

Review article.

Symbiosis in Deep-Water Corals

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Received October 7, 2003; Accepted December 20, 2003

Abstract

Deep or cold-water corals house a rich fauna of more or less closely associated animals. This fauna has been poorly studied, and most of the records are sporadic observations of single species. In this review we compile available records of invertebrates associated with alcyonarian, antipatharian, gorgonian, and scleractinian deep-water corals, including our own previously unpublished observations. Direct observations of the location of mobile species on deep-water corals are few and samples of deep-water corals often contain a mixture of sediments and broken corals. The nature of the relationship between the associated species and the coral is therefore in most cases uncertain. We present a list of species that can be characterised as symbionts. More than 980 species have been recorded on deep-water corals, of these 112 can be characterised as symbionts of which, 30 species are obligate to various cnidarian taxa. Fifty-three percent of the obligate deep-water coral symbionts are parasites, 47% are commensals. The obligate symbionts are rarer than their hosts, which implies that reduced coral abundance and distribution may be critical to the symbionts' ecology. Most of the parasites are endoparasites (37%), whereas ectoparasites and kleptoparasites are less common (13 and 3%, respectively). There are no clear examples of mutualistic symbiotic relationships with deep-water corals, but the behaviour of some of the common associates have equally strong elements of mutualism and parasitism.

Presented at the 4th International Symbiosis Congress, August 17–23, 2003, Halifax, Canada

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Comparisons of the symbiont fauna of deep-water corals and shallow or warm-water corals revealed that the diverse decapod and gastropod fauna symbiotic with shallow water corals is not paralleled in the deep-water coral community. Possible effects on the symbionts from damage to deep-water corals by fisheries are discussed.

Keywords: Symbiosis, commensalism, parasitism, deep-water corals, Alcyonacea, Gorgonacea, Scleractinia, Antipatharia

1. Introduction

It is well known that corals in the photic zone of temperate and tropical waters form complex habitats with a high diversity of associated organisms that often form close relations with their hosts. In contrast, little is known about the associated fauna of deep-water corals, especially deep-water gorgonians, and the role of corals in deep-water as habitat for other species is poorly understood. At the same time, there is a growing concern that human activities (e.g. fishing and oil-exploration) along the continental shelf edges and slopes may represent a threat to coral habitats in these environments. As fish stocks in shallower water have been overexploited, fisheries are moving into deeper water. Deep-water corals are thought to be particularly at risk because of their arborescent morphology and assumed slow growth.

What is a "coral" differs between studies. In this paper we include cnidarian species belonging to the orders Alcyonacea (soft corals), Gorgonacea (horny corals), Scleractinia (stone corals) and Antipatharia (black corals). Deep-water corals are found in all of the world's oceans and the Mediterranean Sea, and are most common at depths between 200 and 1000 m (Jungersen, 1917; Broch, 1935, 1957; Madsen, 1944; Zibrowius, 1980; Cairns, 1994). In fjords, they can occur much shallower. In total, there are more than 600 species of deep-water corals (Cairns et al., 1999). Among these, scleractinians such as *Desmophyllum*, *Goniocorella*, *Lophelia*, *Oculina* and *Solenosmilia* are able to form reefs (Stanley and Cairns, 1988).

Shallow water coral habitats accommodate a high diversity of algae, invertebrates and fish (McCloskey, 1970; Connell, 1978). In deep water, plants are absent, and in this paper we will focus on the invertebrates. The coral inhabitants demonstrate a great variety of life histories, and often occur together with corals in symbiotic relationships. Symbiosis can be defined as the relationship of two species living together (de Bary, 1879). Symbiosis is divided into three different categories (van Beneden, 1876) defined on the basis of the effect of the symbiont on the host: 1) mutualism: both species benefit of the relationship, 2) commensalism: the symbiont profit from staying with the host, while the host is unaffected, and 3) parasitism: the symbiont benefits, but

the host suffers from the relationship. These categories lie on a continuum, and it should be kept in mind that placement of a symbiosis into any of these three categories is likely to vary with conditions and perceived benefits to each partner. The symbiosis can be obligatory or facultative for one or both of the species. The term obligate has been defined in two different ways in the literature: occurrence restricted to only one host taxon, or involvement in only one of the three types of symbiotic relationships. If not specified, in this review "obligate" is used for symbionts only inhabiting corals. Commensalism is the most common relationship between corals and invertebrates. In an evolutionary context both parasitic and mutualistic symbiotic relationships may have evolved from commensalistic relationships (Smyth, 1960). On the other hand, parasitism can have been the initial relationship for many mutualistic and commensalistic relationships (Campbell, 1990). In many cases it can be hard to distinguish parasitism from predation, and there is an overlap between partial predation and parasitic feeding. This is evident in the literature where one species might be regarded as a parasite by one author, while regarded as a predator by another.

Little is known about the fauna associated with deep-water corals compared to shallow water corals. The deep-water coral that has been best studied with regards to associated fauna is the scleractinian *Lophelia pertusa*. Around 800 species have been recorded from this coral in the north-east Atlantic (Fosså and Mortensen, 1998; Rogers, 1999). Very little is known about the fauna associated with deep-water gorgonians, but previous studies indicate that they often house a large assemblage of mobile crustaceans and ophiuroids clinging to coral branches (Storm, 1901; Strømngren, 1970).

In this review we compile available information about associations between deep-water corals and invertebrates, and we present a list of species that can be characterised as symbionts, with some new and previously unpublished observations included. The deep-water coral associated fauna is compared with observations from shallow water corals.

2. Deep-Water Corals as Habitat

Most deep-water corals grow attached to hard substrates such as bedrock and larger stones (cobble and boulder). Stones in glacial till are a common substrate for corals in the North Atlantic (Mortensen et al., 2001; Mortensen et al., in press). Seabeds with irregular topography are known to support *Lophelia* reefs and stands of gorgonians (Genin et al., 1986; Mortensen et al., 2001; Mortensen et al., in press). Deep-water corals are also a peculiar part of the fauna of many fjords in Norway, northwest North America, and New Zealand, were they occur much shallower than at the shelf. The deep-water coral locations are

exposed to water with an oceanic origin, with temperatures commonly ranging from 6 to 10°C, and salinity >35. The currents at these locations are relatively strong, and are mainly driven by tidal forces.

Most corals have an arborescent morphology with branches elevated into faster flowing water above the relatively still boundary layer closer to the bottom. In addition, the orientation of colonies perpendicular to prevailing water currents in many species maximizes the amount of water flowing through the polyps at any given time (Wainwright and Dillon, 1969). This enables the polyps in the colony to have maximum feeding access to water currents flowing across the gorgonian branches. This advantage is also passed on to any rheophilic, filter-feeding epizoid animal associated with the colony. In addition, filter feeding organisms may also derive nutrition from detritus or micro-organisms commonly found trapped in the mucus secreted from the gorgonian colonies (Patton, 1972).

Deep-water coral reefs typically have a circular or elongated outline with a longest extension of up to ca 1000 m. They commonly display vertical zones with living coral atop and skeleton fragments at increasing stages of decay towards the foot of the reef (Mortensen et al., 1995). Four different microhabitats can be recognised within the coral colonies: 1) the smooth surface of living corals, 2) the detritus laden surface of dead corals, 3) the cavities inside dead skeleton, and 4) the free space between the coral branches. Many microhabitats very similar to these can also be found on bottoms without corals, therefore the majority of species found with corals are facultative symbionts.

3. Symbionts with Deep-Water Corals

The diversity of animals found together with deep-water corals is high (Reed et al., 1982; Reed and Mikkelsen, 1987; Jensen and Frederiksen, 1992; Rogers, 1999). In this study we compiled data on 983 invertebrate species reported from 74 deep-water coral species. Most of these associated species are also known from other habitats. Presumably firm substratum in a high current environment is a limited resource in deep-water and thus the corals provide an important habitat for sessile invertebrates. Direct observations of location of mobile species on deep-water corals are largely lacking. Furthermore, samples of deep-water corals often contain a mixture of sediments and broken corals. The nature of the relationship between the associated organism and the host coral is therefore often uncertain.

Even though the majority of species recorded as associated with deep-water corals also occur in other habitats, many of them show clear signs of adaptations to living with corals. Among the species known to be associated with *Lophelia* reefs, several have direct development or very short planktonic

larval stages. This ensures that the offspring stay within the coral habitats, which exhibit a highly patchy distribution.

Table 1 gives an overview of invertebrates reported to be more frequent or abundant on live (including the microhabitat of exposed skeleton) deep-water corals than other habitats. Only 114 of the 983 species recorded on deep-water corals can be characterised as symbionts. Of these, 36 species are obligate (or likely to be obligate) to various cnidarian taxa (Table 1). Fifty-three percent of the obligate deep-water coral symbionts are parasites, whereas commensals account for 47% of the number of species. Most of the parasites are endoparasites (37%), whereas ectoparasites and kleptoparasites are less common (13 and 3% respectively). There are no documented clear examples of mutualistic symbiotic relationships with deep-water corals, but the behaviour of some of the common species associated with the corals have equally strong elements of mutualism and parasitism (i.e. Mortensen, 2001: *Eunice norvegica*).

Foraminifera

There is a large number of foraminiferans living attached to hard substrates in deep-water, and many of these (e.g. *Cibicides lobatulus*) are common on dead parts of organisms rising above the seabed, such as corals and sponges. To our knowledge only the parasite *Hyrrokkin sarcophaga* and the possibly commensal *Planispirinoides bucculentus* have direct contact with live coral tissue. Both species are facultative symbionts. *H. sarcophaga* is known from *Lophelia pertusa* in the Northeast Atlantic (Mortensen, 2001), whereas *P. bucculentus* is common on the branches of *Capnella florida* (Alcyonacea) collected from the shelf break off Nova Scotia (own observations).

Cnidaria

Seven species of Actinaria are reported as commensals mainly on gorgonians. Two of these (*Amphianthus inornata* and *Sagartia acanella*) are obligate on the gorgonians *Acanella arbuscula* and *A. normanni*, respectively, in the North Atlantic (Verrill, 1883; Whiteaves, 1901; Bronsdon et al., 1993). Several epizoanthid actinarians grow as pseudocolonies on different gorgonians and *L. pertusa* (Storm, 1901; Dons, 1944; Carlgren, 1945). In the Northeast Channel, off Nova Scotia, *Epizoanthus* sp. has been observed as a parasite gradually overgrowing and killing *P. resedaeformis* (Mortensen et al., in press). *Protanthea simplex* is so common on *L. pertusa* that Dons (1944) introduced the Norwegian common name "korallnellik", which translates to "coral carnation". The octocoral *Alcyonium (Parerythropodium) coralloides* is recorded as a commensal mainly on gorgonians in the Mediterranean (Weinberg and

Weinberg, 1979). McFadden (1999) found one distinct morphotype of this species, which she believes is a separate species, only on gorgonians.

Polychaeta

Polynoidae is the most common family of symbiotic polychaetes on deep-water corals. Five of the 12 species listed in Table 1 are obligate to antipatharian and gorgonian corals (Pettibone, 1991a,b; Martin and Britayev, 1998). *Harmothoe oculinarum* lives on *Lophelia pertusa*, often inside tubes of the polychaete *Eunice norvegica* (Dons, 1944; Jensen and Frederiksen, 1992; Mortensen, 2001). The nature of this relationship is not known, but it seems likely that the coral is essential for *H. oculinarum* since it has not been reported from polychaete tubes in other habitats. The polychaete is bright white and blends in with the coral. *Eunice norvegica* is more common on *L. pertusa* than in other hard bottom habitats in the North Atlantic (Dons, 1944; Jensen and Frederiksen, 1992; Mortensen, 2001). It commonly feeds on food particles captured by the coral's polyps, and may thus be regarded as a facultative kleptoparasite (Mortensen, 2001). However, it also exhibit mutualistic behaviour since it cleans the coral surface and attacks invading mobile organisms (Mortensen, 2001). *E. pennata* and *E. dubiata* are reported as facultative kleptoparasitic commensals or mutualists on *Madrepora oculata* (Martin and Britayev, 1998). An other example of kleptoparasitic commensal or mutualist is *Haplosyllis anthogorgicola* which is reported as obligate on *Anthogorgia bocki* in the Japanese seas (Utinomi, 1956). *Lumbrineris flabellicola* is perhaps the polychaete with the widest array of coral hosts in deep-water. It is obligate commensal on cnidarians, mainly scleractinians, but also occurs on unidentified hydroids and zoantharians (Zibrowius et al., 1975). It has been recorded from 22 scleractinian species in the Pacific and Indian Ocean (Miura and Shirayama, 1992; Zibrowius et al., 1975; Cairns and Zibrowius, 1997).

Crustacea

The lamippid copepod *Enalcyonium olssoni* is an obligate endoparasite in octocorals. It was recently observed for the first time inside *P. resedaeformis* (Buhl-Mortensen and Mortensen, 2004a). A new lamippid species was found living in galls which it induces in its host *P. arborea*. There are very few gall-forming lamippid copepods, and this species represents a new genus described by Buhl-Mortensen and Mortensen (2004b). Cirripedia is the most species rich group of symbiotic crustaceans on deep-water corals. Most of these belong to the order Ascothoracica, which comprises obligate endoparasites. These cirripeds

form permanent galls on the branches of the coral (Moyses, 1983; Grygier, 1990). The stalked barnacle *Ornatoscalpellum (Scalpellum) stroemii* is a facultative commensalist common on gorgonians off Nova Scotia (Buhl-Mortensen and Mortensen, in press). It is frequently found on exposed skeleton of *Primnoa resedaeformis* and on hydroids attached to the coral. *O. stroemii* is also recorded from the Norwegian coast on the gorgonians *Paramuricea placomus*, *P. resedaeformis* and *Isidella lofotensis* (Broch, 1924). The early observations of *O. stroemii* on *P. resedaeformis* were so frequent that Ström (1788) named it *Lepas gorgoniae*.

Furthermore, Linné named the host *P. resedaeformis*, *Gorgonia lepadifera*, due the resemblance between the scalpellid and the polyps of its gorgonian host (Broch, 1918). Two less known species collected from the skeleton of gorgonians are one new *Heteralepas* species (on *P. resedaeformis*) and *Arcoscalpellum michelottianum* (on *Keratoisis ornata*) from offshore Nova Scotia (own observations). *A. michelottianum* has a wide distribution, but very few records worldwide. Amphipods and isopods dominate the associated fauna on deep-water gorgonians in terms of abundance (Storm, 1901; Strømngren, 1972; Buhl-Mortensen and Mortensen, 2004a), but so far no obligate symbionts have been identified. The decapods occurring on deep-water corals are dominated by anomuran and palaemonid shrimps. *Munidopsis serricornis* (Lovén, 1853) (syn. *Galathodes tridentata*) is a commensal seemingly obligate to cnidarians, mainly occurring on *L. pertusa* in the Northeast Atlantic (Dons, 1944; Jensen and Frederiksen, 1992; Mortensen, 2001), but is also reported from *P. placomus* (Storm, 1901).

In the Northwest Atlantic, *Eumunida picta* occurs on *L. pertusa* and *Primnoa resedaeformis* (Nizinski et al., in press; Buhl-Mortensen and Mortensen, 2004). The shrimps *Pandalus propinquus*, *Caridion gordonii*, and *Synalpheus townsendi* are facultative commensals on deep-water corals in the Atlantic Ocean. The two first have been reported from *Paragorgia arborea* and *L. pertusa* (Storm 1901; Buhl-Mortensen and Mortensen, 2004a), while the latter is found on the *Oculina* reefs off Florida (Reed et al., 1982). *Periclimenes franklini*, a symbiont with gorgonian deep-water corals in the Coral Sea, is to our knowledge, the only report of symbiotic shrimps from the Pacific Ocean (Bruce, 1990).

Mollusca

All of the symbiotic gastropods on deep-water corals are parasites or predators. Most of these have been found on the *Oculina* reefs off Florida (Reed and Mikkelsen, 1987). *Alvania jeffreysi* is probably a predator and has been reported from *L. pertusa* and gorgonians off Norway (Storm, 1901; Fosså and Mortensen, 1998).

Table 1. List of symbiotic invertebrates recorded from deep-water corals (Alcyonacea, Antipatharia, Gorgonacea and Scleractinia). Dependence: symbionts dependence of coral host (F = facultative, O = obligate). Relation: type of relation with the coral host (C = commensal, E = endoparasite, K = kleptoparasite, M = mutualist, P = parasite). * = also known from seapens (Pennatulacea).

Symbiont	Host coral(s)	Dependence	Relation	General distrib.	Reference
PROTOZOA					
Foraminifera					
<i>Hyrrokkia sarcophaga</i>	Cedhagen, 1994	F	P	North Atlantic	Mortensen (2001)
<i>Planispirinoides bucculentus</i>	Brady, 1884	F	?	Off Nova Scotia	Own observation
CNIDARIA					
Actinaria					
<i>Amphiantus inornatus</i>	Gravier, 1918	O	C	North Atlantic	Bronsdon et al. (1993)
<i>Epizoanthus norvegicus</i>	Koren & Danielssen, 1877	F	C	North Atlantic	Dons (1944); Carlgren (1945)
<i>Epizoanthus</i> sp.		F	C/P	North Atlantic	Storm (1901); Mortensen et al. (in press)
<i>Protanthea simplex</i>	Carlgren, 1891	F	C	NE Atlantic	Dons (1944); Jensen & Frederiksen (1992)
<i>Dactyloanthus antarcticus</i>	Clubb, 1908	F	C	Chilean fjords	Dayton et al. (1997)
<i>Sagartia acanella</i>		O	C	Off Nova Scotia	Verrill (1883); Whiteaves (1901)
<i>Synanthus mirabilis</i>	Verrill, 1899	?	C	Off Nova Scotia	Verrill (1883); Whiteaves (1901)
Alcyonaria					
<i>Alcyonium (Parerythropodium) coralloides</i>		F	C	Mediterranean	Weinberg & Weinberg (1979)
<i>Alcyonium (Parerythropodium) sp.</i>		O	C	Mediterranean	McFadden (1999)
POLYCHAETA					
Polynoidea					
<i>Bayerpolynoe floridensis</i>	Pettibone, 1991	O	C	Florida	Pettibone (1991b)
<i>Benhamipolynoe antipathicola</i>	Benham	O	C	Off New Zealand	Pettibone (1989)
<i>Brychionoe karenae</i>	Hanley & Burke, 1991	O	C	Tasman Sea	Martin & Britayev (1998)

Table 1. Continued

Symbiont	Host coral(s)	Dependence Relation	General distrib.	Reference
<i>Eunoe spinulosa</i> Verrill, 1879	<i>Acanella arbuscula</i> , <i>Acanthogorgia armata</i>	O? C	Off Nova Scotia	Own observation
<i>Gorgoniapolytnoe bayeri</i> Pettibone, 1991	<i>Narella clavata</i>	? C	North Pacific	Pettibone (1991a)
<i>Gorgoniapolytnoe caeciliae</i> Fauvel, 1913	<i>Acanthogorgia aspera</i> , <i>Candidella imbricata</i> , <i>Corallium johnsoni</i> , <i>Corallium niobe</i> , <i>Corallium tricolor</i>	O C	North Atlantic	Pettibone (1991a)
<i>Gorgoniapolytnoe galapagensis</i> Pettibone, 1991	<i>Narella ambigua</i>	? C	Eastern Central Pacific	Pettibone (1991a)
<i>Gorgoniapolytnoe guadalupensis</i> Pettibone, 1991	<i>Corallium imperiale</i>	? C	Eastern Central Pacific	Pettibone (1991a)
<i>Gorgoniapolytnoe muzikae</i> Pettibone, 1991	<i>Acanthogorgia bocki</i> , <i>Candidella helminthophora</i> , <i>Corallium</i> sp.	F C	North Pacific	Pettibone (1991a)
<i>Harmothoe acanellae</i> Verrill	<i>Acanella arbuscula</i> , <i>Acanthogorgia armata</i> , <i>Anthomastus grandiflorus</i>	O C	NW Atlantic	Martin & Britayev (1998)
<i>Harmothoe oculinarum</i> Storm, 1879	<i>Lophelia pertusa</i>	O? C?	NE Atlantic	Dons (1944); Jensen & Frederiksen (1992); Mortensen (2001) Jensen & Frederiksen (1992)
<i>Neopolynoe paradoxa</i> Storm, 1888	<i>Lophelia pertusa</i>	? C	NE Atlantic	Martin & Britayev (1998)
Eunicidae				
<i>Eunice</i> cf. <i>dubiata</i> Fauchald, 1974	<i>Madrepora oculata</i>	F C/K?	North Atlantic	Dons (1944); Mortensen (2001)
<i>Eunice norvegica</i> (L., 1758)	<i>Lophelia pertusa</i> , <i>Madrepora oculata</i>	F K/M	North Atlantic	Jensen & Frederiksen (1992); Mortensen (1992); Mortensen (2001)
<i>Eunice pennata</i> O.F. Müller, 1776	<i>Lophelia pertusa</i> , <i>Madrepora oculata</i> , <i>Primnoa resedaeformis</i>	F C/ K? M?	North Atlantic	Jensen & Frederiksen (1992); Martin & Britayev (1998); Buhl-Mortensen & Mortensen (in press)
Hesionidae				
<i>Leocrates chinensis</i> Kinberg, 1866	Corals	F C	Circumtropical to subtropical	Pettibone (1970)

Table 1. Continued

Symbiont	Host coral(s)	Dependence Relation	General distrib.	Reference
<i>Leocrates giardi</i> Gravier, 1900	Corals	F C	Red Sea, Central Pacific, China Sea	Pettibone (1970)
Lumbrineridae				
<i>Lumbrineris flabellicola</i> Fage, 1936	<i>Acoanthocyathus spiniger</i> , <i>Balanophyllia cellulosa</i> , <i>Balanophyllia</i> sp., <i>Caryophyllia transversalis</i> , <i>C. grayi</i> , <i>C. sarsiae</i> , <i>C. smithi</i> , <i>C. spinigera</i> <i>C. spinicarens</i> , <i>Ceratotrochus duodecimcostatus</i> , <i>Conotrochus brunneus</i> , <i>Dendrophyllia cornigera</i> , <i>D. cornucopia</i> , <i>Desmophyllum cristagalli</i> , <i>Flabellum chunii</i> , <i>F. lamellulosum</i> , <i>F. patens</i> , <i>F. pavonium</i> , <i>Flabellum</i> sp., <i>Rhizotrochus typus</i> , <i>Stephanocyantus mosseteyanus</i> , <i>Truncatoflabellum inconstans</i>	O C	Japanese seas, Philippine and Indonesian regions, Cairns & Zibrowius (1997) Indian Ocean	Miura & Shirayama (1992); Zibrowius et al. (1975); Cairns & Zibrowius (1997)
Sphaerodoridae				
<i>Sphaerodorum guilbaulti</i> Rullier, 1974	<i>Paragorgia arborea</i>	O ?	Cuba, Caribbean	Martin & Britayev (1998)
Spintheridae				
<i>Spinther arcticus</i> M. Sars, 1851	<i>Lophelia pertusa</i>	F C/P	North Atlantic, North Pacific, Mediterranean	Jensen & Frederiksen (1992); Kirkegaard (1992); Martin & Britayev (1998)
<i>Spinther oniscoides</i> Johnston, 1865	<i>Lophelia pertusa</i>	F C/P	North Atlantic, Mediterranean	Jensen & Frederiksen (1992); Kirkegaard (1992)

Table 1. Continued

Symbiont	Host coral(s)	Dependence Relation	General distrib.	Reference
Syllidae				
<i>Haplosyllis anthogorgicola</i> Utinomi, 1956	<i>Acanthogorgia bocki</i>	O K	Japanese seas	Utinomi (1956)
ARTHROPODA				
Pycnogonida				
<i>Colossendeis colossea</i> Wilson, 1881	<i>Paramuricea borealis</i>	F C	NE USA	Hecker et al. (1980)
Crustacea				
Copepoda				
<i>Enalcyonium</i> cf. <i>olssoni</i> de Zulueta, 1908	<i>Alcyonium digitatum</i> , <i>Primnoa resedaeformis</i>	O P	North Atlantic	Bresciani & Lützen (1962); Buhl-Mortensen & Mortensen (2004a)
<i>Lamippidae</i> sp. Nov.	<i>Paragorgia arborea</i>	O P	Nova Scotia	Buhl-Mortensen & Mortensen (2004b)
<i>Lichomolgidae</i> indet.	<i>Paragorgia arborea</i>	? P?	Nova Scotia	Buhl-Mortensen & Mortensen (2004a)
Tanaidacea				
<i>Apseudes spinosus</i> M. Sars, 1858	<i>Lophelia pertusa</i>	F C	North Atlantic	Jensen & Frederiksen (1992); Fosså & Mortensen (1998)
Cirripedia				
Ascothoracida				
<i>Cardomanica longispinata</i> Grygier, 1984	<i>Chrysoyorgia elegans</i>	O E	Bahamas, Lesser Antilles	Grygier (1984); Grygier (1990a)
<i>Introcornia australis</i> Grygier 1990	<i>Lophelia pertusa</i>	O E	Off St. Paul Island, southern Indian Ocean	Grygier (1990b)
<i>Introcornia conjugans</i> Grygier, 1982	<i>Caryophyllia decapali</i>	O E	Shikoku Island, Japan	Grygier (1982)
<i>Isidascus bassindalei</i> Moyses, 1983	<i>Acanella arbuscula</i>	O E	NE Atlantic	Moyses (1983)
<i>Thalassomembracis acanthosphaericus</i> Grygier, 1984	<i>Chrysoyorgia elegans</i>	O E	Bahamas	Grygier (1984)
<i>Thalassomembracis atlanticus</i> Grygier, 1990	<i>Chrysoyorgia quadriflex</i>	O E	SW of British Isles	Grygier (1990a)
<i>Thalassomembracis bayeri</i> Grygier, 1985	<i>Chrysoyorgia desbonni</i>	O E	Yucatan Channel	Grygier (1984)
<i>Thalassomembracis bilobus</i> Grygier, 1984	<i>Chrysoyorgia</i> cf. <i>papillosa</i>	O E	Hawaii	Grygier (1984)

Table 1. Continued

Symbiont	Host coral(s)	Dependence Relation	General distrib.	Reference
<i>Thalassomembracis conquistador</i> Grygier, 1984	<i>Chrysoorgia</i> sp.	O	Moluccas	Grygier (1984)
<i>Thalassomembracis orientalis</i> Grygier, 1985	<i>Chrysoorgia</i> sp.	O	Philippines	Grygier (1984)
<i>Thalassomembracis tetraedus</i> Grygier, 1985	<i>Chrysoorgia papillosa</i>	O	Madagascar	Grygier (1984)
Thoracica				
<i>Acasta hirsuta</i>	<i>Euplexaura</i> sp.	?	?	Broch (1931)
<i>Acasta gregaria</i> Utinomi, 1959	<i>Euplexaura</i> sp.	?	?	Utinomi (1959)
<i>Arcoscalpellum michelottianum</i>	<i>Keratois ornata</i>	F	Off Nova Scotia	Own observation
<i>Aurivillialepas calyculus</i> Aurivillius, 1898	Scleractinians	?	Azores	Newman et al. (2002)
<i>Conopea calceola</i> Ellis, 1758	Gorgonians.	O?	West Africa	Darwin (1854); Nilsson-Cantell (1938)
	<i>Rhipidogorgia</i> sp.		Persian Gulf, Indian Ocean	
<i>Solidobalanus auricoma</i> Hoek, 1913	<i>Acanthogorgia</i> sp.	F	Indian Ocean, North of New Zealand	Nilsson-Cantell (1938)
<i>Chirona hammeri</i> Ascanius, 1767	<i>Lophelia pertusa</i> , <i>Primnoa resedaeformis</i>	F	North Atlantic	Broch (1924); Dons (1944); Burdon-Jones & Tambbs-Lyche (1960); Own observation
<i>Heteralepas cornuta</i> Darwin, 1852	<i>Acanthogorgia</i> sp.	F	Indian Ocean, West Indies, West Africa	Nilsson-Cantell (1938)
<i>Heteralepas meteorensis</i> Carriol, 1998	<i>Callogorgia</i> sp.	?	Azores	Young (2001)
<i>Heteralepas</i> n. sp.	<i>Keratois ornata</i>	?	?	Own observation
<i>Neopyrgoma lobata</i> Gray, 1825	Scleractinians	?	Nova Scotia	Ross & Newman (2002)
<i>Ornatoscalpellum stroemii</i> M. Sars, 1859	<i>Isidella</i> sp., <i>Keratois ornata</i>	F	North Atlantic	Broch (1924); Dons (1944); Own obs.
<i>Pyrgoma japonica</i> Weltner, 1897	<i>Lophelia</i> sp.	?	Tokyo Bay	Ross & Newman (2002)
<i>Pyrgoma kuri</i> Hoek, 1913	<i>Caryophyllia</i> sp.	O	Indian Ocean, Moluccas	Ross & Newman (2002)
<i>Pyrgoma sinica</i> Renl, 1986	<i>Dendrophyllia</i> sp.	O	South China Sea	Ross & Newman (2002)
<i>Scillaelepas grimaldi</i> Aurivillius, 1898	Scleractinians	?	Azores	Newman et al. (2002)
<i>Scillaelepas superba</i> Pilsbry, 1907	Scleractinians	?	Western Atlantic	Newman et al. (2002)
<i>Scillaelepas</i> sp.	<i>Lophelia pertusa</i>	?	NE Atlantic	Newman et al. (2002)

Table 1. Continued

Symbiont	Host coral(s)	Dependence Relation	General distrib.	Reference
Amphipoda				
<i>Aeginella spinosa</i> Boeck, 1861	<i>Paragorgia arborea</i> , <i>Primnoa resedaeformis</i> , <i>Lophelia pertusa</i>	F C	North Atlantic	Strømngren (1970); Jensen & Frederiksen (1992); Fosså & Mortensen (1998); Buhl-Mortensen & Mortensen (2004a)
<i>Jassa pusilla</i> G.O. Sars, 1894	<i>Paragorgia arborea</i> , <i>Paramuricea placomus</i> , <i>Primnoa resedaeformis</i> , <i>Lophelia pertusa</i>	F C	Norwegian coast, Off Nova Scotia	Strømngren (1970); Fosså & Mortensen (1998); Buhl-Mortensen & Mortensen (2004a)
<i>Maxillipus commensalis</i>	Gorgonians	?	Papua New Guinea	Thomas (1996)
<i>Metopa brazeli</i> Goës, 1866	<i>Paragorgia arborea</i> , <i>Primnoa resedaeformis</i> , <i>Lophelia pertusa</i>	F C	Norwegian coast, Off Nova Scotia	Burdon-Jones & Tambis-Lyche (1960); Buhl-Mortensen & Mortensen (2004a)
<i>Proaeginina norvegica</i> Stephensen, 1931	<i>Paragorgia arborea</i> , <i>Lophelia pertusa</i>	F C	Norwegian coast, Off Nova Scotia	Dons (1944); Buhl-Mortensen & Mortensen (in press)
<i>Proboloites calcarata</i> G.O. Sars, 1882	<i>Paragorgia arborea</i> , <i>Primnoa resedaeformis</i>	F C	North Atlantic	Buhl-Mortensen & Mortensen (2004a)
<i>Stenopleustes malmgreni</i> Boeck	<i>Paragorgia arborea</i> , <i>Primnoa resedaeformis</i>	F C?	Norwegian coast, Off Nova Scotia	Vader (1969); Buhl-Mortensen & Mortensen (2004a)
<i>Stenopleustes nodifer</i> G.O. Sars, 1882	<i>Primnoa resedaeformis</i> , <i>Lophelia pertusa</i>	F C	North Atlantic	Strømngren (1970); Buhl-Mortensen & Mortensen (in press)
Isopoda				
<i>Astacilla longicornis</i> Sowerby, 1806	<i>Paramuricea placomus</i> , <i>Lophelia pertusa</i>	F C	Norwegian coast	Strømngren (1970); Storm (1901)
<i>Janira maculosa</i> Leach, 1814	<i>Paragorgia arborea</i> , <i>Lophelia pertusa</i>	F C	NE Atlantic	Jensen & Frederiksen (1992); Fosså & Mortensen (1998); Storm (1901)

Table 1. Continued

Symbiont	Host coral(s)	Dependence Relation	General distrib.	Reference
<i>Munna boeckii</i> Krøyer, 1839	<i>Paragorgia arborea</i> , <i>Primnoa resedaeformis</i> , <i>Lophelia pertusa</i> ,	F C	North Atlantic	Jensen & Frederiksen (1992); Fosså & Mortensen (1998); Buhl-Mortensen & Mortensen (2004a)
Decapoda				
Caridea				
<i>Caridion gordonii</i> Bate, 1858	<i>Paragorgia arborea</i> , <i>Lophelia pertusa</i>	F C	Norwegian coast	Storm (1901); Dons (1944)
<i>Pandalus propinquus</i> G.O. Sars, 1870	<i>Paragorgia arborea</i> , <i>Lophelia pertusa</i>	F C	North Atlantic	Storm (1901); Buhl-Mortensen & Mortensen (2004a)
<i>Periclimenes franklini</i> Bruce, 1990	<i>Primnoa resedaeformis</i> ,	O		Bruce (1990)
<i>Synalpheus townsendi</i>	<i>Lophelia pertusa</i> ,	F C	Coral Sea Florida	Reed et al. (1982)
Anomura				
<i>Galathea intermedia</i> Lilljeborg, 1851	<i>Oculina varicosa</i> <i>Lophelia pertusa</i>	F C	Norwegian coast, Cape Verde	Burdon-Jones & Tamba-Lyche (1960); Wirtz & Udekem d'Acoz (2001)
<i>Eumunida picta</i>	<i>Lophelia pertusa</i> , <i>Primnoa resedaeformis</i>	F C	Western Atlantic	Nizinski et al. (submitted); Buhl-Mortensen & Mortensen (2004a)
<i>Galathea rostrata</i>	<i>Oculina varicosa</i>	F C	Florida, SW North Atlantic	Reed et al. (1982)
<i>Munidopsis serricornis</i> Lovén, 1852	<i>Paramuricea placomus</i> , <i>Lophelia pertusa</i> ,	O? K?	Norwegian coast	Storm (1901); Dons (1944); Fosså & Mortensen (1998); Mortensen (2001)
<i>Nematopaguroides pusillus</i>	<i>Oculina varicosa</i>	F C	Florida, SW North Atlantic	Reed et al. (1982)
<i>Pagurus piercei</i>	<i>Oculina varicosa</i>	F C	Florida, SW North Atlantic	Reed et al. (1982)
Brachyura				
<i>Euchirograpsus americanus</i>	<i>Oculina varicosa</i>	F C	Florida, SW North Atlantic	Reed et al. (1982)

Table 1. Continued

Symbiont	Host coral(s)	Dependence Relation	General distrib.	Reference
<i>Micropanope barbadensis</i>	<i>Oculina varicosa</i>	F C	Florida, SW North Atlantic	Reed et al. (1982)
<i>Micropanope scutipes</i>	<i>Oculina varicosa</i>	F C	Florida, SW North Atlantic	Reed et al. (1982)
<i>Pseudomedusa distinctus</i> Rathbun	<i>Oculina varicosa</i>	F C	Florida, SW North Atlantic	Reed et al. (1982)
MOLLUSCA				
Gastropoda				
<i>Alvania jeffreysi</i> Waller, 1864	<i>Lophelia pertusa</i>	F P?	Norwegian shelf and coast	Jensen & Frederiksen (1992); Fosså & Mortensen (1998)
<i>Alvania</i> sp.	Gorgonians	F P?	Norwegian coast	Storm (1901)
<i>Coralliophila</i> sp. 2	<i>Oculina varicosa</i>	O P	Florida, SW North Atlantic	Reed & Mikkelsen (1987)
<i>Latiaxis mansfieldi</i> McGinty, 1940	<i>Oculina varicosa</i>	O P	Florida, SW North Atlantic	Reed & Mikkelsen (1987)
Bivalvia				
<i>Acesta excavata</i> J.C. Fabricius, 1779	<i>Lophelia pertusa</i>	F C	NE Atlantic	Dons (1944); Jensen & Frederiksen (1992); Fosså & Mortensen (1998)
<i>Bentharca nodulosa</i> Müller, 1776	<i>Lophelia pertusa</i>	F C	NE Atlantic	Dons (1944); Burdon-Jones & Tambis-Lyche (1960); Jensen & Frederiksen (1992)
<i>Delectopecten vitreus</i> Gmelin, 1791	<i>Acanthogorgia armata</i> , <i>Paragorgia arborea</i> , <i>Primnoa resedaeformis</i> , <i>Lophelia pertusa</i>	F C	North Atlantic	Verrill (1883); Dons (1944); Jensen & Frederiksen (1992); Fosså & Mortensen (1998); Buhl-Mortensen & Mortensen (in press)

Table 1. Continued

Symbiont	Host coral(s)	Dependence Relation	General distrib.	Reference
ECHINODERMATA				
Ophiuroidea				
<i>Asteronyx loveni</i> J. Müller & Troschel, 1842*	<i>Acanella arbuscula</i> , <i>Paramuricea placomus</i> , <i>Paramuricea grandis</i> , <i>Radicipes</i> sp., <i>Ellisella barbadensis</i> , <i>Ellisella barbadensis</i> , <i>Antipathes abietina</i> , <i>Antipathes</i> sp., <i>Ellisella barbadensis</i> , <i>Antipathes</i> sp., Gorgonians, <i>Lophelia pertusa</i>	O C	NE Atlantic	Fujita & Ohta (1988); Hecker et al. (1980); Mortensen (1927)
<i>Asterochema tenue</i> Lyman		O	Jamaica	Emson & Woodley (1987)
<i>Asteropora annulata</i>		F	Jamaica	Emson & Woodley (1987)
<i>Asterogordius cacaotica</i>		F	Jamaica	Emson & Woodley (1987)
<i>Gorgonocephalus caputmedusae</i> (L., 1758)		F	Norwegian coast	Mortensen (1927); Storm (1901); Dons (1944); Burdon-Jones & Tams-Lyche (1960)
<i>Gorgonocephalus eucnemis</i> J. Müller & Troschel, 1842	<i>Eunephthia</i> sp.	F	North Atlantic	Mortensen (1927)
<i>Gorgonocephalus lamarcki</i> J. Müller & Troschel, 1842	<i>Paragorgia arborea</i> , <i>Paramuricea placomus</i> , <i>Primnoa resedaeformis</i> , <i>Lophelia pertusa</i> Gorgonians	F	P/C Nova Scotia, Norwegian coast	Whiteaves (1901); Dons (1944); Buhl-Mortensen & Mortensen (in press)
<i>Hermiuryale pustulata</i>		F	Jamaica, Caribbean	Emson & Woodley (1987)
<i>Ophiacantha abyssicola</i> G.O. Sars, 1871	<i>Paragorgia arborea</i> , <i>Primnoa resedaeformis</i> , <i>Lophelia pertusa</i>	F	North Atlantic	Dons (1944); Burdon-Jones & Tams-Lyche (1960); Jensen & Frederiksen (1992); Buhl-Mortensen & Mortensen (in press)

Table 1. Continued

Symbiont	Host coral(s)	Dependence Relation	General distrib.	Reference
<i>Ophiacantha anomala</i> G.O. Sars, 1871	<i>Paragorgia arborea</i> , <i>Primnoa resedaeformis</i> , <i>Lophelia pertusa</i>	F C	North Atlantic	Dons (1944); Burdon-Jones & Tams-Lyche (1960); Jensen & Frederiksen (1992); Buhl-Mortensen & Mortensen (in press) Whiteaves (1901); Dons (1944); Fosså & Mortensen (1998) Hecker et al. (1980); John Gage (pers. comm.)
<i>Ophiomitrella clavigera</i> Ljungman, 1865	<i>Paramuricea placomus</i> <i>Lophelia pertusa</i>	F C	North Atlantic	
<i>Ophiomusium lymani</i> W. Thompson, 1873*	Gorgonians, <i>Acanella arbuscula</i>	F C	NE USA	
Asteroidea <i>Novodinia antillensis</i> A.H. Clark, 1934	Gorgonians	F C	Bahamas	Emson & Young (1994)
<i>Odinia americana</i>	<i>Paragorgia arborea</i>	F C	Nova Scotia	Whiteaves (1901)

Echinodermata

For deep-water corals *Ophiuroidea* is the only class comprising known symbiotic species. *Asteronyx loveni* has been found on *Radicipes* sp. (Fujita and Ohta, 1988), *Paramuricea* sp. (Hecker et al., 1980) and on *Funiculina quadrangularis* (Mortensen, 1927), and can be regarded as obligate to anthozoans. *Asteroschema tenue* is an obligate commensal on *Ellisella barbadensis* (Emson and Woodley, 1987). Basket stars (Gorgonocephalidae) are commonly found on gorgonians. *Gorgonocephalus caputmedusae* and *G. lamarckii* are common on *Paragorgia aborea* (Mortensen, 1927; Storm, 1901). Juveniles of *Gorgonocephalus eucnemis* occur parasitic on *Eunephthia* (Mortensen, 1927).

4. Comparison between Host Taxa

Symbionts (both obligate and facultative) are reported from 74 species of deep-water corals: 33 gorgonians, 29 scleractinians, seven alcyonaceans, and five antipatharians. The highest number of symbiotic species (65) was found for gorgonians. Fifty-three species were found with scleractinians, whereas alcyonarians and antipatharians both had five species each. Twenty-nine percent of the symbionts on deep-water gorgonians were obligate, where the comparable number for scleractinians was 11%. Cirripedia was the most species rich group in gorgonians, whereas for scleractinians crustacean decapods were as species rich as cirripeds. For antipatharians, polynoid polychaetes was the richest group, represented by 3 species. No taxonomic groups were typical for the alcyonarians.

5. Comparison of the Symbiont Fauna on Deep versus Shallow Water Corals

The diversity in shallow water reef communities is very high (McCloskey, 1970; Connell, 1978). Few faunistic studies cover several of the different habitats found in this biotope simultaneously because of the taxonomical challenges and complex habitat structure.

Our survey of available literature on obligate invertebrate symbionts in shallow water corals revealed 311 species from 210 coral species. Facultative symbionts of shallow water corals are not included in this review, but the number is much higher than for deep-water corals.

The ranking of the most common symbiotic taxa is very different for shallow and deep-water corals (Table 2). This picture is probably correct for most taxa, but for some it may simply reflect different research efforts. The deep-water

Table 2. Comparison between shallow and deep-water corals of the percentage composition of symbiotic species belonging to different taxa. obl. = obligate symbionts. fac. = facultative symbionts. unknown = unknown status.

	Shallow (obl.)*	Deep (obl.)	Deep (fac.)	Deep (unknown)
Protozoa				
Foraminifera	0	0	2	0
Porifera	1	0	0	0
Cnidaria	3	3	4	1
Polychaeta	5	11	8	4
Arthropoda				
Pycnogonida	0	0	1	0
Cirripedia	5	14	5	10
Copepoda	34	2	1	1
Tanaidacea	0	0	1	0
Amphipoda	1	0	7	1
Isopoda	0	0	3	0
Decapoda	29	2	12	0
Mollusca				
Gastropoda	15	2	2	0
Bivalvia	5	0	3	0
Echinodermata				
Ophiuridea	2	2	10	0
Asteroidea	0	0	2	0
No of species	311	36	61	17

*Data compiled from: Bayer (1961), Bruce (1970), Bruce (1976), Bruce (1990), Bruce (1994), Castro (1976), Clark (1976), Cronin et al. (1995), Darwin (1854), Demond (1957), de Zulueta (1908), Fujioka and Yamazota (1983), Gamo and Shinpo (1992), Garth and Hopkins (1968), Gerhart (1990), Glynn (1983), Goh (1991, 1996), Goh and Chou (1994a), Goh et al. (1999), Gohar and Soliman (1969), Grygier (1981), Harris (1975), Hickson (1906), Hoeksema and Achituv (1993), Humes and Stock (1973), Humes (1990), Humes (1993), Humes (1994), Kay and Switzer (1974), Liu and Hsieh (2000), Maes (1967), Martin and Britayev (1998), Miller (1972), Nakasone et al. (1986), Newman and Ladd (1974), Ng and Goh (1996), Nishi (1992), Odinetz-Collart and Richer de Forges (1985), Patton (1972), Patton (1976), Pettibone (1991a), Pettibone (1991b), Purchon and Purchon (1981), Reed et al. (1982), Ridder (1980), Robertson (1970), Ross and Newman (1999), Rudman (1991), Ruesing and Harvell (1990), Scott (1985), Spotte et al. (1995), Taylor (1968), ten Hove (1989), Thomas (1996), Tsuchiya and Yonaha (1992), Udekem d'Acoz (2001), Utinomi (1956), Weinberg and Weinberg (1979), Wirtz and Udekem d'Acoz (2001), Young (1989), and references found therein.

corals have been poorly investigated and it is likely that more symbionts will be identified as the research intensifies. One extreme example of how focused

research may result in a high representation of a single taxonomical group is the very high number of parasitic copepods on shallow water corals (e.g. Humes and Stock, 1973; Humes, 1990; Humes, 1993). The association of copepods with shallow water gorgonians has been known for a long time (de Zulueta, 1908), whereas this group has been overlooked in deep-water corals.

6. Why are there more Obligate Symbionts in Shallow-Water Corals than in Deep-Water Corals?

The average number of obligate symbionts per host coral species is two times higher for shallow water corals (1.2 per host) than for deep-water corals (0.6 per host). This introduces the obvious question: why are there more obligate symbionts in shallow-water corals than in deep-water corals? One answer could simply be that the food supply in shallow water coral reefs is mainly produced within the habitat, with the corals' production as an essential part. The deep-water corals and their associated species receive their food mainly through advection from sources outside the coral habitat, and specialisations in feeding strategies are not directed by the corals to the same extent. The high number of obligate symbionts in shallow water corals may also reflect the general pattern where interspecific obligate relationships are less common for high latitude biotopes in general, compared to the tropics (Rhode, 1978; Beaver, 1979). Several conditions can be used to explain this pattern, including time needed for development of such relationships, frequency of disturbance, and variability of nutrient supply. The frequency of disturbance at the depths inhabited by deep-water corals is probably low compared to tropical reef environments. However, at a geological time-scale the high latitudinal deep-water coral habitats have been subject to dramatic climatic changes, leading to regional extinctions during periods of glaciations. Therefore, the oldest *Lophelia* reefs in the Northeast Atlantic are less than 10,000 yr. old (Mortensen et al., 2001). The nutrient supply probably show stronger seasonal variations due to migration of dominant zooplankton and phytoplankton blooms. These environmental conditions are believed to disfavour specialisation and increased species diversity.

Further studies of deep-water coral communities in low latitudinal deep-waters could shed light on the hypothesis that interspecific obligate relationships are more common in the tropics than for high latitude biotopes in general. Habitats with many examples of obligate mutualistic symbiosis in the sea (e.g. coral reefs, and hydrothermal vents) characteristically have energy sources that are not available to the key organisms without help from the symbionts. No such "unavailable" energy sources have been identified in deep-water coral habitats.

Another possible explanation for the low diversity of obligate deep-water coral symbionts is restricted larval dispersal potential combined with widely separated habitat patches. Among the species known to be associated with *L. pertusa*, several have direct development or very short planktonic larval stages. An example is the internal brooding common in ophiacanthid ophiuroids (Mortensen, 1924), and in eunicid polychaetes (Kirkegaard, 1992). The ability to live in a variety of habitats may represent an adaptation for species with short larval periods to ensure successful dispersal in the long run. However, little is known about the life history for most of the species occurring on deep-water corals, and there are still large gaps in our understanding of the ecology of deep-water coral reefs and their associated species.

7. Threats to Symbionts in Deep-Water Corals

There is a growing concern that human activities (e.g. fishing and oil-exploration) along the continental shelf edges and slopes may represent a threat to coral habitats in these environments (Rogers, 1999; Fosså et al., 2002; Reed 2002; Mortensen et al., in press). As fish stocks in shallower water have been overexploited, fisheries are moving into deeper water. In general, intense bottom fishing has a strong negative effect on colonial and larger sessile benthic organisms (Sainsbury, 1997). Because of their arborescent growth form deep-water corals seem to be particularly vulnerable to encounters with fishing gear. There are several documented cases that bottom trawling is extremely destructive (Fosså et al., 2002), and recovery of deep-water corals from damage can be expected to be slow because of their low growth rates (assumed to be on the order of 1–2 cm per year) (Andrews et al., 2002). Damage of coral habitats in shallow waters have led to changed community structure (Sainsbury et al., 1997). The effects of damage to coral habitats on coral symbionts in deep-water is little known. Mortensen et al. (in press) showed that damages to deep-water gorgonians increase the frequency of lethal parasite infections. Since the obligate symbionts are rarer than their hosts, it is likely that reduced coral abundance and distribution may be critical to the successful reproduction and reproduction of the symbionts. It is important to incorporate the associated community, including the symbionts when assessing the status of deep-water corals.

Acknowledgement

This study was funded by the Environmental Studies Research Fund (ESRF), Department of Fisheries and Oceans (DFO), and the National Science and Engineering Council (NSERC) in Canada. We are grateful to Don Gordon and E.

Kenchington at Bedford Institute of Oceanography, Dartmouth, Canada for fruitful collaboration and discussions.

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