i> Chan et al., 2017	6	IP	0.00	1	L	16
<i>T. dentata</i> (Darwin, 1854)	>21	IP	2.36	21	L	2,11,28,33,46
<i>T. dongshaensis</i> Chan et al., 2017	4	IP	0.00	1	L	16
<i>T. doni</i> Chan et al., 2017	5	IP	2.67	4	L	16
<i>T. isfae</i> Achituv & Langsam, 2009	2	IP	0.00	1	L	6
<i>T. jensi</i> Brickner et al., 2010	3	IP	0.00	1	L	12
<i>T. longidonta</i> Chan et al., 2017	12	IP	3.00	2	L	16
<i>T. margaretae</i> Brickner et al., 2010	3	IP	0.00	1	L	12
<i>T. mizrachae</i> Brickner et al., 2010	3	IP	0.00	1	L	12
<i>T. niuea</i> Achituv, 2004	1	IP	-	1	L	2
<i>T. noae</i> Achituv & Hosie 2013	5	IP	0.00	1	L	4
<i>T. orientalis</i> (Ren, 1986)	3	IP	2.00	2	L	33,35
<i>T. paulayi</i> Asami & Yamaguchi, 2001	>3	IP	0.00	1	L	11,33,52
<i>T. sarae</i> Brickner et al., 2010	5	IP	0.00	1	L	12
<i>T. synthesysae</i> Achituv & Langsam, 2009	4	IP	0.00	1	L	6
<i>T. taiwanus</i> Chan et al., 2017	3	IP	0.00	1	L	16
<i>T. tureiae</i> Achituv & Langsam, 2005	1	IP	-	1	L	5

Nr. Records, minimum number of records; regions: At, Atlantic, IP, Indo-Pacific; S_{TD}, host specificity index; Nr. hosts, number of host corals; substrate: L, live coral, ^afeeds on coral tissue, ^bunidentified live coral. References: [1] Achituv (2001); [2] Achituv (2004); [3] Achituv and Hoeksema (2003); [4] Achituv and Hosie (2013); [5] Achituv and Langsam (2005); [6] (Achituv and Langsam, 2009); [7] Achituv and Newman (2002); [8] Achituv and Simon-Blecher (2006); [9] Achituv et al. (2009); [10] Annandale (1924); [11] Asami and Yamaguchi (2001); [12] Brickner et al. (2010); [13] Buhl-Mortensen and Mortensen (2004); [14] Chan et al. (2013a); [15] (Chan et al., 2013b); [16] Chan and Liu (2017); [17] Chan et al. (2018); [18] Chen et al. 2012; [19] Darwin (1854); [20] Galkin (1981); [21] Galkin (1982); [22] Hoeksema et al. (2017); [23] Hoeksema et al. (2012); [24] Jones and Hosie (2016); [25] Kim et al. (2019); [26] Kim et al. (2021); [27] Kolosváry (1947); [28] Malay, M.C.D., 2010. Speciation and Diversification in the Indo-West Pacific: Inferences from the Molecular Systematics of Reef-associated Crustaceans. Doctoral dissertation, University of Florida, USA; [29] Mokady et al. (1999); [30] Ogawa (2000); [31] Ogawa and Matsuzaki (1992); [32] Ogawa and Nomura (2010); [33] Paulay and Ross (2003); [34] Poltarukha and Dautova (2007); [35] Ren (1986); [36] Ross (2000a); [37] Ross (2000b); [38] Ross and Newman (1973); [39] Ross and Newman (1995); [40] Ross and Newman (1999); [41] Ross and Newman (2000); [42] Ross and Newman (2002); [43] Ross and Pitombo (2002); [44] Scott (1987); [45] Shahdadi et al. (2014); [46] Simon-Blecher et al. (2007); [47] Simon-Blecher et al. (2016); [48] Stewart et al. (1989); [49] Tsang et al. (2014); [50] Veglia et al. (2018); [51] Xu, W., 2019. Phenotypic plasticity of coral-inhabiting barnacles: variations among age, locations on hosts and host species. MSc. Dissertation. Institute of Ecology and Evolutionary Biology, College of Life Science, National Taiwan University, Taiwan; [52] Zweifler et al. (2020); [53] Fig. 1B.

3. Results

3.1. Host range of coral-associated invertebrates

Totals of 203 coral-associated invertebrates and 335 host coral species were recorded (Supplementary Table S1). Data on Pyrgomatidae comprised 186 records from 53 studies, on Cryptochiridae

92 records from 39 studies, Serpulidae 75 records from 47 studies, and Lithophaginae 59 records from 29 studies (Tables 1–4). The species number of all four symbiont groups together was higher in the Indo-Pacific ($n = 176$) than in the Atlantic region ($n = 23$). In addition, four species occurred in both regions. The number of host species were 266 and 62, respectively, with another seven species occurring in both regions. When all symbiont groups were

Table 2
Range of host coral species of the coral gall crab family Cryptochiridae (54 species) based on published records.

Species	Nr. records	Region	S _{TD}	Nr. hosts	Substrate	References
Cecidocarcinus Kropp & Manning, 1987						
<i>C. brychius</i> Kropp & Manning, 1987	2	At	2.00	2	L	15
<i>C. zibrowii</i> Manning, 1991	1	IP	-	1	L	18
Cryptochirus Heller, 1861						
<i>C. coralliodytes</i> Heller, 1861	4	IP	1.67	3	L	10
<i>C. planus</i> (Takeda & Tamura, 1983)	1	IP	-	1	L	36
Dacryomaia Kropp, 1990						
<i>D. edmonsoni</i> (Fize & Serène, 1956)	3	IP	1.00	2	L	4,26
<i>D. japonica</i> (Takeda & Tamura, 1981)	3	IP	2.33	3	L	2634
Detocarcinus Kropp & Manning, 1987						
<i>D. balsi</i> (Monod, 1956)	8	At	2.67	6	L	15,26
Fizesereneia Takeda & Tamura, 1980						
<i>F. daidai</i> Zayasu, 2013	2	IP	0.00	1	L	39
<i>F. heimi</i> (Fize & Serène, 1956)	6	IP	1.00	4	L	5,26
<i>F. ishikawai</i> Takeda & Tamura, 1980	1	IP	-	1	L	33
<i>F. latisella</i> Kropp, 1994	12	IP	1.00	5	L	13,26
<i>F. panda</i> van der Meij, 2015	12	IP	1.00	3	L	28
<i>F. stimpsoni</i> (Fize & Serène, 1956)	3	IP	0.00	1	L	5,33
<i>F. tholia</i> Kropp, 1994	6	IP	0.00	1	L	13,24
Fungicola Serène, 1968						
<i>F. fagei</i> (Fize & Serène, 1956)	18	IP	1.73	6	L	5 8
<i>F. syzygia</i> van der Meij, 2015	59	IP	1.69	11	L	22
<i>F. utinomi</i> (Fize & Serène, 1956)	37	IP	1.93	10	L	5,8,22
Hapalocarcinus Stimpson, 1859						
<i>H. marsupialis</i> Stimpson, 1859	7	IP	1.83	4	L	5
Hiroia Takeda & Tamura, 1981						
<i>H. krempfi</i> (Fize & Serène, 1956)	12	IP	1.00	3	L	4,5
Kropparcinus Badaro et al., 2012						
<i>K. siderastreicola</i> Badaro et al., 2012	112	At	2.33	3	L	1,20,30,37
Lithoscaptus Milne-Edwards, 1862						
<i>L. doughnut</i> Wong et al., 2023	1	IP	-	1	L	38
<i>L. grandis</i> (Takeda & Tamura, 1983)	1	IP	-	1	L	36
<i>L. helleri</i> (Fize & Serène, 1957)	18	IP	1.61	8	L	5,26
<i>L. nami</i> (Fize & Serène, 1957)	3	IP	0.00	1	L	5
<i>L. pacificus</i> (Edmondson, 1933)	2	IP	0.00	1	L	3
<i>L. paradoxus</i> Milne-Edwards, 1862	4	IP	1.50	4	L	26,38
<i>L. pardalotus</i> Kropp, 1995	7	IP	0.00	1	L	14
<i>L. prionotus</i> Kropp, 1994	8	IP	2.00	2	L	13,36
<i>L. scottae</i> Wong et al., 2023	14	IP	2.00	2	L	38
<i>L. semperi</i> van der Meij, 2015	15	IP	0.00	1	L	23
<i>L. tri</i> (Fize & Serène, 1956)	3	IP	1.00	3	L	5
<i>L. tuerkayi</i> van der Meij, 2017	6	IP	1.00	2	L	29
Luciades Kropp & Manning, 1996						
<i>L. agana</i> Kropp & Manning, 1996	1	IP	-	1	L	9,16
Neotroglocarcinus Takeda & Tamura, 1980						
<i>N. dawydoffi</i> (Fize & Serène, 1956)	15	IP	1.00	5	L	5,27
<i>N. hongkongensis</i> (Shen, 1936)	11	IP	1.50	4	L	4,11,13,27
Opecarcinus Kropp & Manning, 1987						
<i>O. aurantius</i> Kropp, 1989	4	IP	0.00	1	L	12
<i>O. cathyae</i> van der Meij, 2014	9	IP	1.00	2	L	21
<i>O. crescentus</i> (Edmondson, 1925)	20	IP	1.58	10	L	4,12
<i>O. granulatus</i> (Shen, 1936)	3	IP	2.00	2	L	12
<i>O. hypostegus</i> (Shaw & Hopkins, 1977)	203	A	1.57	7	L	6,20,32
<i>O. lobifrons</i> Kropp, 1989	5	IP	0.00	1	L	12
<i>O. peliops</i> Kropp, 1989	2	IP	0.00	1	L	12
<i>O. pholeter</i> Kropp, 1989	8	IP	2.00	2	L	12
<i>O. sierra</i> Kropp, 1989	7	IP	1.00	3	L	12,29
Pelycomaia Kropp, 1990						
<i>P. minuta</i> (Edmondson, 1933)	3	IP	2.33	3	L	3,26
Pseudocryptochirus Hiro, 1938						
<i>P. viridis</i> Hiro, 1938	29	IP	1.00	5	L	5,7,11,19
Pseudohapalocarcinus Fize & Serène, 1956						
<i>P. ransoni</i> Fize & Serène, 1956	5	IP	1.00	2	L	5,26,29
Sphenomaia Kropp, 1990						
<i>S. pyriformis</i> (Edmondson, 1933)	3	IP	2.00	3	L	3
Troglocarcinus Verrill, 1908						
<i>T. corallicola</i> Verrill, 1908	36	At	2.67	26	L	2,15,20,31,32
Utinomiella Kropp & Takeda, 1988						
<i>U. dimorpha</i> (Henderson, 1906)	10	IP	1.00	4	L	4,17,35
Xynomaia Kropp, 1990						
<i>X. boissoni</i> (Fize & Serène, 1956)	9	IP	2.67	3	L	5
<i>X. sheni</i> (Fize & Serène, 1956)	4	IP	1.00	2	L	5,26
<i>X. verrilli</i> (Fize & Serène, 1957)	3	IP	2.00	2	L	5
Zibrovina Kropp & Manning, 1996						
<i>Z. galea</i> Kropp & Manning, 1996	3	IP	0.00	1	L	16

Nr. records, minimum number of records; regions: At, Atlantic, IP, Indo-Pacific; S_{TD}, host specificity index; Nr. hosts, number of host corals; substrate: L, live coral. References: [1] Badaro et al. (2012); [2] Canário et al. (2015); [3] Edmondson (1933); [4] Fang et al. (2005); [5] Fize and Serène (1957); [6] García-Hernández et al. (2020); [7] Hiro (1938); [8] Hoeksema et al. (2012); [9] Komatsu and Takeda (2013); [10] Kropp (1988a); [11] Kropp (1988b); [12] Kropp (1989); [13] Kropp (1994); [14] Kropp (1995); [15] Kropp and Manning (1987); [16] Kropp and Manning (1996); [17] Limviriyakul et al. (2016); [18] Manning (1991); [19] van der Meij (2012); [20] van der Meij (2014a); [21] van der Meij (2014b); [22] van der Meij (2015a); [23] van der Meij (2015b); [24] van der Meij (2015c); [25] van der Meij (2017); [26] van der Meij and Nieman (2016); [27] van der Meij and Reijnen (2014); [28] van der Meij et al. (2015a); [29] van der Meij et al. (2017); [30] Nogueira et al. (2014); [31] Scott, P.J.B., 1985. Aspects of living coral associates in Jamaica. Proc. 5th Int. Coral Reef Congr. 5, Tahiti, pp 345–350; [32] Shaw, J.K., Hopkins, T.S., 1977. The distribution of the family Hapalocarcinidae (Decapoda, Brachyura) on the Florida middle ground. Proc. 3rd Int. Coral Reef Symp. 1, Miami, USA, pp 177–183; [33] Takeda (1980); [34] Takeda and Tamura (1981a); [35] Takeda and Tamura (1981b); [36] Takeda and Tamura (1983); [37] van Tienderen and van der Meij (2016); [38] Wong et al. (2023); [39] Zayasu et al. (2013).

Table 3

Range of host-coral species of the tubeworm family Serpulidae (31 associates) based on published records.

Species	Nr. records	Region	S _{TD}	Nr. hosts	Substrate	References
Floriprotis Uchida, 1978						
<i>F. sabiuraensis</i> Uchida, 1978	7	IP	2.29	7	L	3,24,34,42
Pseudovermilia Bush, 1907						
<i>P. fuscostriata</i> ten Hove, 1975	3	At	3.00	2	L, A	23
<i>P. madracicola</i> ten Hove, 1989	3	At	1.00	2	L	24
Serpula Linnaeus, 1758						
<i>S. watsoni</i> Willey, 1905	1	IP	-	1	L, D	31
Spirobranchus Blainville, 1818						
<i>S. aloni</i> Perry et al., 2018	16	IP	4.00	4	L, A	37
<i>S. corniculatus</i> (Grube, 1862)	>100	IP	2.99	67	L, A, R, S	16,20,28,29,30,36,39,45
<i>S. dendropoma</i> Mörch, 1863	2	At	0.00	1	L, M	1,5,22
<i>S. gardineri</i> Pixell, 1913	9	IP	2.83	4	L	12,25,36
<i>S. giganteus</i> (Pallas, 1766)	>100	At	3.14	31	L, O ^a , SP ^a	9,13,15,17,19,21,40
<i>S. incrassatus</i> Krøyer in Mörch, 1863	1	IP	-	1	L, R	4,44
<i>S. laticapus</i> (Marenzeller, 1884)	2	IP	5.00	2	L, S	2,4,42
<i>S. nigranucha</i> (Fischli, 1903)	1	IP	-	1	L	24
<i>S. polycerus</i> (Schmarda, 1861)	5	At	4.00	4	L, R	18,21,27,46
<i>S. richardsmithi</i> Pillai, 2009	>11	IP	2.58	11	L	14,39,45,47
<i>S. tetracerus</i> (Schmarda, 1861) complex	12	IP	3.44	9	L, M, S	22,25,36,34,39,45
Hydroides Gunnerus, 1768						
<i>H. elegans</i> (Haswell, 1883)	-	IP, At	-	1	L, D, S	34,43
<i>H. exaltata</i> (Marenzeller, 1884)	-	IP	-	1	L, D	34
<i>H. trompi</i> Bastida et al., 2003	-	IP	-	1	L	7
<i>H. parva</i> (Treadwell, 1902)	-	At	-	1	L, A, M, SP	6
<i>H. mongeslopezi</i> Rioja, 1958	-	At	-	1	L	6
<i>H. similoides</i> Bastida-Zavala & ten Hove, 2002	-	At	-	1	L, R	6
<i>H. lirs</i> Kupriyanova et al., 2015	1	IP	-	1	L	26
Vermiliopsis Saint-Joseph, 1894						
<i>V. glandigera</i> Gravier 1906 <i>pygidialis</i> (Willey, 1905)	9	IP	2.83	4	L, D, A	2,26,32,34
Salmacina Claparède, 1870						
<i>S. dysteri</i> (Huxley, 1855)	2	IP	3.00	2	L	34
<i>S. ceciliae</i> Nogueira & ten Hove, 2000	2	A	0.00	1	L	35
Paraprotis Uchida, 1978						
<i>P. dendrova</i> Uchida, 1978	1	IP	-	1	L, D	34
Rhodopsis Bush, 1905						
<i>R. pusilla</i> Bush, 1905	1	IP	-	1	L	8,34
Josephella Caullery & Mesnil, 1896						
<i>J. marenzelleri</i> Caullery & Mesnil, 1896	1	IP	-	1	L	34
Pomatostegus Schmarda, 1861						
<i>P. actinoceras</i> Mörch, 1863	2	IP	3.00	2	L, S, R	38,41
<i>P. stellatus</i> (Abildgaard, 1789)	7	At, IP	2.90	7	L, D, A, M	1,11,10,33,34
<i>P. kroyeri</i> Mörch, 1863	4	IP	1.00	2	L, D, A, S	7

Nr. records, minimum number of records; regions: At, Atlantic, IP, Indo-Pacific; S_{TD}, host specificity index; Nr. hosts, number of host-corals; substrate: L, live coral, D, dead coral, A, artificial substrate, S, shell, R, rock, M, mangrove, O, octocoral, SP, sponge, U, unknown, ^asecondary host. References: [1] Augener (1927); [2] Bailey-Brock (1972); [3] Bailey-Brock (1985); [4] Bastida-Zavala (2008); [5] Bastida-Zavala (2009); [6] Bastida-Zavala and ten Hove (2002); [7] Bastida-Zavala et al. (2016); [8] Ben-Eliafiu and ten Hove (1989); [9] Ben-Tzvi et al. (2006); [10] Borger (2005); [11] DeLoach and Humann (1999); [12] Fiege and ten Hove (1999); [13] García-Hernández and Hoeksema (2017); [14] Hoeksema and ten Hove (2014); [15] Hoeksema et al. (2015); [16] Hoeksema et al. (2016); [17] Hoeksema and ten Hove (2017a); [18] Hoeksema and ten Hove (2017b); [19] Hoeksema et al. (2017); [20] Hoeksema et al. (2018b); [21] Hoeksema et al. (2020); [22] ten Hove (1970); [23] ten Hove (1975); [24] ten Hove (1989); [25] ten Hove (1994); [26] Kupriyanova et al. (2015); [27] Marsden (1992); [28] Martin and Britayev (1998); [29] Martin and Britayev (2018); [30] Molodtsova et al. (2016); [31] Nishi (1992); [32] Nishi (1993); [33] Nishi (1995); [34] Nishi (1996); [35] Nogueira and ten Hove (2000); [36] Perry et al. (2017); [37] Perry et al. (2018); [38] Sánchez-Ovando and Bastida-Zavala (2021); [39] van der Schoot, R.J., 2015. Host specificity of *Spirobranchus* species (Blainville, 1818) on Koh Tao, Gulf of Thailand. Master's thesis, University of Amsterdam, Netherlands; [40] Skinner et al. (2012); [41] Treadwell (1928); [42] Uchida (1978); [43] Vine and Bailey-Brock (1984); [44] Woodward (1961); [45] pers. comm. H.A. ten Hove. [46] Unpublished photographic record B.W. Hoeksema; [47] Fig. 3B.

pooled, the mean number of hosts was 8.3 for Atlantic, and 5.6 for Indo-Pacific symbiont species.

With 95 species, Pyrgomatidae is the most speciose group of coral-associates (Table 1). The localities and host for three *Cantellius* spp. are unknown, i.e., *Cantellius octavus*, *Cantellius preobrazhenskyi* and *Cantellius quintus* (Ross and Newman, 1973; Galkin, 1982). *Pyrgospongia stellula* was only recorded from a sponge (Achituv and Simon-Blecher, 2006). Four species have been described to feed on coral tissue (Ross and Newman, 1969, 2000; Ross, 2000b). With 56 host species, *Galkinius indica* is the most host-generalist coral barnacle.

For each of all 54 species of Cryptochiridae, at least one host coral has been recorded at species level (Table 2). Five species have only one host record. With 26 host species, *Troglocarcinus corallicola* is the most host-generalist coral gall crab.

Out of 547 serpulid species, 31 species (6%), belonging to 11 genera, have been recorded as coral associates (Table 3). The majority of

these tubeworms ($n = 19$) have also been recorded from a variety of alternative substrates. With 67 host coral species, *Spirobranchus corniculatus* is the most generalist serpulid. It has also been recorded from artificial substrates (van der Schoot, 2015; Perry et al., 2017) and bivalve shells (van der Schoot et al., 2016), which therefore makes the relationship with host coral species facultative. *Hydroides* spp. have been described to associate with live coral, however host species were unknown until this study. A host coral of *Hydroides lirs* (see Kupriyanova et al., 2015) was identified here for the first known time based on photographs supplied by Dr. Elena Kupriyanova, Australian Museum, Sydney, Australia.

The subfamily Lithophaginae contains six genera and 59 species, 23 of which (39%) are recorded from live corals, and 10 also from dead coral or rock (Table 4). With 17 scleractinian host species, *Leiosolenus levigatus* has the widest host range. It has also been recorded from various alternative substrates such as dead coral (Kleemann, 1980) and rock (Kleemann and Maestrati, 2012).

Table 4
Range of host coral species of the date mussel subfamily Lithophaginae (23 associates) based on published records.

Species	Nr. records	Region	S_{TD}	Nr. hosts	Substrate	References
Fungiacava Soot-Ryen, 1969						
<i>F. eilatensis</i> Soot-Ryen, 1969	>20	IP	1.93	11	L	6,7,9,10,11,20,29
Leiosolenus Carpenter, 1857						
<i>L. aristatus</i> (Dillwyn, 1817)	>6	At, IP	3.00	6	L, D, R	3,5,12,25,27
<i>L. bisulcatus</i> (d'Orbigny, 1853)	>5	At	2.80	5	L, D, R	21,23,25
<i>L. calyculatus</i> (Carpenter, 1857)	>4	IP	0.00	1	L, S	3,4
<i>L. dahabensis</i> (Kleemann, 2008)	10	IP	-	1	L	15
<i>L. dixonae</i> (Scott, 1986)	9	At	1.00	3	L	22
<i>L. hancocki</i> (Soot-Ryen, 1955)	>10	IP	2.33	3	L, D	2,3
<i>L. hanleyanus</i> (Reeve, 1857)	>6	IP	2.73	6	L, D	7,15,24
<i>L. hastasius</i> (Olsson, 1961)	1	IP	-	1	L	3
<i>L. kleemanni</i> (Valentich-Scott, 2008)	>10	IP	3.00	2	L	26
<i>L. kuehneli</i> (Kleemann, 1977)	>3	IP	1.00	3	L	7,11,13
<i>L. lessepsianus</i> (Vaillant, 1865)	>9	IP	2.00	9	L	1,11,13,15,16
<i>L. levigatus</i> (Quoy & Gaimard, 1835)	>17	IP	2.72	17	L, D, R	11,13,14,15
<i>L. lima</i> (Jousseau in Lamy, 1919)	>13	IP	2.76	13	L	11,13,24
<i>L. lischkei</i> M. Huber, 2010	12	IP	3.00	2	L	7
<i>L. malaccanus</i> (Reeve, 1857)	>9	IP	2.78	9	L, D, R	12,15
<i>L. obesus</i> (Philippi, 1847)	1	IP	-	1	L, D, R	13,17
<i>L. parapurpureus</i> (Kleemann, 2008)	6	IP	2.00	2	L	15
<i>L. peruvianus</i> (d'Orbigny, 1845)	1	IP	-	1	L	24
<i>L. plumula</i> (Hanley, 1843)	>4	IP	0.00	1	L, R	3,15,21
<i>L. purpureus</i> (Kleemann, 1980)	>10	IP	2.56	10	L	11,13,16
<i>L. simplex</i> (Iredale, 1939)	>15	IP	2.58	15	L, D	11,13,19,28
Lithophaga Röding, 1798						
<i>L. punctata</i> Kleemann & Hoeksema, 2002	>5	IP	2.00	5	L	10

Nr. records, minimum number of records; regions: At, Atlantic, IP, Indo-Pacific; S_{TD} , host specificity index; Nr. hosts, number of host-corals; substrate: L, live coral, D, dead coral, S, shell, R, rock. References: [1] Arnaud and Thomassin (1976); [2] Cantera and Contreras (1988); [3] Cantera et al. (2003); [4] Carpenter (1857); [5] Coan et al. (2000); [6] Goreau et al. (1969); [7] Highsmith (1980); [8] Hoeksema and Achituv (1993); [9] Hoeksema and Gittenberger (2008); [10] Hoeksema and Kleemann (2002); [11] Kleemann (1980); [12] Kleemann (1990); [13] Kleemann (1995); [14] Kleemann (1996); [15] Kleemann and Maestrati (2012); [16] Mokady et al. (1994); [17] Owada (2007); [18] Owada (2008); [19] Owada (2009); [20] Owada and Hoeksema (2011); [21] Scott, P.J.B., 1985. Aspects of living coral associates in Jamaica. Proc. 5th Int. Coral Reef Congr. 5, Tahiti, pp 345–350; [22] Scott (1986); [23] Scott (1988); [24] Soliman (1969); [25] Valentich-Scott and Dinesen (2004); [26] Valentich-Scott and Tongkerd (2008); [27] Vinagre et al. (2018); [28] Yahel et al. (2009); [29] Zibrowius and Arnaud (1994).

3.2. Influence of the number of records on S_{TD}

The S_{TD} of a symbiont species is positively related to the total number of records. Two of the four symbiont groups show a significant correlation between the number of records and S_{TD} (Fig. 5). In all symbiont groups, the R-value is low, indicating a weak relationship. The regression analysis in which species with less than three records were excluded shows only a significant relationship for Pyrgomatidae but not for the other three groups (Fig. 5). All P and R values decreased and all trendlines became less steep when species with less than three records were removed (Fig. 5; Supplementary Table S2), indicating less bias in the number of records on S_{TD} .

3.3. Comparisons between symbiont groups and biogeographic regions

Host specificity in some symbiont groups, in particular cryptochirids, was very high, occasionally involving only one host. S_{TD} differed significantly across symbiont groups and between biogeographic regions.

Inclusion of rarely recorded species (all species) resulted in significant differences between Pyrgomatidae and Serpulidae, and Pyrgomatidae and Lithophaginae (Fig. 6A). When species with low records were excluded ($n \geq 3$), Serpulidae was significantly less host-specific, showing a higher S_{TD} than Pyrgomatidae and Cryptochiridae, but not Lithophaginae (Fig. 6B).

According to S_{TD} , the Indo-Pacific symbionts are significantly more host-specific than those in the Atlantic, approximately 2× with low-record species included and 1.5× without (Fig. 7). When only species with three or more records were included, the median S_{TD} of the Indo-Pacific species was higher than when all species were included (Fig. 7B). This results in a smaller difference between Atlantic and Indo-Pacific symbiont species; the corre-

sponding P value, however, was smaller too (Fig. 7; Supplementary Table S3).

3.4. The host's perspective

The 335 host coral species and 197 symbiont species that were examined participated in nearly 1000 unique host-associate combinations (Supplementary Table S1). Taxonomically, the host species are divided over three classes, 27 families and 114 genera. Considering scleractinian hosts, the associated species were not equally distributed over the 36 extant families (Hoeksema and Cairns, 2023) since only 24 families contain at least one host species. Among scleractinian families with reef corals only Coscinaraeidae (eight species) and Plerogyridae (14 species) were recorded without hosts. Merulinidae showed the highest number of host-symbiont associations (Table 5), although it is not the largest scleractinian family, which indicates a high degree of hospitability. Caryophylliidae contains many more species (most of which are not reef-dwelling) but has only 10 host species and 23 associations. *Porites* was the most inhabited genus, with 59 unique symbiont-host relationships, even though cryptochirids were absent. The most favoured host species were *Favites abdita* and *Pocillopora damicornis* with, respectively, 14 and 13 symbiont species (Table 6). Three non-scleractinian families had host corals, of which Milleporidae was the most hospitable, predominantly inhabited by serpulid species.

A majority of host species (54%) had two or more associates, making hosts with a single symbiont most common (46%) (Table 6). Host families that contained the most host species (Merulinidae, Fungiidae, Acroporidae, Agariciidae) were almost evenly inhabited by the four symbiont groups (Fig. 8). The absence of Cryptochiridae in Poritidae and Acroporidae is remarkable. Measured by S_{TD} , Serpulidae showed the lowest host specificity; their distribution over

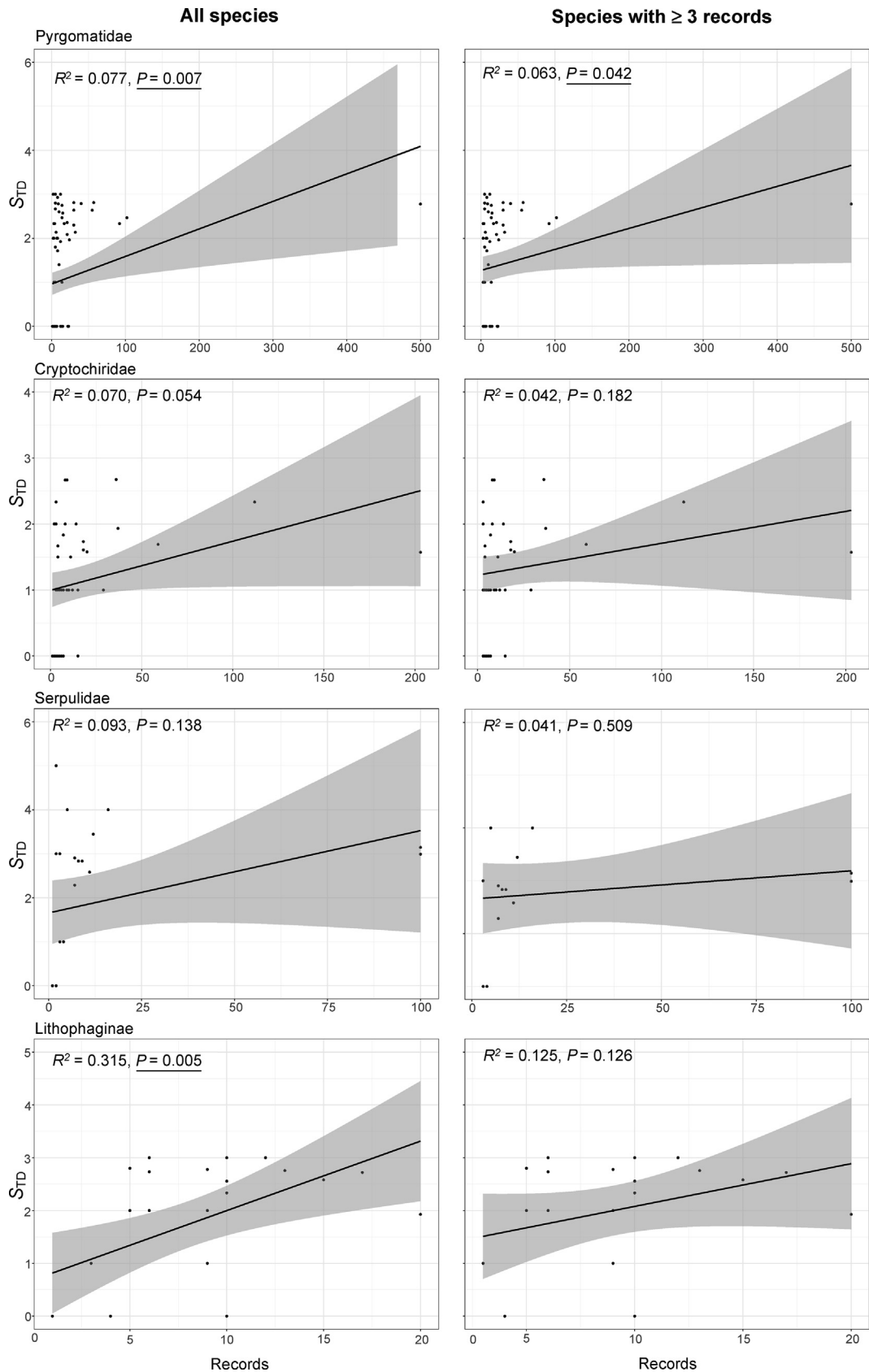


Fig. 5. Linear regression per symbiont group between the number of records of a symbiont species (independent variable) and the index of host coral specificity (S_{TD}) (response variable). Underlined P -values are significant. Grey areas represent the 95% confidence level interval for predictions from the linear model. Analyses with all species included, and those with only three or more records, are shown.

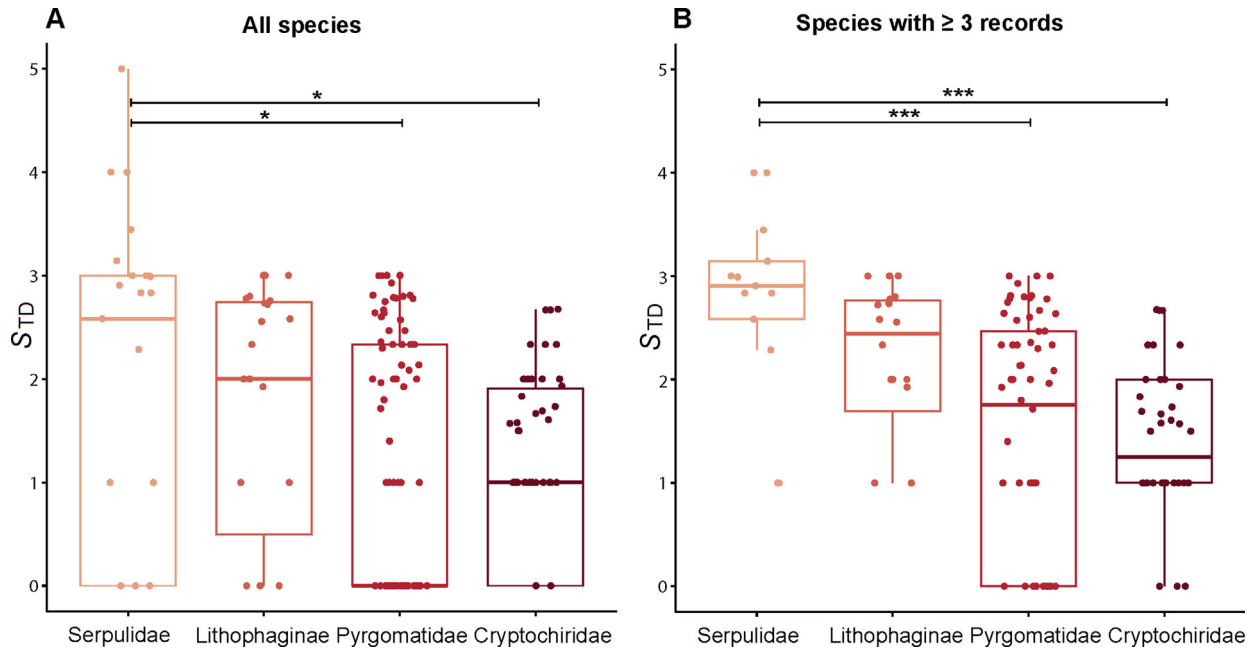


Fig. 6. Comparison of the index of host coral specificity (S_{TD}) within pairs of symbiont taxa. The boxplots are drawn from Q1 to Q3, and the horizontal line in the middle represents the median value. The symbiont groups are ranked in order of decreasing S_{TD} . (A) All species included, regardless the number of records; (B) only species with three or more records. * $P < 0.05$, *** $P < 0.001$.

host families was very uneven (Fig. 8). Serpulid records among Fungiidae are rare and absent in Lobophyllidae. Lithophaginae and Pyrgomatidae are present in all popular scleractinian host families, each with 15 or more host species and showing a relatively even distribution. Furthermore it is remarkable that the invasive sun coral (*Tubastraea coccinea*) is inhabited by two Atlantic symbionts, the serpulid *Spirobranchus giganteus* and the date mussel *Leiosolenus aristatus*.

4. Discussion

This study presents an overview of the currently recorded host-associate relationships of four species-rich groups of coral-associated invertebrates. The number of species in all four symbiont groups is higher in the Pacific than in the Atlantic region (Fig. 7; Tables 1–4), which is in line with earlier studies on tropical marine biogeography (Ekman, 1953; Briggs, 1974; Paulay, 1997; Spalding et al., 2001).

4.1. Host ranges

4.1.1. Cryptochiridae and Pyrgomatidae

All cryptochirid species were described to be associated exclusively with live coral, thus no records of alternative substrates for coral gall crabs were found. Also, all but four pyrgomatid species were exclusively associated with live coral. Three coral barnacles with unknown hosts are therefore considered potentially coral-associated. Of one barnacle, *Pyrgospongia stellula*, the only recorded host is a sponge, which is why a new genus was erected to accommodate this species (Achituv and Simon-Blecher, 2006). It is possible that *P. stellula* may not even be a pyrgomatid species and should perhaps be placed in the balanid subfamily Archaeobalaninae (Achituv and Simon-Blecher, 2006; van Syoc et al., 2015), which would require a molecular phylogenetic analysis.

4.1.2. Serpulidae and Lithophaginae

Tube worms and boring mussels were predominantly recorded on a large variety of alternative substrates, which is consistent with a more facultative need for hosts, whereas their host ranges are wide, especially in serpulids. The total of 67 coral hosts for *S. corniculatus* is the highest number found in the present study, although many publications on coral-dwelling serpulids do not mention the host's identity. Lithophaginae shows a narrower host range, with a maximum of 17 hosts for *L. levigatus*. This finding is in contrast with what might be expected, as 10 out of 23 boring mussels also excavate rock or dead coral.

4.2. Observation effort

The low number of host coral species for the mussel *L. levigatus* can partly be explained by a difference in observation effort (expressed in number of studies). The Lithophaginae are relatively understudied, as on average only 0.4 studies per symbiont species could be included. The Serpulidae and Lithophaginae were the most-studied symbiont taxa; serpulids are covered by 44 studies for 31 associated species, resulting in an average of 1.4 studies per serpulid and 1.3 studies per lithophagin symbiont species. The Pyrgomatidae and Cryptochiridae are moderately studied with, respectively, 0.3 and 0.7 studies per symbiont species. This effect is also present within symbiont groups, since certain symbiont species are recorded in multiple studies while others are reported only once. Various taxonomic publications about serpulids do not mention the host identity, because they are based on museum specimens that were collected without substrate (e.g. Pillai, 2009; Willette et al., 2015; Kupriyanova et al., 2022). In some regional studies, host coral identifications can be correct but erroneous symbiont identifications are used, such as the Atlantic *Spirobranchus giganteus* reported from East Pacific *Pocillopora* corals (Mercier et al., 2022). Some older records from the Indo-Pacific are based on similar misidentifications or on superseded synonyms (e.g., DeVantier et al., 1986; Dai and Yang, 1995; Nishi and Nishihira, 1996; Floros et al., 2005). It is obvious that all sym-

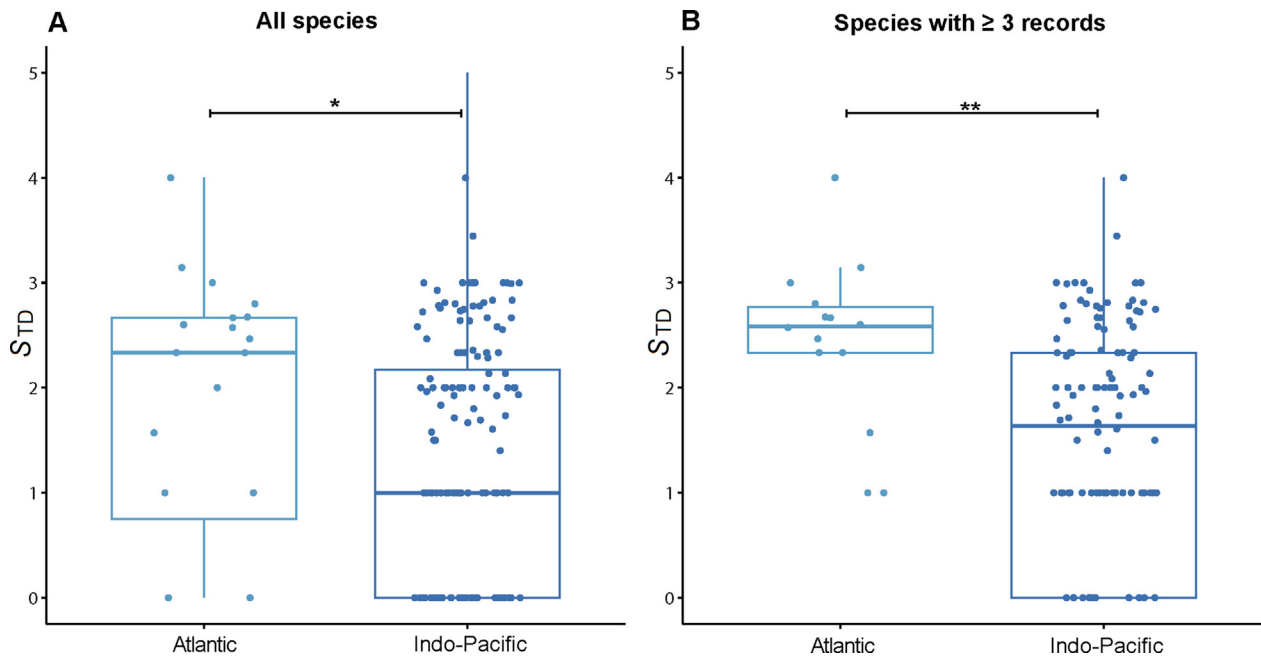


Fig. 7. Comparison of the index of host coral specificity (S_{TD}) between two biogeographic regions. The boxplots are drawn from Q1 to Q3, the horizontal line in the middle represents the median value. All symbiont groups were pooled and divided over the Atlantic and the Indo-Pacific regions. The symbiont groups are ranked in order of decreasing S_{TD} . (A) All species included, regardless the number of records; (B) only species with three or more records. * $P < 0.05$, ** $P < 0.01$.

biont groups show additional and more reliable symbiont-host records with the use of new taxonomic techniques and the recognition of new, cryptic species (Valentich-Scott and Tongkerd, 2008; Perry et al., 2018; Kim et al., 2021; Wong et al., 2023).

As a consequence, host coral ranges in the present study have to be considered incomplete but because the associated groups are the largest and most studied, they are expected to be the best available. It remains unclear whether symbiont species with many records are also very abundant on coral reefs, or only appear so due to an increased observation effort. The latter might be caused by a remarkable appearance of a symbiont species, as is the case with *Spirobranchus* spp. due to their colourful branchial crown (Kleemann, 2008; ten Hove and Kupriyanova 2009; Idris et al., 2022). This phenomenon is also noticed in the comparison of biogeographic regions, with a lower observation effort in the Atlantic than in the Indo-Pacific (Fisher et al., 2011).

4.3. Evaluation of S_{TD}

In this study the use of S_{TD} is evaluated, both by a multiple scenario approach and by assessing the relationship between S_{TD} and the number of records. The regression analyses showed only weak relationships between the number of records and S_{TD} . This is consistent with the original description of the index, which states that the index is independent of observation effort (Poulin and Mouillot, 2003). The weak relationship found in the present study can be explained by a positive relationship between record and host numbers i.e., the number of hosts increases with additional records, thereby affecting S_{TD} . The $R^2_{(adj.)}$ and P values of the regression analyses decreased and increased, respectively, when rarely recorded symbiont species were excluded, thereby indicating their biasing effect on S_{TD} . The dataset in which low record symbiont species were excluded is therefore considered the most representative. As host ranges of the symbiont species are not complete, S_{TD} and the corresponding differences between symbiont groups should be considered indicative. They may improve if records of host ranges become more complete. Future research on coral-

associated invertebrate species should therefore clearly document the host species on or in which the symbiont was found.

4.4. Variation across biogeographic regions

According to S_{TD} values in the present study, Atlantic symbionts are on average more host-generalist than those in the Indo-Pacific. This difference appears paradoxical because the Indo-Pacific has approximately 10 times more reef coral species than the Atlantic, implying that symbionts have more potential hosts available to them. Actually, Atlantic symbiont species have a higher taxonomic diversity among their hosts than their Indo-Pacific counterparts, which is not dependent on the size of the host range. In earlier taxonomic and phylogenetic studies on coral gall crabs (Cryptochiridae), similar differences in host specificity were noticed between the Indo-Pacific and the Atlantic (Kropp and Manning, 1987; van der Meij, 2014a; Chan et al., 2020b) but the present study covers more taxa and it is more quantitative in its approach.

It is suggested that the host range is limited by suitable host species that are present in a certain area (Poulin, 2011). As the number of scleractinian reef coral species in the Indo-Pacific is more than 10-fold that of the Atlantic (Veron, 2000; Hoeksema and Cairns, 2023), Indo-Pacific symbiont species have a larger range of potential hosts and the total number of coral associates is also expected to be much higher. A wide host range, however, does not necessarily result in low host specificity according to S_{TD} , as this index also depends on the taxonomic distinctness of the hosts. As mentioned before, and in addition to the larger species diversity in the Indo-Pacific region, there are on average more coral species per genus and family than in the Atlantic region (Hoeksema and Cairns, 2023). From an evolutionary perspective, groups of host-specific symbionts in the Indo-Pacific have a larger potential number of new hosts that are closely related (of the same genus) and therefore could become slightly less host-specific. Generalist symbionts are less selective in their host choice and may settle on a range of hosts that are not closely related.

Table 5

Host families with at least one host species (ranked according to decreasing number of host-symbiont relationships). Number of relationships, the total unique symbiont-host relationships found in this study; number of species, total number of species in the host family; number of host species, total number of host species of a host family found in this study.

Host families	Number of relationships	Number of species	Number of host species
Scleractinia			
Merulinidae Verrill, 1865	240	150	60
Fungiidae Dana, 1846	142	54	36
Acroporidae Verrill, 1901	137	271	62
Agariciidae Gray, 1847	75	47	26
Poritidae Gray, 1840	70	99	22
Pocilloporidae Gray, 1840	67	54	19
Dendrophylliidae Gray, 1847	45	165	22
Lobophylliidae Dai & Horng, 2009	38	60	13
Faviidae Milne Edwards & Haime, 1857	34	23	15
Caryophylliidae Dana, 1846	20	286	11
Rhizangiidae d'Orbigny, 1851	19	31	5
Psammocoridae Chevalier & Beauvais, 1987	14	10	5
Oculinidae Gray, 1847	12	20	7
Montastraeidae Yabe & Sugiyama, 1941	12	1	1
Astrocoeniidae Koby, 1890	10	6	3
Leptastreidae Rowlett, 2020	10	8	3
Pachyseridae Hoeksema & Benzioni, 2023	8	14	2
Meandrinidae Gray, 1847	8	7	4
Euphylliidae Alloiteau, 1952	8	23	4
Plesiastreidae Dai & Horng, 2009	6	1	2
Oulastreidae Vaughan, 1919	3	1	1
Cladocoridae Milne Edwards & Haime, 1857	2	4	2
Astrangiidae Milne Edwards & Haime, 1857	1	15	1
Diploastraeidae Chevalier & Beauvais, 1987	2	1	1
Anthoathecata			
Milleporidae Fleming, 1828	14	16	6
Stylasteridae Gray, 1847	2	330	1
Scleractyonacea			
Coralliidae Lamouroux, 1812	1	42	1

Table 6

Hospitality expressed as the number of symbiont species per coral host. Rounded percentages of each number within a total per symbiont group is presented between parentheses. Only *Favites abdita* has a maximum of 14 symbiont species.

Nr. symbiont species	Nr. hosts for Pyrgomatidae	Nr. hosts for Cryptochiridae	Nr. hosts for Serpulidae	Nr. hosts for Lithophaginae	Total nr. of hosts
1	117 (52%)	106 (77%)	77 (74%)	68 (80%)	140 (42%)
2	48 (22%)	23 (17%)	17 (16%)	10 (12%)	71 (21%)
3	31 (14%)	9 (7%)	6 (6%)	4 (5%)	47 (14%)
4	17 (8%)	1 (1%)	1 (1%)	1 (1%)	26 (8%)
5	3 (1%)	1 (1%)	2 (2%)	1 (1%)	16 (5%)
6	4 (2%)	1 (1%)	1 (1%)	1 (1%)	13 (4%)
7	2 (1%)				11 (3%)
8					4 (1%)
9	1 (<1%)				2 (1%)
10					4 (1%)
12					1 (<1%)
13					1 (<1%)
14					1 (<1%)

In addition to the availability of suitable host species, several other drivers of host specificity are involved. Over time, host ranges of a symbiont taxon can change. Pyrgomatid barnacles, for example, show an evolutionary direction towards a generalist strategy (Ogawa and Matsuzaki, 1992). Mechanisms causing a decrease in host specificity are host switching events (Hoeksema et al., 2018b; Potkamp and Franssen, 2019), colonization of new host species, and exclusive speciation of host species (Poulin, 2011). Other mechanisms can cause an increase in host specificity, e.g. co-speciation or independent evolution in which host selectivity is increased by the symbiont species (Poulin, 2011). Based on their S_{TD} , Atlantic symbionts may have undergone more evolutionary host range expansion and/or Indo-Pacific symbionts more evolutionary host diversification. Recent host range expansions have been demonstrated by the Atlantic host-generalist serpulid *Spirobranchus giganteus* and the date mussel *Leiosolenus aristatus*, both of which have started an association with invasive *Tubastraea* spp. from the Indo-Pacific, which were introduced in the Atlantic since the 1930s (Hoeksema and ten Hove, 2017a; Vinagre et al., 2018). Symbionts in the native range of *Tubastraea* spp., such as some corallivorous snails of the genera *Epidendrium* and *Phestilla* (Gittenberger and Gittenberger, 2005; Yiu and Qiu, 2023), have not yet been reported from the Atlantic.

Finally, it has to be noted that various groups of coral associates are well represented in the Indo-Pacific but strikingly absent in the Atlantic. Examples are: epitoniid gastropods (Gittenberger and Gittenberger, 2005), gall-forming, endolithic gastropods (Gittenberger and Gittenberger, 2011), acoel flatworms (Kunihiro et al., 2019), and corallivorous nudibranchs (Yiu and Qiu, 2022, 2023). Some other coral-associated groups are poorly represented in the Atlantic, such as sessile ctenophores (Alamaru et al., 2017; Glynn et al., 2019) and zancleid hydrozoans (Montano et al., 2017a; Maggioni et al., 2022a). The present study benefitted from four selected groups of coral associates being well represented in studies covering both the Atlantic and the Indo-Pacific.

4.5. Variation across symbiont groups

Considering host specificity between symbiont groups, the facultative relationship of coral-associated species makes it plausible that the symbiont species exploits a relatively wide range of host species. The high S_{TD} for both coral-associated serpulids and date mussels in the present study is therefore in line with this expectation, as many species in these symbiont groups were recorded on abiotic substrates. Serpulidae shows the highest S_{TD} of all four symbiont groups, which is significantly higher than the S_{TD} of both the Pyrgomatidae and the Cryptochiridae. The relatively high host specificity for cryptochirids is in line with the obligate relationship

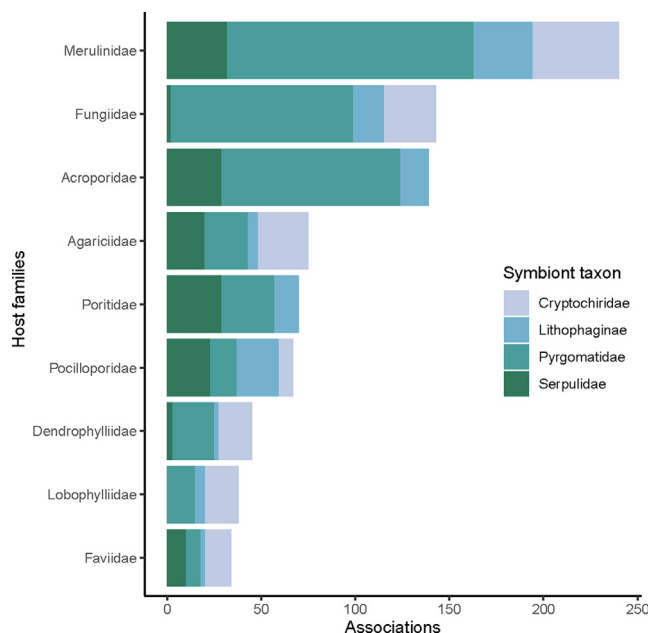


Fig. 8. Hospitality among host coral families with more than 30 unique associations according to their total numbers of unique symbiont-host associations divided over the four target taxa.

with their host. In earlier studies a high degree of host specialization was mentioned (Kropp and Manning, 1987; van der Meij et al., 2015b), but this was not based on a direct comparison with other symbiont taxa, as in the present study. The high host specificity of pyrgomatid barnacles also corresponds to the obligate relationships with their hosts (Ross and Newman, 1973; Ogawa and Matsuzaki, 1992). Moreover, sponge-inhabiting barnacles were also found to show a high degree of host specificity (van Syoc et al., 2015), suggesting that this trait may be characteristic of associated barnacles in general.

4.6. What makes a hospitable host?

Host coral families were not represented equally in this study (Fig. 8). Merulinidae showed the most unique symbiont-host relationships, and contained the highest number of host species. Acroporidae is the largest scleractinian reef coral family with 271 species (Hoeksema and Cairns, 2023), of which only 52 were recorded as hosts. Dendrophylliidae, a family composed of 165 species of which 90% is azooxanthellate (Cairns, 2001), was poorly represented with only 22 host species and 39 unique associations. The unequal taxonomic distribution in host species is consistent with results of a review study (Stella et al., 2011). However, the most inhabited taxa found in that study did not coincide with the present one, which can be explained by the difference in assessed taxa. The most inhabited genus studied by Stella et al. (2011) was *Porites*, which so far has not been found to be inhabited by cryptochirids. However, there is a possible gall crab record in the Caribbean poritid *Porites astreoides* (Lympiraki et al., 2022; Fig. 2B) and confirmed records of the gall crab genus *Opecarcinus* in two *Porites* spp. in the Red Sea, which were, however, located close to regular hosts species of the genus *Pavona* (Bähr et al., 2023). It is as yet unclear why certain host species are more preferred by coral associates than others, but it is for instance possible that the host's microbiome plays a role herein, as suggested for coral-dwelling hydroids (Bonito and McInnis, 2019).

The co-evolutionary history of corals and groups of symbiotic invertebrates is also an important component contributing to the

host dependence of the latter, which may be most relevant in the host-specific Pyrgomatidae and Cryptochiridae, and less so for the more substrate generalist taxa Serpulidae and Lithophaginae. Host switches and host range extensions of symbionts may occur where regular hosts are not available, as observed in a relatively isolated population of a gall crab living with an atypical host coral (Hoeksema et al., 2018b). Relationships may perhaps also start by accident, as for example in a commensal shrimp observed on a nudibranch snail (Hoeksema and Fransen, 2017) instead of its regular anthozoan hosts (Brinkmann and Fransen, 2016; García-Hernández and Schizas, 2021). In contrast to the host-specific Pyrgomatidae and Cryptochiridae of the present study, there are also crustacean families that live in symbiosis with hosts from different phyla, such as the pea crab family Pinnotheridae (de Gier and Becker, 2020; Hultgren et al., 2022) and commensal shrimps of the family Palaemonidae (Horká et al., 2016; de Gier et al., 2022). A large difference between the above-mentioned host-specific taxa and the two host-generalist taxa is that the latter are also occurring on abiotic substrates. This is shown by separate studies on serpulid worms (Hadfield et al., 2021; Nishi et al., 2022; Kupriyanova et al., 2023) and date mussels (Kleemann, 1990; Owada, 2007; Ricci et al., 2015).

The following morphological and ecological traits can be considered when evaluating whether a host coral is hospitable or not: (i) attached versus free-living corallum, (ii) massive versus branching coral growth form, (iii) large versus small body size, (4) host coral defences, and (5) bathymetrical range.

4.6.1. Host coral growth form: attached versus free-living

Pyrgomatidae, Cryptochiridae, and Lithophaginae are more represented in free-living corals than Serpulidae. Attached corals usually provide a more stable habitat than free-living corals, which can be mobile, especially when they are small (Ohara et al., 2021; Herrán et al., 2022; Bayley and Mogg, 2023; Mehrotra et al., 2023). The underside of free-living corals, such as most species of Fungiidae, may provide shelter to epibionts (Hoeksema et al., 2013b; Rauch et al., 2019) but when they become overturned (Jokiel and Cowdin, 1976; Hoeksema and Bongaerts, 2016), epibionts become exposed to predators (Gittenberger and Hoeksema, 2013). Serpulid associates are strongly underrepresented in the associate fauna of Fungiidae, 80% of which are free-living (Gittenberger et al., 2011; Benzoni et al., 2012). When a coral is overturned, a serpulid worm may not have space to extend its radioles and capture food. The only fungiid known to host a serpulid symbiont is attached (Hoeksema and ten Hove, 2014). Coral barnacles are much smaller than serpulids and a few of them have been observed to live underneath mushroom corals (Fig. 1F). Date mussels and gall crabs can find protection inside their holes (Kleemann and Hoeksema, 2002; Hoeksema et al., 2012, 2022b; van der Meij et al., 2015a) which may help them to survive when a free-living host is overturned.

4.6.2. Host coral growth form: massive versus branching

Some symbiont species live partly embedded in coral skeleton, whereas others can survive very well on the coral surface. Massive corals offer much volume and exposure, whereas branching corals offer much surface space and shelter. The host species with the highest record of associated species are the branching *Pocillopora damicornis* ($n = 14$) and the massive *Favites abdita* ($n = 13$). The first has tightly arranged branches that may provide more protection from predation than host corals with widely spaced branches (Vytopil and Willis, 2001; Stella et al., 2010). *Favites abdita*, however, has a massive growth form and is mostly preferred by pyrgomatid species. *Spirobranchus* worms are present in both branching and massive species, especially in the latter (Montebon and Yap, 2009; van der Schoot and Hoeksema, 2022). This could be related

to less obstructed current speeds, allowing a better delivery of food particles to the filter-feeding serpulid (Strathman et al., 1984). A massive growth form may also offer more protection against predators since a large part of the worm tube is embedded in the coral skeleton (Muller et al., 2020). Most species of Acroporidae are branching and are not inhabited by gall crabs (Bähr et al., 2023). Instead, Atlantic *Acropora* spp. are inhabited by gall-forming crabs of the family Domeciidae (Hoeksema and García-Hernández, 2020), making the absence of cryptochirids in these corals even more enigmatic.

4.6.3. Host coral growth form: large versus small body size

Small coral species consisting of single polyps are able to act as hosts for barnacles that are almost the same size as the host (Karasawa and Kobayashi, 2022). The only symbiont recorded from the smallest mushroom coral species, *Cycloseris boschmai*, is a barnacle (Hoeksema, 2014; Fig. 12e). Mushroom corals that reproduce asexually by autotomy, resulting in the production of many small coral fragments (Hoeksema and Waheed, 2011; Hoeksema et al., 2018a), are also able to act as hosts for barnacles (Fig. 1E). Some small gall crabs require little space and have been found to dwell in between the septa of mushroom corals (van der Meij et al., 2015b; Hoeksema et al., 2018b). Solitary corals of the genera *Heterocyathus* and *Heteropsammia* are relatively small and have been reported to host small bivalves inside their cavities, although not all of them are mytilids (Arnaud and Thomassin, 1976; Herrán et al., 2022). Many mushroom coral species (Fungiidae) have thin skeletons. Endolithic mytilids of the genus *Fungiacava*, which are only associated with species of this family (Table 4), can fit inside their hosts by adapting their position parallel to the corallum surface (Hoeksema and Gittenberger, 2008; Fig. 2), whereas individuals of the host-generalist genus *Leiosolenus* are usually positioned perpendicular to the upper surface, allowing them to penetrate deep into massive corals (Hoeksema et al., 2022b).

4.6.4. Host coral defences

The host's tolerance to the settlement of an associated species is another factor that determines its suitability as a host. Larvae of coral-associated barnacles settle on live coral tissue, which triggers a chemical defence response from the coral. The settling larva has to be able to repel this hostile activity for successful settlement; this only occurs in specific symbiont-host combinations (Liu et al., 2016). The settlement of barnacles and serpulids may evoke an inflammatory reaction in some host corals, such as *Porites* spp., which can be visible as pink colorations (Palmer et al., 2008; Samimi-Namin et al., 2010).

4.6.5. Shallow- versus deep-living hosts

Scleractinian families from which no host species were recorded mainly consist of azooxanthellate, solitary, deep-water species (Hourigan et al., 2017). Most deep-water corals are solitary with a small body size (e.g. Cairns, 1979, 2000; Cairns and Kitahara, 2012; Kitahara and Cairns, 2021), offering little space for epibionts. Five coral species are known to form deep-water reefs, all of which are branching: *Desmophyllum pertusum* (Linnaeus, 1758), *Goniocorella dumosa* (Alcock, 1902), *Madrepora oculata* Linnaeus, 1758, *Oculina varicosa* Le Sueur, 1820, and *Solenosmilia variabilis* Duncan, 1873 (Reed, 2002; Fallon et al., 2014; Arnaud-Haond et al., 2017; Buhl-Mortensen et al., 2017; Raddatz et al., 2020; Orejas et al., 2021; Anderson et al., 2022). Their branches are very thin, except at their base, forming dense, complex networks that create space for epifauna, but not so much for species that live partly embedded in the coral skeleton. Due to their depth, these reefs are not easy to sample for studies on associated fauna.

4.7. Relevance for coral reef conservation

The importance of associated fauna in the conservation of coral reef biodiversity has been expressed in earlier studies (Stella et al., 2011; Hoeksema, 2017; Montano, 2022). Conservation managers of coral reef areas have to be aware that much of what needs to be conserved is hidden (Hoeksema, 2017). Some host coral species in need of conservation are unique in their genus, reflecting phylogenetic distinctness (Huang, 2012; Curnick et al., 2015). This may affect Caribbean scleractinians, such as *Helioseris cucullata* (Ellis and Solander, 1786) and *Mussa angulosa* (Pallas, 1766) (Hoeksema et al., 2017; García-Hernández and Schizas, 2021). The Indo-Pacific reef coral *Heliofungia actiniformis* has a geographic range that is slightly larger than the Coral Triangle (Hoeksema, 1989, 2007). It needs special protection because it is harvested for the international aquarium trade (Knittweis and Wolff, 2010). For its conservation, it is relevant to know that it is the only host species of the commensal shrimp *Cuapetes kororensis* (Bruce, 1977) and the pipe fish *Siokunichthys nigrolineatus* Dawson, 1983 (Hoeksema, 2017). A coral can also be an important host because it is hospitable to a large range of associates, such as *Pocillopora verrucosa* (Cantera et al., 2003; Stella et al., 2011) and *Heliofungia actiniformis* (Hoeksema et al., 2012). In this way, they contribute significantly to coral reef biodiversity. The present study follows a quantitative approach by directly comparing coral taxa regarding the composition and species richness of their associated fauna. The new information can be applied to conservation strategies that not only focus on coral cover, but also on the protection of important and unique reef corals and their associated fauna.

On the other hand, coral-associated fauna could also have a negative impact on coral reef diversity when they occur in plague proportions and directly increase the mortality of their preferred hosts, occasionally in combination with coral bleaching, e.g. coral-livorous snails (Hoeksema et al., 2013a; Rice et al., 2019), or when they cause their hosts to become more susceptible to diseases, e.g. boring mussels and other corallivorous snails (Wong et al., 2016; Montano et al., 2022). Such negative impacts may overrule possible positive roles of coral symbionts in protecting their hosts against predators and diseases (DeVantier et al., 1986; Montano, et al., 2017b; Samsuri et al., 2018).

4.8. Future research directions

The recorded host ranges are currently extensive but likely incomplete. The results should therefore be interpreted with some caution, although we have learned that a few additional host records do not make a difference when the minimum threshold of three records is applied. It is recommended that new research should focus on deep-water species (Buhl-Mortensen and Mortensen, 2004). More taxonomists specializing in coral-associated fauna should try to identify and report the host species, which so far has not always been the case, such as in Serpulidae. Regarding date mussels, more effort should be made in future studies to identify the associated species, which means that host corals initially need to be broken (Hoeksema et al., 2022b), but this can be prevented later on when information on date-mussel DNA becomes available for barcoding. Although we have been dealing with four major symbiont groups, future studies on host specificity should also focus on other groups of associated fauna, which can be ecologically relevant if their species are harmful to their hosts, e.g. acael flatworms, feather duster worms, and worm snails. Future studies may also focus on which host corals are the most susceptible to damage caused by associated fauna. The results will contribute to a better understanding of coral reef biodiversity and can be applied to reef coral conservation.

4.9. Conclusion

This study presents an updated list of host species of four important groups of coral-associated invertebrates. The host specificity index (S_{TD}) sheds light on the characteristics of interspecific associations and the vulnerability of coral associated fauna, especially as many reef corals are now threatened with extinction (Carpenter et al., 2008). This is the first known study in which host specificity of coral symbionts is compared quantitatively between the Indo-Pacific and Atlantic oceans, indicating that Indo-Pacific symbionts are on average one-and-a-half to two times more host-specific than the more generalist Atlantic species. Symbiont groups with more generalist species (serpulid worms and date mussels) also contain species that are able to settle on abiotic substrates, whereas symbiont groups specialized to live on biotic substrates (coral barnacles and coral gall crabs) appear to be more host-specific.

Acknowledgements

The first author was funded by the Dutch Research Council (NWO) Doctoral Grant for Teachers Programme (nr. 023.015.036). We are grateful to Dr. Elena Kupriyanova (Australian Museum, Sydney) for supplying pictures of the specimen of *Hydroides lirs* and its host. We want to thank Dr. Benny K.K. Chan (Academia Sinica, Taiwan) for confirming the identity of the barnacle in Fig. 1B. We are also grateful to two anonymous reviewers, the editorial assistant, and the editor for their constructive comments.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ijpara.2023.09.002>.

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