

**THE BIOLOGY AND ECOLOGY OF HAWAIIAN BLACK CORALS
(CNIDARIA: ANTHOZOA: HEXACORALLIA: ANTIPATHARIA)**

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ABSTRACT

Antipatharians, commonly known as black corals, are treasured by many cultures for medicinal purposes and to produce jewelry. Despite their economic and cultural importance, very little is known about the basic biology and ecology of black corals, because most species inhabit deeper-water environments (> 50 m) which are logistically challenging to study. The objectives of this dissertation were to (1) comprehensively review the literature on the biology and ecology of black corals worldwide, (2) provide a taxonomic guide to the shallow-water (<200 m) antipatharian fauna from the Hawaiian Archipelago, and (3) examine sexual reproductive processes within *Antipathes griggi*, the dominant species targeted by the Hawaiian black coral fishery. The literature review reveals that despite encompassing close to 240 species that are found in diverse environments, there are a number of generalities in the biology and ecology of black corals. Most antipatharian species are found in tropical and subtropical regions below depths of 50 m, on areas with hard substrates, low-light and strong currents. Antipatharians are generally slow-growing and long-lived organisms with longevities ranging from decades to millennia. With the exception of a few predators, antipatharians appear to be little impacted by predation. Like other corals, antipatharians can be habitat engineers of importance to a myriad of associated fish and invertebrates, several of which are adapted to live exclusively on black corals.

A taxonomic guide to the shallow-water (<200 m) antipatharian fauna of the Hawaiian Archipelago was created by examining all available museum specimens from

Hawaiian waters, as well as type material from species collected outside of Hawai‘i.

Based on these examinations eight species are identified from Hawai‘i including (1)

Antipathes griggi Opresko, 2009, (2) *Antipathes grandis* Verrill, 1928, (3) *Stichopathes echinulata* Brook, 1889, (4) an undescribed *Stichopathes* sp., (5) *Cirrhopathes* cf. *anguina* Dana, 1846, (6) *Aphanipathes verticillata* Brook, 1889, (7) *Acanthopathes undulata* (Van Pesch, 1914), and (8) *Myriopathes* cf. *ulex* (Ellis & Solander, 1786).

The sexual reproduction of *Antipathes griggi* was investigated using histological techniques. The results indicate that *A. griggi* is likely gonochoric with a 1:1 sex-ratio, and spawns continuously between June and December when temperatures are highest. Although, *A. griggi* can be found to depths of 100 m, it is rare below the 75 m depth limit at which commercial harvest occurs in Hawai‘i. Thus, the supposed depth refuge from harvest does not really exist, thereby calling into question population models used for the management of the Hawaiian black coral fishery.

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CHAPTER 1. INTRODUCTION

The Hawaiian Islands are part of the geographically longest and geologically oldest volcanic chains on Earth. Extensive coral reefs exist on every island and shallow bank of the archipelago from the island of Hawai'i past Kure Atoll, over 2000 miles to the northwest (Grigg 1988a; Grigg 1997; Fletcher et al. 2008; Grigg et al. 2008). The vast geographic isolation of the Hawaiian Archipelago has produced a unique biodiversity that is marked by one of the highest levels of marine endemism recorded on Earth (Roberts et al. 2002; DeMartini & Friedlander 2004; Cowie & Holland 2006; Parrish & Baco 2007). While Hawai'i's terrestrial and shallow-water (40 m) marine biodiversity have been well surveyed and documented (Eldredge & Evenhuis 2003; Eldredge 2006), organisms that inhabit Hawai'i's deeper marine ecosystems remain only marginally explored (Baco 2007; Parrish & Baco 2007). Antipatharians, commonly known as black corals, represent one of such particularly undersurveyed taxonomic groups, as evidenced by the high rates of species discoveries from recent deep-water surveys around the Hawaiian Islands (Opresko 2003b; Opresko 2005a; Baco 2007; Parrish & Baco 2007).

The Antipatharia is an anthozoan order within the subclass Hexacorallia encompassing 7 families, 43 genera and over 235 species (Cairns 2007; Daly et al. 2007; Bo 2008). The order is characterized by (1) a skeleton that is primarily proteinaceous and covered with minute skeletal spines, (2) polyps with six unbranched tentacles that are non-retractile, (3) six primary mesenteries, and (4) exclusively colonial organisms (Opresko 1972; Opresko & Baron-Szabo 2001; Daly et al. 2003; Daly et al. 2007; Bo

2008). Black corals occur worldwide in all oceans from polar to tropical regions, and have a wide depth distribution ranging from 2 m for tropical wire corals (Brook 1889; Davis & Cohen 1968; Parrish & Baco 2007; Bo 2008) down to abyssal depths of over 8,600 m for species in the western Pacific (Pasternak 1977; Molodtsova et al. 2008). Despite this wide bathymetric range, black corals are primarily found in deep waters below the photic zone, with over 75% of the currently described species occurring below 50 m (Cairns 2007). At these depths black corals are often abundant and dominant components of the sessile invertebrate fauna (Genin et al. 1986; Opresko & Genin 1990; Chave & Malahoff 1998; Grigg 2001; Rogers et al. 2007; Bo et al. 2009b), and create habitat for a myriad of species and associates (Grigg 1964; Goenaga 1977; Grange 1991; Buhl-Mortensen & Mortensen 2004; Boland & Parrish 2005; Love et al. 2007; Molodtsova & Budaeva 2007; Tazioli et al. 2007). However, because most species are found below the depth limits of conventional SCUBA diving, very little is known about the basic biology and ecology of black corals.

In Hawai‘i black corals are of particular importance, not just from an ecological perspective, but also from a cultural and economic one. First, black corals are dominant habitat-forming species on Hawaiian deep reefs (>50 m) (Grigg 1965; Grigg 1976; Chave & Malahoff 1998; Grigg 2001; Grigg 2004; Boland & Parrish 2005; Baco 2007; Kahng & Kelley 2007; Parrish & Baco 2007). Second, black corals are important culturally as they represent the official gemstone of the State of Hawai‘i and were traditionally used in Hawaiian culture for medicinal purposes (Kaaiakamanu & Akina 1922; Nagata 1971; Chun 1994). Third, Hawai‘i is the only place in the United States, and only one of few

places in the world, where black coral is harvested commercially for the precious coral jewelry industry, a multi-million dollar business that employs close to 650 people statewide (Grigg 2001; Morgan 2005; Parrish & Baco 2007; Grigg 2010; Tsounis et al. 2010). The fishery started in 1958 when large black coral beds were discovered off Lahaina on the island of Maui (Bayer 1961; Weaver 1961; Gage 1962; Grigg 1964). Since its inception, the fishery has been supplied by SCUBA divers that collect the coral at depths between 40-75 m, primarily in the Au‘au Channel between the islands of Maui and Lāna‘i, and to a lesser extent in the waters off South Kaua‘i (Grigg 2001; Parrish & Baco 2007; Grigg 2010). Deep-water surveys (40-110 m) performed in the Au‘au Channel in 1975 and 1998, suggested a stability in both recruitment and growth of commercially valuable black coral populations, and thus indicated that the fishery had been sustainable over this time period (Grigg 2001). However, subsequent surveys performed in the channel in 2001 indicated a substantial decline in the abundance of black coral colonies, with likely causes including increases in harvesting pressure and overgrowth of black coral colonies by the invasive octocoral *Carijoa* sp. (Grigg 2003; Grigg 2004; Kahng & Grigg 2005). Together, these factors renewed scrutiny on the black coral fishery and raised questions about whether regulations need to be redefined in order to maintain a sustainable harvest (Grigg 2004). Unfortunately, very little is known about the basic life history of black corals which complicates effective management of the resource (Grigg 2004). Three black coral species have been reported as being targeted by the Hawaiian precious coral fishery: *Antipathes griggi* Opresko, 2009 (formerly *A. dichotoma*), *Antipathes grandis* Verrill, 1928 and *Myriopathes ulex* (Ellis & Solander, 1786) (formerly *Antipathes ulex*) (Grigg 1976; Grigg 2001; Boland & Parrish 2005;

Parrish & Baco 2007; Grigg 2010; Wagner et al. 2010; Wagner et al. 2011a). However, over 90% of the coral harvested by the fishery consists of *A. griggsi* (Oishi 1990; Parrish & Baco 2007).

As a result of collaborations between scientists and the Hawaiian black coral fishery, antipatharian populations have been well documented in Hawai‘i (Grigg 1964; Grigg 1965; Grigg 1976; Grigg & Opresko 1977; Grigg 1993; Montgomery & Crow 1998; Grigg 2001; Montgomery 2002; Grigg 2004; Boland & Parrish 2005; Kahng & Grigg 2005; Kahng & Kelley 2007; Wagner et al. 2010; Wagner et al. 2011a), especially in comparison to most other geographic locations (Etnoyer & Morgan 2005).

Consequently some baseline data already exists for this group in Hawai‘i, and several specimens have previously been collected in Hawaiian waters and are available for further investigation. Therefore there is a unique opportunity to study black corals in Hawai‘i. Furthermore, as a result of the general scarcity of information available on antipatharians, the study of Hawaiian black corals provides the opportunity to learn new things among a widely understudied group.

The purpose of this dissertation is to examine the biology and taxonomy of Hawaiian black corals. As in other parts of the globe, antipatharians are found across a wide depth range in Hawaiian waters, with species reported from subtidal to abyssal depths (Chave & Jones 1991; Chave & Malahoff 1998; Parrish & Baco 2007). Due to logistical constraints of obtaining deep-sea samples, this study is mainly focused on those species found at depths down to 200 m, and includes, but is not limited to, commercially

valuable species. One of the advantages of focusing on the 0-200 m depth range, is that it includes mesophotic coral reef ecosystems, which are light-dependent coral reef ecosystems found below the depth limits of conventional SCUBA diving (40 m), and extending to the deepest portion of the photic zone, which may be over 150 m in some tropical locations with high water clarity (Puglise et al. 2009; Hinderstein et al. 2010; Kahng et al. 2010). Mesophotic coral reef ecosystems are notoriously undersurveyed worldwide, and in some areas they are even less sampled than those systems found in deeper waters (Pyle 1996; Menza et al. 2008; Puglise et al. 2009; Hinderstein et al. 2010; Kahng et al. 2010; Rooney et al. 2010; Wagner et al. 2011a). By focusing on depths containing these understudied systems, this dissertation seeks to address various gaps in our knowledge. Specifically, the objectives of this dissertation are to: (1) review the literature on the biology and ecology of black corals worldwide, (2) taxonomically describe Hawaiian antipatharian species, and (3) examine sexual reproductive processes within the commercially valuable black coral species *A. griggsi*.

CHAPTER 2. LITERATURE REVIEW

Introduction

Antipatharians, commonly known as black corals, represent a taxonomic order within the anthozoan subclass Hexacorallia that encompasses 7 families, 43 genera and over 235 species (Daly et al. 2007; Bo 2008). Many black coral species have been treasured by humans due to their presumed ability to fend off evil and ailments. In fact, the name of the order Antipatharia is derived from the Greek words "*anti*" and "*pathos*," and literally means against evil or disease (Castorena & Metaca 1979; Kenyon 1984; Romero 1997). Objects or remedies made out of black coral have been used in many cultures. In Indonesian folklore, black coral bracelets have been considered to increase virility and cure rheumatism (Grigg 1984; Tsounis et al. 2010). Around the Red Sea, black corals were used as an aphrodisiac and to cure eye diseases (Castorena & Metaca 1979). In Chinese traditional medicine, black corals are said to relieve pain, reduce fever, stop bleeding, and soften hard mass (Qi et al. 2009; Bai et al. 2011). In ancient Greco-Roman culture, black coral powder was applied to wounds before and after cranial surgery (Mariani-Costantini et al. 2000). In Hawaiian culture, a mixture of black coral powder and various other natural ingredients was used to remedy mouth sores and lung diseases (Kaaiakamanu & Akina 1922; Nagata 1971; Castorena & Metaca 1979; Chun 1994). Besides these therapeutic uses, several black coral species have been used to manufacture jewelry and art, and consequently have been harvested commercially in many regions around the globe, including throughout Asia, Hawai'i, Latin America, the Caribbean, the Mediterranean and the Red Sea (Gage 1962; Grigg 1975; Noome &

Kristensen 1976; Grigg & Opresko 1977; Castorena & Metaca 1979; Olsen & Wood 1980; Humann 1983; Grigg 1984; Kenyon 1984; Kerstitch 1989; Grigg 1993; Romero 1997; Grigg 2001; Maldonado 2003; Padilla & Lara 2003; Warner 2005; Parrish & Baco 2007; Deudin et al. 2010; Huang & Ou 2010; Tsounis et al. 2010. In addition to targeted commercial harvesting, black corals are also inadvertently caught in bottom trawls (Probert et al. 1997; Opresko 1998; Koslow et al. 2001; Häussermann & Försterra 2007; Murillo et al. 2010). As a result of overexploitations of black coral populations in several regions (Noome & Kristensen 1976; Romero 1997; Maldonado 2003; Padilla & Lara 2003), some governments have banned harvesting of antipatharians (Olsen & Wood 1980; Grange 1985; Grange 1988; Moon & Song 2005). Additionally, black corals are regulated on a global scale by the Convention on International Trade in Endangered Species of Wild Flora and Fauna (CITES), an intergovernmental treaty that controls the international trade of animals and plants. Since 1981 all species of black coral have been added to CITES Appendix II, which contains species that are vulnerable to become overexploited, but that are not yet at risk of extinction (Grigg 1984; Romero 1997; Green & Hendry 1999; Bruckner 2001; Reyes & Santodomingo 2002; Harriott 2003; Tsounis et al. 2010).

Despite the importance of black corals in the culture and economy of many societies, very little is known about the basic biology and ecology of these organisms. This is in large part due to the remoteness of the habitats that most species inhabit, but also due to a historical lack of studies focusing on black corals (Brook 1889; Van Pesch 1914; Pax 1918; Hyman 1940; Grigg & Opresko 1977; Pax et al. 1987; Cairns 2007). To

date, the limited information on the biology and ecology of antipatharians has not been comprehensively reviewed, and the majority of summaries on this group are found in taxonomic monographs that were published close to a century ago (Brook 1889; Cooper 1903; Schultze 1903; Roule 1905; Cooper 1909; Van Pesch 1914; Pax 1918; Totton 1923). The purpose of this chapter is to address this lack of a recent synthesis within the Antipatharia, by presenting a comprehensive literature review on the biology and ecology of black corals. This review covers previously published information on black corals worldwide and throughout their entire depth range, from subtidal to abyssal depths. That said, a vast majority of studies involving antipatharians have been conducted in shallow water (< 50 m), the findings from which may not necessarily be consistent with deep-water (>50 m) species. Furthermore, this review does not include information on the taxonomy and systematics of black corals, which can be found in a series of recent taxonomic revisions and summaries (Opresko 2001; Opresko 2002; Opresko 2003b; Opresko 2004; Opresko 2005a; Opresko 2006; Daly et al. 2007; Bo 2008).

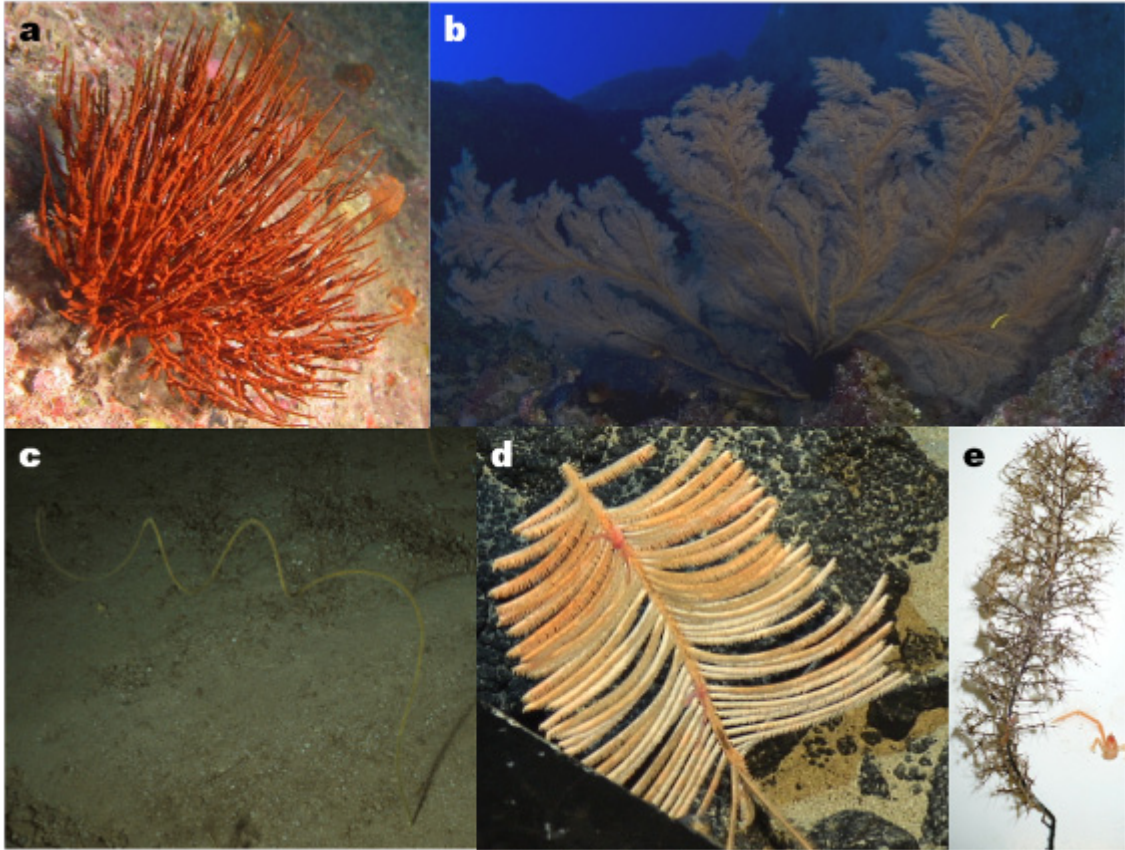
Materials and methods

A literature search was performed on any and all information regarding black corals using electronic searches at the libraries of the (1) University of Hawai‘i at Mānoa and (2) the Smithsonian Institution. Further articles were identified by searching through reference lists of articles obtained through the above mentioned searches. A total of 407 articles were reviewed for information on the biology and ecology of antipatharians, and included peer-reviewed journal articles, reports from oceanographic expeditions, proceedings from scientific conferences, dissertations, theses and edited book chapters.

General morphology

Antipatharians are exclusively colonial organisms with a wide range of colony morphologies (**Figure 2.1**). In general, black coral colonies are either unbranched (i.e., wire or whip corals) or branched like a bush, fan, feather or bottle-brush (**Figure 2.1**). Colony heights range from just a few centimeters for some species within the genus *Antipathes*, to heights of many meters for wire corals in the genera *Cirrhopathes* and *Stichopathes* (Bo 2008). Unlike their close related scleractinians, antipatharian corals do not build reef structures and are thus considered ahermatypic. Colonies are generally firmly attached to the substrate through a basal plate, with the exception of some species within the genera *Bathypathes* and *Schizopathes*, which have a modified, hook-like holdfast for support in soft sediments and mud (Pax 1918; Grigg & Opresko 1977; Pasternak 1977; Grasshoff 1981a; Opresko 1997; Opresko 2002). The skeleton of antipatharians is secreted by axial epithelial tissues of the polyps in concentric layers around a central hollow core, the central canal (Daly et al. 2007). The color of the skeleton ranges from black to golden brown, and is covered with minute skeletal spines. These skeletal attributes give rise to the common names of the order Antipatharia: black corals or thorny corals. Covering the skeleton is a thin layer of tissue, the coenenchyme, from which the polyps arise. Antipatharian tissues do not contain any mineralized structures such as spicules or sclerites, and vary in coloration between brown, red, orange, pink, green, yellow, white and grey (**Figure 2.1**). Polyps typically range in size from a few millimeters to about one centimeter, and bear six, unbranched tentacles encircling the oral cone and mouth (Opresko & Sanchez 2005; Daly et al. 2007). The polyps are bilaterally symmetrical and possess six primary mesenteries, and zero, four or

Figure 2.1. Different colony morphologies of antipatharians. **a.** bush-like, **b.** fan-shaped, **c.** wire-like, **d.** feather-like and **e.** bottle-brush (Photographs courtesy of **a.** Sam Kahng, **b.** Greg McFall and **c-d.** the Hawai'i Undersea Research Laboratory).



six secondary mesenteries (Opresko & Sanchez 2005; Daly et al. 2007). The muscular system supporting the polyps is only poorly developed in the Antipatharia, so that tentacles can only contract slightly but not retract like other anthozoans (Brook 1889; Van Pesch 1914; Hyman 1940; Goldberg & Taylor 1989a; Daly et al. 2003).

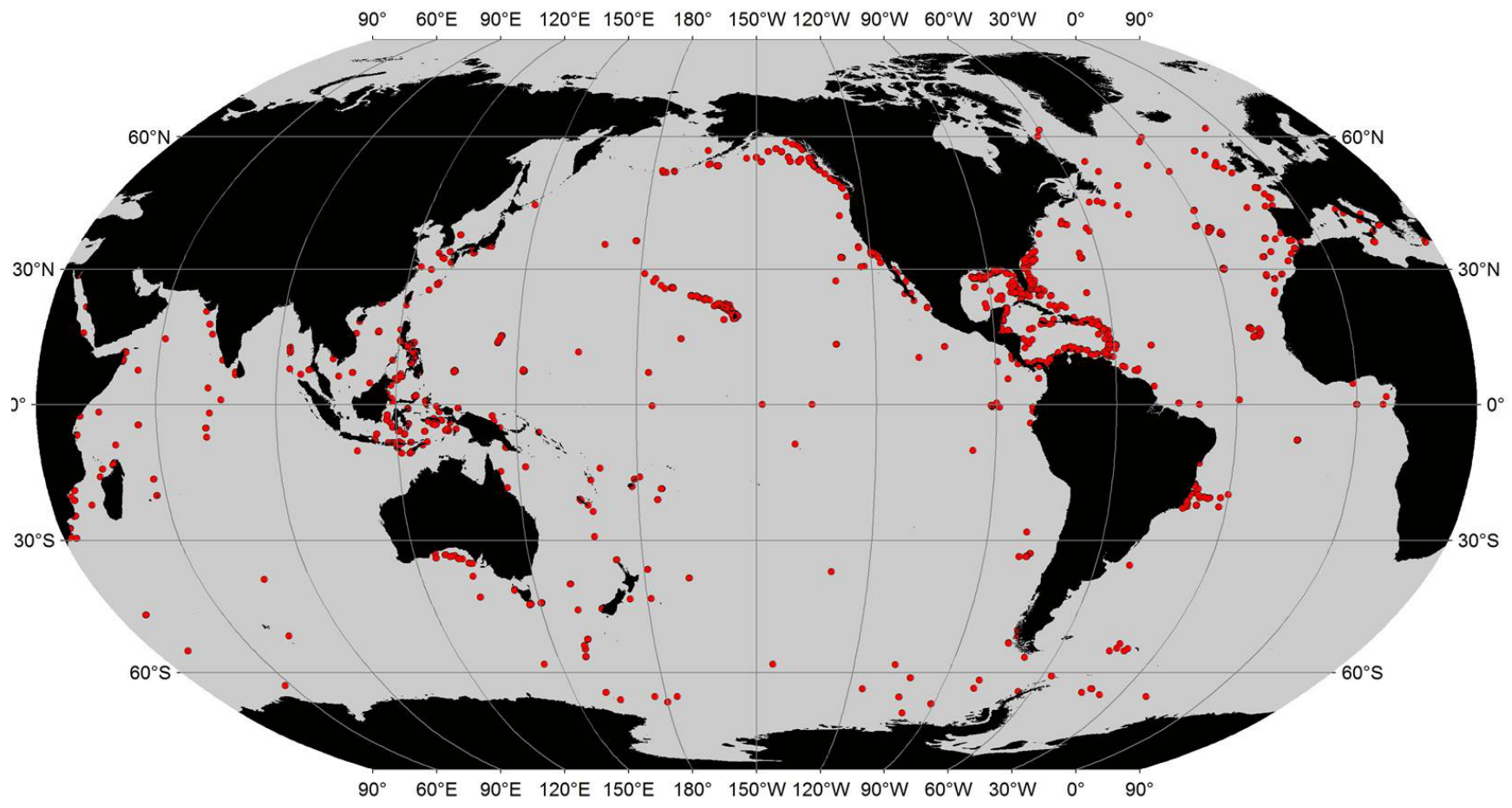
Biogeography

Black corals are restricted to marine ecosystems and are found in all oceans from tropical to polar latitudes; however, they are particularly abundant in tropical and subtropical regions (**Figure 2.2**). To date, black corals have not been found in areas with brackish waters, although some species inhabit areas with decreased salinities such as the fiords of New Zealand (**Figure 2.2**). In addition to their wide geographic range, black corals are found over a wide depth gradient, that spans from waters as shallow as 2-4 m for wire corals in the tropical Pacific (Brook 1889; Davis & Cohen 1968; Parrish & Baco 2007; Bo 2008), down to depths of 8,600 m for *Bathypathes patula* in the in the Northwestern Pacific (Pasternak 1977; Molodtsova et al. 2008). Despite this wide bathymetric range, over 75% of described antipatharian species are restricted to depths below 50 m (Cairns 2007). Additionally, there are no records of black corals from intertidal zones, perhaps reflecting that antipatharians are sensitive to air exposure (Bo 2008).

Studies on the biogeographical distributions of individual species are very scarce within the Antipatharia, because a large proportion of black coral species are only known from their type locality and consequently have very limited known ranges (Roberts &

Hawkins 1999; Opresko 2001; Opresko 2002; Opresko 2003b; Opresko 2004; Molodtsova 2005; Opresko 2005a; Opresko 2006). The restricted known ranges of most species are in part due to the remoteness of antipatharian habitats which make observations and collections logistically challenging, but also due to taxonomic problems within the order Antipatharia (Molodtsova 2005; Cairns 2007; Daly et al. 2007; Bo 2008). Numerous antipatharian species have been described from poorly preserved or incomplete specimens (Opresko 1972; Molodtsova 2005; Opresko & Sanchez 2005; Daly et al. 2007; Bo 2008). Additionally, missing type material and inadequate species descriptions have resulted in numerous species names that cannot be reliably verified (Daly et al. 2007; Bo 2008). Consequently, species identifications are often only tentative within the Antipatharia. The few discussions on the biogeographical distribution of antipatharians are mostly limited to reports from oceanographic expeditions (Dana 1846; Pourtales 1871; Pourtales 1874; Brook 1889; Schultze 1902; Thomson 1905; Cooper 1909; Van Pesch 1914; Totton 1923; Thomson & Renet 1931; Pasternak 1977; Grasshoff 1981b; Grasshoff 1985; Grasshoff 1989). Additionally, inventories of the antipatharian fauna have been published for several regions around the globe including the waters surrounding East Africa and the Mergui Archipelago (Summers 1910), the Maldiva and Laccadive Islands (Cooper 1903), Diego Garcia and the Northern Indian Ocean (Cooper 1909), the Gulf of Manaar (Thomson & Simpson 1905), Japan (Silberfeld 1909; Pax 1932), Korea (Moon & Song 2005; Moon & Song 2008a; Moon & Song 2008b), China (Zou & Zhou 1982; Zhou & Zou 1984; Zou & Zhou 1984; Zhou & Zou 1987; Zhou & Zou 1992), Indonesia and the Moluccan Archipelago (Schultze 1896a; Schultze 1896b; Bo 2008), Antarctica (Thomson 1905; Thomson & Renet 1931), the

Figure 2.2. Map of biogeographical distribution of antipatharian corals using records from the literature and museum specimens housed at the National Museum of Natural History, Smithsonian Institution.



Mariana Islands (Paulay et al. 2003; Parrish & Baco 2007), the Hawaiian Archipelago (Grigg & Opresko 1977; Chave & Malahoff 1998; Parrish & Baco 2007), the Aleutian Islands (Heifetz et al. 2005), Alaska (Heifetz 2002) the Gulf of Mexico (Opresko 2009a), the Caribbean (Opresko & Sanchez 2005), Brazil (Echeverria 2002; Loiola & Castro 2005), Madeira (Johnson 1899), the Canary Islands (Brito & Ocaña 2004), the Bay of Biscay (Roule 1905; Hickson 1907; Grasshoff 1981b), and the Mediterranean (Bo 2008; Bo et al. 2008). Antipatharians are also important faunal components on seamounts throughout the world (Grasshoff 1985; Genin et al. 1986; Molodtsova 2005; Baco 2007; Rogers et al. 2007), and a checklist of the antipatharian fauna of seamounts is presented by Rogers et al. (2007).

Habitat requirements

Despite the great geographic and bathymetric range of antipatharians (**Figure 2.2**), there are a number of generalities in terms of the physical habitats of black corals. First, the vast majority of antipatharians require hard substrates to which they can firmly attach, with the exception of some species within the genera *Bathypathes* and *Schizopathes*, which have a modified holdfast for support in soft sediments and mud (Pax 1918; Grigg & Opresko 1977; Pasternak 1977; Grasshoff 1981a; Opresko 1997; Opresko 2002). Second, because black corals are suspension feeders (see below), they require areas with strong and temporally dependent currents (Grigg 1964; Grigg 1965; Goenaga 1977; Warner 1981; Grigg 1984; Genin et al. 1986; Grange & Singleton 1988; Moffitt et al. 1989; Opresko & Genin 1990; Grigg 1993; Chave & Malahoff 1998; Ocaña et al.

2006; Bright 2007; Parrish & Baco 2007; Tazioli et al. 2007; Bo 2008). Consequently, colonies are typically found in areas where the surrounding topography accelerates currents, such as on the crest of seamounts, pinnacles and knobs (Genin et al. 1986; Opresko & Genin 1990; Mortensen et al. 2007; Parrish & Baco 2007). Third, black corals are typically absent in areas that are surrounded by high sediment cover (Fraser & Sedberry 2008). Unlike other cnidarians, antipatharian tissues have no structural protection against abrasive forces, and muscular systems are only poorly developed, so that tentacles can only contract slightly but not retract into a groove like other anthozoans (Hyman 1940; Goldberg & Taylor 1989a; Kim et al. 1992; Daly et al. 2003; Bo 2008). As a result, sediments suspended in currents can be detrimental to the soft tissues of antipatharians (Grigg 1964; Grigg 1965). Fourth, despite their wide depth range (2-8,600 m), black corals are predominantly found in low-light environments below the photic zone. Over 75% of antipatharian species are found at depths below 50 m (Cairns 2007), and when antipatharians do occur in shallower water (< 50 m), they are found in areas where light intensities are substantially reduced, such as inside caves or crevices, underneath overhangs, on steep vertical walls, or in areas with high water turbidity (Grigg 1964; Grigg 1965; Goreau & Goreau 1973; Goenaga 1977; Grange & Singleton 1988; Oakley 1988; Ramsay & Mason 1990; Sanchez et al. 1998; Sanchez 1999; Vega et al. 2002; Opresko & Sanchez 2005; Warner 2005; Sink et al. 2006; Parrish & Baco 2007; Tazioli et al. 2007; Lam & Morton 2008; Monteiro et al. 2008). In particular, the fjords of New Zealand contain some of the shallowest (> 4 m) populations of black corals on the planet, because of a tannin-rich low salinity layer (3-4 m deep) that substantially reduces light levels (Grange & Singleton 1988; Grange 1991; Miller 1997; Kregting & Gibbs

2006). Interestingly, the requirement for low light does not appear to affect antipatharians throughout their entire growth. In several shallow-water (<40 m) regions, black corals are usually attached to the substrate in shaded microenvironments such inside crevices, however, the colonies frequently grow towards the light (Grigg 1964; Grigg 1965; Goenaga 1977; Oakley 1988). Based on these observations it has been speculated that antipatharians have negatively phototactic larvae (Grigg 1964; Grigg 1965; Goenaga 1977; Oakley 1988). However, to date there is only a single study reporting direct observations of larvae (Miller 1996), and it remains unknown whether black coral larvae move away from light.

Population densities

In areas with favorable conditions, some species of antipatharians can attain particularly high population densities (see **Table 2.1**), and build monotypic aggregations that extend over large areas. Such dense aggregations are commonly referred to as black coral beds, some of which are of economic importance to humans, because they contain species that are used to manufacture jewelry. Furthermore, black coral beds represent important reservoirs of biodiversity, because they typically host distinct communities inhabited by a myriad of organisms (Grigg 1964; Boland & Parrish 2005; Yoklavich & Love 2005; Tissot et al. 2006; Bright 2007; Bo 2008; Bo et al. 2008; Bo et al. 2009b). The highest densities among antipatharians have been recorded for several species of wire corals (*Stichopathes* spp. and *Cirrhopathes* spp.). In particular, *Stichopathes spiessi* populations can reach densities of up to 20 colonies/m² on deep-water (550-1150 m)

Table 2.1. Previously published data on population densities of antipatharians.

Species	Family	Location	Depth (m)	Population density (colonies / m ²)	Reference(s)
<i>Antipates</i> cf. <i>atlantica</i>	Antipathidae	Providencia Island, Caribbean	30–50	≤ 1.47	(Sanchez et al. 1998)
<i>Antipathes atlantica</i>	Antipathidae	Caribbean coast off Colombia	15–50	0–0.5	(Sanchez 1999)
<i>Antipathes caribbeana</i>	Antipathidae	Providencia Island, Caribbean	30–50	≤ 2.19	(Sanchez et al. 1998)
<i>Antipathes caribbeana</i>	Antipathidae	Caribbean coast off Colombia	15–50	0–0.9	(Sanchez 1999)
<i>Antipathes</i> cf. <i>dichotoma</i>	Antipathidae	Palau	6–75	≤ 0.25	(Grigg 1975)
<i>Antipathes gracilis</i>	Antipathidae	Caribbean coast off Colombia	15–50	0–0.1	(Sanchez 1999)
<i>Antipathes grandis</i>	Antipathidae	Hawai'i	40–146	0–1.5	(Grigg 1974)
<i>Antipathes grandis</i> , <i>Antipathes griggi</i>	Antipathidae	Hawai'i	35–110	0–1.0	(Grigg 2001; Grigg 2004)
<i>Antipathes griggi</i>	Antipathidae	Hawai'i	40–70	0.05 (mean)	(Grigg 1976)
<i>Antipathes griggi</i>	Antipathidae	Hawai'i	58–70	0–0.047	(Wagner et al. 2011a)
<i>Stichopathes paucispina</i>	Antipathidae	Eastern North Pacific seamounts	>1000	<<1	(Opresko & Genin 1990)
<i>Stichopathes spiessi</i>	Antipathidae	Eastern North Pacific seamounts	550–1150	≤ 20	(Genin et al. 1986; Opresko & Genin 1990)
<i>Stichopathes</i> spp.	Antipathidae	Caribbean coast off Colombia	15–50	0.1–3.8	(Sanchez 1999)
<i>Stichopathes</i> spp.	Antipathidae	Providencia Island, Caribbean	30–50	≤ 7.32	(Sanchez et al. 1998)
<i>Stichopathes</i> spp. (N=2)	Antipathidae	Puerto Rico	15–70	≤ 0.5	(Goenaga 1977)
Antipathrian spp. (N=16)	Antipathidae, Aphanipathidae, Myriopathidae	Indonesia	5–45	≤ 0.5	(Tazioli et al. 2007)
Antipathrian spp. (N=7)	Antipathidae, Myriopathidae	Jamaica	≤ 35	0.1–2.5	(Warner 2005)
<i>Antipathes caribbeana</i> , <i>Stichopathes lutkeni</i> , <i>Plumapathes pennacea</i>	Antipathidae, Myriopathidae	Cozumel, Mexico	20–75	0.07 (mean)	(Padilla & Lara 2003)
<i>Antipathes caribbeana</i> , <i>Stichopathes lutkeni</i> , <i>Plumapathes pennacea</i>	Antipathidae, Myriopathidae	Banco Chinchorro, Mexico	20–75	0.5 (mean)	(Padilla & Lara 2003)
<i>Aphanipathes salix</i>	Aphanipathidae	St. Croix	15–46	0.0092–0.0314	(Olsen & Wood 1980)
<i>Antipathella subpinnata</i>	Myriopathidae	Mediterranean	≤ 100	≤ 5.2	(Bo 2008; Bo et al. 2008; Bo et al. 2009b)
<i>Antipathella</i> spp.	Myriopathidae	New Zealand	4–40	0.25 (mean)	(Grange 1985)
<i>Myriopathes ulex</i>	Myriopathidae	Hawai'i	58–70	0–0.690	(Wagner et al. 2011a)
<i>Plumapathes pennacea</i>	Myriopathidae	St. Croix	15–46	0.0087–0.0175	(Olsen & Wood 1980)
<i>Plumapathes pennacea</i>	Myriopathidae	Caribbean coast off Colombia	15–50	0–0.6	(Sanchez 1999)
<i>Leiopathes</i> sp.	Leiopathidae	Hawai'i	375–450	0.002–0.003	(Grigg 1988b)

seamounts in the eastern North Pacific (Genin et al. 1986; Opresko & Genin 1990). Such dense aggregations of wire corals are also common in many deep-water (> 150 m) environments around Hawai‘i, although population densities have not yet been reported (Chave & Malahoff 1998; Parrish et al. 2002). Dense populations of *Stichopathes* spp. are also widespread throughout several shallower (< 50 m) locations in the Caribbean (see **Table 2.1**), with maximum densities of up to 7.32 colonies/m² (Sanchez et al. 1998). In the Mediterranean, *Antipathella subpinnata* forms massive aggregations of up to 5.2 colonies/m² at depths ranging between 70-100 m (Bo 2008; Bo et al. 2008; Bo et al. 2009b). In slightly shallower-water (5-70 m), dense black coral populations exist in several locations around the globe including in Indonesia, New Zealand, Palau, Hawai‘i and the Caribbean, with densities ranging between 0-2.5 colonies/m² (**Table 2.1**). On the other end of the spectrum, several black coral species do not form massive aggregations (Grigg 1988b; Chave & Jones 1991; Chave & Malahoff 1998). Although, population densities are typically not reported for antipatharian species with low population densities (**Table 2.1**), several of these occur in deeper water (>300 m), and include several species in the family Leiopathidae and Schizopathidae (Grigg 1988b; Chave & Jones 1991; Chave & Malahoff 1998). Taken together, the available information suggests that densities are highly variable among antipatharian corals, but that at least some species can reach particularly high densities to the point of becoming ecologically dominant.

Feeding and nutrition

Several studies have made inferences about the feeding biology of antipatharians based on the occurrence and orientation of colonies in relation to the dominant flow

regime (Grigg 1964; Warner 1981; Genin et al. 1986; Tazioli et al. 2007). Black corals are typically found in areas with strong and temporally dependent currents (see above). The limited field observations suggest that black corals are suspension feeders with direct interception being the dominant mode of food capture, and that zooplankton is the major component of their diet (Grigg 1964; Goenaga 1977; Warner 1981; Goldberg & Taylor 1989b; Ocaña et al. 2006; Carlier et al. 2009). In areas where current direction is primarily uni-directional, fan-shaped antipatharians are common and oriented perpendicular to currents (Grigg 1964; Grigg 1965; Warner 1981; Grange 1988; Opresko & Sanchez 1997; Tazioli et al. 2007; Peccini & MacDonald 2008), an orientation that maximizes contact between feeding surfaces and suspended food (Grigg 1972). Additionally, polyps usually face the downcurrent side of fans, which may be because food particles are more readily caught in turbulent eddies on the leeward side of fans than in the direct current flow (Warner 1981). Alternatively, polyp orientation may not be related to food capture, but rather controlled by abrasive forces which can be detrimental to exposed antipatharian tissues (Grigg 1964; Grigg 1965; Kim et al. 1992; Tazioli et al. 2007).

Several studies have described the feeding behavior of antipatharians in aquarium cultures (Grigg 1964; Goenaga 1977; Lewis 1978). Grigg (1964) noted that the presence of food caused *Antipathes griggi* (as *A. grandis*) to guide ciliary currents towards its mouth, and that the mouth was capable of expanding to up to three times its normal size in order to ingest larger food particles such as amphipods, copepods and chaetognaths. Additionally, Grigg (1964) noted that *A. griggi* polyps expanded throughout the day and

concluded that feeding is thus not restricted to specific hours. Lewis (1978) studied the feeding behavior of three shallow-water (<40 m) species from the West Indies, and made similar observations to those of Grigg (1964). Polyps expanded throughout the day and the presence of food caused polyp expansion, tentacle extension and wide mouth opening (Lewis 1978). Additionally, black corals produced mucus nets over their body surfaces which were used to trap food particles, and were subsequently moved into mouths via ciliary currents (Lewis 1978). Furthermore, polyps ingested food particles by thrusting tentacles towards their mouths, and caught live zooplankton with the use of nematocysts (Lewis 1978). Goenaga (1977) studied the feeding behavior of two *Stichopathes* spp. in Puerto Rico. In contrast to previous studies (Grigg 1964; Lewis 1978), he noted that colonies expanded more fully and fed more actively during the night. Such nocturnal feeding behavior has also been reported in the field for *Cirrhipathes* spp. in Indonesia, where tentacles contracted throughout the day and completely expanded at night (Tazioli et al. 2007).

Several authors report finding various zooplankton items in the guts of antipatharians, suggesting that carnivorous feeding is important (Goenaga 1977; Warner 1981; Goldberg & Taylor 1989b; Ocaña et al. 2006; Carlier et al. 2009). While phytoplankton feeding has not been reported among antipatharians, it has been documented among various octocoral species from the Red Sea (Fabricius et al. 1995a; Fabricius et al. 1995b; Fabricius et al. 1998), in areas that are also inhabited by black corals (**Figure 2.2**). Given the indiscriminate method of food capture among antipatharians (Lewis 1978), phytoplankton and detritus may also be consumed, but is

Table 2.2. Summary of previously published information on nitrogen stable isotope ratios in black corals, with implications on trophic levels.

Species	Family	Collection location	Collection depth (m)	$\delta^{15}\text{N}_{\text{air}}$ (‰)	$\delta^{15}\text{N}$ relation to other organisms in study	Reference(s)
<i>Antipathes</i> sp.	Antipathidae	Saudi Arabia	2-8	4.5-6.5	No other organisms analyzed; $\delta^{15}\text{N}$ enriched in locations that were historically exposed to sewage	(Risk et al. 2009)
<i>Antipathes</i> sp.	Antipathidae	Palau	5	6.4	Similar to octocorals	(Williams & Grotoli 2010)
<i>Leiopathes glaberrima</i>	Leiopathidae	SE United States	307-679	7.7-8.6	No other organisms analyzed	(Williams et al. 2006; Williams et al. 2007)
<i>Leiopathes glaberrima</i>	Leiopathidae	Mediterranean	520	7.3	Lower than most gorgonians and scleractinians; similar to bivalve <i>Delectopecten vitreus</i>	(Carlier et al. 2009)
<i>Leiopathes</i> sp.	Leiopathidae	Hawai'i	400-500	9.3 ± 0.6	Higher than zoanthid <i>Gerardia</i> sp.	(Roark et al. 2009)
<i>Bathypathes arctica</i>	Schizopathidae	Newfoundland & Labrador	750-1300	10.76 ± 1.16	Higher than octocoral <i>Paragorgia arborea</i> and <i>Primnoa resedaeformis</i> ; lower than several alcyoneceans, pennatulaceans and scleractinians.	(Sherwood et al. 2008)
<i>Rhipidipathes</i> sp.	Stylopathidae	Palau	26	5.8-7.0	Similar to octocorals	(Williams & Grotoli 2010)

less readily found in guts because it is usually not identified. More recently, a number of studies have examined the ratios of nitrogen stable isotopes among various black corals (**Table 2.2**), which is a useful tool to estimate the relative trophic position in food webs because $\delta^{15}\text{N}$ values increase at every trophic level (Kling et al. 1992; Hobson et al. 1994; Post 2002). Carlier et al. (2009) examined the relative trophic position among various deep-water (520-700 m) invertebrates from the Mediterranean including the black coral *Leiopathes glaberrima*. In relation to other deep-sea gorgonians and scleractinians, *L. glaberrima* had lower $\delta^{15}\text{N}$ values, suggesting a lower trophic level (**Table 2.2**; Carlier et al. 2009). Additionally, at one site *L. glaberrima* had the same $\delta^{15}\text{N}$ value as the suspension-feeding bivalve *Delectopecten vitreus* suggesting a similar trophic position (Carlier et al. 2009). Williams & Grottoli (2010) examined stable isotope compositions among various genera of shallow-water (5-105 m) octocorals and antipatharians from Palau, and noted similar $\delta^{15}\text{N}$ values for both groups indicating a similar trophic level (**Table 2.2**). Sherwood et al. (2008) examined stable isotope ratios among several deep-water (47-1433) corals from the Newfoundland and Labrador region. *Bathypathes arctica*, the only antipatharian in the study, had a higher $\delta^{15}\text{N}$ value than the sympatric octocorals *Paragorgia arborea* and *Primnoa resedaeformis*, suggesting a higher trophic level (**Table 2.2**; Sherwood et al. 2008).

Endosymbiotic dinoflagellates within the genus *Symbiodinium*, commonly known as zooxanthellae, provide photosynthetically derived nutrients to a diverse array of corals (Baker 2003; Knowlton & Rowder 2003). To date, however, a mutualistic association between *Symbiodinium* and a black coral has only been reported for one shallow-water

(<40 m) wire coral species from Indonesia (Bo 2008; Bo et al. 2011), although *Symbiodinium* cells have been discovered in low densities in several species (Brook 1889; Van Pesch 1914; Pax 1918; Buchner 1921; Wagner et al. 2011b). Collectively, this suggests that endosymbiotic dinoflagellates are generally not essential in the nutrition of antipatharians.

Sexual reproduction

With the exception of a few studies on shallow-water species (< 50 m), most information on the sexual reproduction of antipatharians is derived from scarce notes on the anatomy of reproductive tissues accompanying taxonomic descriptions (Wagner et al. 2011c). Even though the majority of this information is derived for the examination of a limited number of specimens, previously published data on sexual reproduction exists for at least 56 nominal species, representing > 20% of the described antipatharian fauna (**Table 2.3**). Based on the published information available to date, there appear to be a number of generalities within the order Antipatharia (reviewed by Wagner et al. 2011c). First, of the six primary mesenteries only the two in the transverse plane bear the filaments and gametes (**Table 2.3**). Second, individual polyps are strictly gonochoric because polyps with both oocytes and spermatocysts have not been found within any antipatharian species examined to date (**Table 2.3**). Third, entire colonies are either female or male, with the exception of *Stichopathes saccula* which has mixed colonies with both male and female polyps (Pax et al. 1987). Fourth, there is no evidence for internal fertilization within the Antipatharia, indicating that fertilization and larval

Table 2.3. Summary of previously published information on the sexual reproduction of antipatharians (N/A = not applicable; G = gonochoric; G* = gonochoric based on the study of a limited number of specimens collected over a short time span; Seq. H = sequential hermaphrodite; Sim. H = simultaneous hermaphrodite; PTM = primary transverse mesenteries; APSM = anterior pair of secondary mesenteries; T = tentacle; – = values not reported).

Species	Authority	Family	Collection location	Collection depth (m)	Sex	Gonad location	Oocyte size (µm)	Spermato-cyst size (µm)	Reference(s)
<i>Antipathes assimilis</i>	(Brook, 1889)	Antipathidae	Strait of Magellan	320	G*	PTM	–	224	(Brook 1889)
<i>Antipathes contorta</i>	(Brook, 1889)	Antipathidae	Strait of Magellan	320	G*	–	340	–	(Brook 1889)
<i>Antipathes dichotoma</i>	Pallas, 1766	Antipathidae	Mediterranean	201-256	G*	PTM	250	100	(Brook 1889; Van Pesch 1914)
<i>Antipathes dubia</i>	(Brook, 1889)	Antipathidae	Japan	–	G*	PTM	80-120	–	(Pax 1932)
<i>Antipathes ericoides</i>	(Milne-Edwards, 1857)	Antipathidae	Indonesia, East Timor	5-34	G*	PTM	65	–	(Van Pesch 1914)
<i>Antipathes grandis</i>	Verrill, 1928	Antipathidae	Hawai'i	28-111	G*	PTM	13-125	–	(Wagner et al. 2011c)
<i>Antipathes griggi</i>	Opresko, 2009	Antipathidae	Hawai'i	23-99	G*	PTM, T	16-131	–	(Grigg 1976; Wagner et al. 2011c)
<i>Antipathes minor</i>	(Brook, 1889)	Antipathidae	Strait of Magellan	320	G*	PTM	–	–	(Brook 1889)
<i>Antipathes plana</i>	Cooper, 1909	Antipathidae	Indonesia	113	G*	–	–	40-60	(Van Pesch 1914)
<i>Antipathes</i> spp.	N/A	Antipathidae	Indo-Pacific	–	G	PTM, T	–	–	(Schmidt & Zissler 1979)
<i>Cirripathes anguina</i>	(Dana, 1846)	Antipathidae	Indonesia	36	G*	PTM	–	–	(Van Pesch 1914)
<i>Cirripathes cf. anguina</i>	(Dana, 1846)	Antipathidae	Indonesia, Hawai'i	10-35	G*	PTM	12-137	≤120	(Gaino et al. 2008; Gaino & Scoccia 2008; Wagner et al. 2011c)
<i>Cirripathes contorta</i>	(Van Pesch, 1914)	Antipathidae	Indonesia	9-45	G*	PTM, APSM	–	–	(Van Pesch 1914)
<i>Cirripathes propinqua</i>	Brook, 1889	Antipathidae	New Guinea	7	G*	PTM	–	–	(Brook 1889)
<i>Cirripathes rumphii</i>	(Van Pesch, 1914)	Antipathidae	Indonesia, East Timor	30-113	G*	PTM	–	55	(Van Pesch 1914)
<i>Cirripathes</i> sp.	N/A	Antipathidae	Indonesia	40	Seq. H	PTM	40-200	–	(Bo 2008)
<i>Cirripathes</i> sp.	N/A	Antipathidae	Indo-Pacific	–	G	PTM, T	–	–	(Schmidt & Zissler 1979)
<i>Cirripathes spiralis</i>	(Blainville, 1834)	Antipathidae	Arafura Sea, Indonesia	32-469	G*	PTM	–	–	(Van Pesch 1914)
<i>Pseudocirripathes mapia</i>	Bo et al. 2009	Antipathidae	Indonesia	17-32	G*	–	80-140	–	(Bo et al. 2009a)
<i>Pteropathes fragilis</i>	Brook, 1889	Antipathidae	St. Paul's Rocks	18-146	G*	PTM	–	–	(Brook 1889)
<i>Stichopathes ceylonensis</i>	Thompson & Simpson, 1905	Antipathidae	Arafura Sea	984	G*	PTM	–	–	(Van Pesch 1914)
<i>Stichopathes echimulata</i>	Brook, 1889	Antipathidae	Hawai'i	129-130	G*	PTM	16-101	–	(Wagner et al. 2011c)
<i>Stichopathes gracilis</i>	(Gray, 1857)	Antipathidae	Indonesia, Morocco	73	G*	PTM	–	–	(Schultze 1903; Van Pesch 1914)
<i>Stichopathes</i> sp.	N/A	Antipathidae	Hawai'i	10-59	G*	PTM	7-132	–	(Wagner et al. 2011c)
<i>Stichopathes</i> spp. (N=2)	N/A	Antipathidae	Puerto Rico	15	G	PTM	≤150	–	(Goenaga 1977)

Species	Authority	Family	Collection location	Collection depth (m)	Sex	Gonad location	Oocyte size (µm)	Spermato-cyst size (µm)	Reference(s)
<i>Stichopathes paucispina</i>	(Brook, 1889)	Antipathidae	Eastern North Pacific	> 1000	G*	–	–	–	(Opresko & Genin 1990)
<i>Stichopathes pourtalesi</i>	Brook, 1889	Antipathidae	Caribbean	82-1606	G*	–	–	–	(Brook 1889)
<i>Stichopathes richardi</i>	Roule, 1905	Antipathidae	NE Atlantic	540-1557	G*	PTM	–	–	(Roule 1905)
<i>Stichopathes saccula</i>	Van Pesch, 1914	Antipathidae	Indonesia	560	Sim. H	PTM	–	120	(Van Pesch 1914; Pax et al. 1987)
<i>Stichopathes semiglabra</i>	Van Pesch, 1914	Antipathidae	Indonesia	55-94	G*	PTM	–	–	(Van Pesch 1914)
<i>Stichopathes solorensis</i>	Van Pesch, 1914	Antipathidae	Indonesia	113	G*	PTM	250	–	(Van Pesch 1914)
<i>Stichopathes</i> sp.	N/A	Antipathidae	Indo-Pacific	–	G	PTM, T	–	–	(Schmidt & Zissler 1979)
<i>Stichopathes spiessi</i>	Opresko & Genin, 1990	Antipathidae	Eastern North Pacific	450-990	G*	–	–	–	(Opresko & Genin 1990)
<i>Stichopathes variabilis</i>	(Van Pesch, 1914)	Antipathidae	Indonesia, Borneo	15-567	G*	PTM, T	–	70	(Van Pesch 1914)
<i>Aphanipathes verticillata</i>	Brook, 1889	Aphanipathidae	Hawai'i	88-130	G*	PTM	21-181	–	(Wagner et al. 2011c)
<i>Heliopathes americana</i>	Opresko, 2003	Cladopathidae	Jamaica	2200	G*	–	–	–	(Opresko 2003b)
<i>Heliopathes pacifica</i>	Opresko, 2005	Cladopathidae	North Pacific	3563-4511	G*	–	–	–	(Opresko 2005b)
<i>Hexapathes alis</i>	Molodtsova, 2006	Cladopathidae	Fiji	400-407	G*	–	–	–	(Molodtsova 2006)
<i>Hexapathes australiensis</i>	Opresko, 2003	Cladopathidae	Tasmania	520	G*	–	–	–	(Opresko 2003b)
<i>Hexapathes hivaensis</i>	Molodtsova, 2006	Cladopathidae	Marquesas	416-430	G*	–	–	–	(Molodtsova 2006)
<i>Sibopathes gephura</i>	Van Pesch, 1914	Cladopathidae	East Timor	1224	G*	PTM	≤200	–	(Van Pesch 1914)
<i>Leiopathes</i> sp.	N/A	Leiopathidae	Hawai'i	382	G*	PTM	51-242	–	(Wagner et al. 2011c)
<i>Antipathella subpinnata</i>	(Ellis & Solander, 1976)	Myriopathidae	Mediterranean	51- 247	G*	PTM	≤150	–	(Brook 1889; Gaino & Scoccia 2010)
<i>Antipathella fiordensis</i>	(Grange, 1990)	Myriopathidae	New Zealand	9-22	G	PTM	15-140	–	(Miller 1996; Parker et al. 1997)
<i>Cupressopathes pumila</i>	(Brook, 1889)	Myriopathidae	Indonesia	30	G*	PTM	–	50-300	(Gaino & Scoccia 2009)
<i>Myriopathes lata</i>	(Silberfeld, 1909)	Myriopathidae	Korea	10-45	G*	–	300	–	(Moon & Song 2008b)
<i>Myriopathes ulex</i>	(Ellis & Solander, 1786)	Myriopathidae	Indonesia	113	G*	PTM, T	–	120	(Van Pesch 1914)
<i>Bathypathes alternata</i>	Brook, 1889	Schizopathidae	Hawai'i	1327	G*	PTM	45-370	–	(Wagner et al. 2011c)
<i>Bathypathes patula</i>	Brook, 1889	Schizopathidae	Indo-Pacific	450-2796	G*	PTM	105	–	(Cooper 1909; Van Pesch 1914)
<i>Parantipathes euantha</i>	(Pasternak, 1958)	Schizopathidae	Kurile-Kamchatka Trench	1080	G*	PTM	75-125	–	(Molodtsova & Pasternak 2005)
<i>Parantipathes larix</i>	(Esper, 1790)	Schizopathidae	Bay of Naples	99	G*	PTM	–	–	(Von Koch 1878; Brook 1889; Pax 1914)
<i>Bathypathes alternata</i>	Brook, 1889	Schizopathidae	Hawai'i	1327	G*	PTM	45-370	–	(Wagner et al. 2011c)
<i>Schizopathes affinis</i>	Brook, 1889	Schizopathidae	Indonesia	1573-2796	G*	PTM	< 500	–	(Cooper 1909; Van Pesch 1914)
<i>Tylopathes crista</i>	Brook, 1889	Stylopathidae	Sarmiento Channel	732	G*	PTM	–	–	(Brook 1889)

development likely occurs externally in the water column and not internally within polyps.

Very little is known about the larval biology and reproductive seasonality of antipatharians. To date, larvae have only been observed for members of the species *Antipathella fiordensis* in laboratory cultures (Miller 1996). The ciliated planulae were 200 μm in length and developed within 36 hours of fertilization (Miller 1996). These larvae were negatively buoyant, weak swimmers, likely non-feeding and stayed alive for a maximum of 10 days, but none settled (Miller 1996). The few studies that have examined the reproductive seasonality of black corals, have all been conducted in shallow water (<70 m) (Grigg 1976; Goenaga 1977; Schmidt & Zissler 1979; Parker et al. 1997; Bo 2008; Gaino & Scoccia 2010). All of these studies report seasonal appearances and disappearances of gametes, which at least in some cases have been correlated to seasonal temperature fluctuations (Schmidt & Zissler 1979; Parker et al. 1997; Gaino & Scoccia 2008). Grigg (1976) performed histological observations on *Antipathes griggi* specimens collected in Hawai'i in both July and March. All female samples collected in March contained immature oocytes, whereas those sampled in July contained both mature and immature oocytes, suggesting an annual reproductive cycle culminating in the summer months (Grigg 1976). Goenaga (1977) studied the sexual reproduction of two *Stichopathes* spp. in Puerto Rico, and concluded that reproduction occurred almost year round, although there were slight temporal differences in the appearance of mature gametes between species. Parker et al. (1997) report that *Antipathella fiordensis* has an annual gametogenic cycle that is highly synchronous both

within and between colonies, and spawns in the month of March coinciding with the warmest temperatures in New Zealand. Bo (2008) monitored polyp fecundities of *Cirrhipathes* sp. in Indonesia, and inferred spawning by the disappearance of gametes which occurred multiple times throughout a year. Gaino & Scoccia (2010) examined *Antipathella subpinnata* from the Mediterranean, and found no fertile colonies in September-November when water temperatures were low (14°C), and fertile colonies in August when temperatures were higher (16°C). Schmidt & Zissler (1979) noted that several tropical Indo-Pacific antipatharians reproduced in the summer during a period of approximately two months. Collectively, these studies suggest that the reproductive cycle of various shallow-water (<70 m) antipatharian species is seasonal, and that at least in some cases it correlates to seasonal temperatures fluctuations with peak maturity occurring when water temperatures are higher.

Asexual reproduction

Asexual reproduction is of vast importance to cnidarians (Campbell 1974; Shick et al. 1979; Richmond & Hunter 1990; Fautin 2002), and antipatharians are no exception to this trend (Miller & Grange 1995; Miller 1997; Miller 1998). Modes of asexual reproduction that have been reported for black corals include (1) budding of new polyps (Pax et al. 1987), (2) breakage of fragments which can subsequently reattach to the substrate (Grigg 1964; Grigg 1976; Grigg 1984; Grigg 1993; Bo et al. 2009c), and (3) production of asexual larvae in aquaria under stressful conditions (Miller & Grange 1995; Parker et al. 1997). The two latter modes of asexual reproduction result in the formation of new colonies, whereas the former leads to new polyps on existing colonies. As

exclusively colonial organisms (Daly et al. 2007; Bo 2008), all black corals rely on budding of new polyps as part of their growth. Budding regularly occurs in the spaces between polyps, and leads to small polyps interspersed within branches containing larger polyps (Pax et al. 1987; Wagner et al. 2010; Wagner et al. 2011c). In addition to budding within interpolypar spaces, new buds may also form directly on existing polyps within several antipatharian species (Pax et al. 1987).

Terminal branches of the Hawaiian black corals *Antipathes griggi* and *A. grandis* often break away from colonies, however, this phenomenon is rarely successful in producing new colonies because broken portions hardly ever reattach to the substrate (Grigg 1964; Grigg 1976; Grigg 1984; Grigg 1993). Signs of colony fracture are also common on skeletons of *Stichopathes* cf. *maldivensis* and *Cirripathes* cf. *anguina* from Indonesia, suggesting that breakage of the corallum occurs often (Bo 2008; Bo et al. 2009c). However, regeneration of anchorages has not been observed in broken portions, suggesting that this mode of asexual reproduction is rarely successful (Bo 2008; Bo et al. 2009c). The artificial transplantation of black coral fragments has been attempted for *Antipathes* sp. in Cuba (Gonzalez et al. 1997), *Stichopathes* cf. *maldivensis* and *Cirripathes* cf. *anguina* in Indonesia (Bo et al. 2009c), and *Antipathes griggi* in Hawai'i (Montgomery 2002), with mean survival rates of 93%, 80%, 68% and 45%, respectively. Collectively, these high survival rates indicate that asexual reproduction via fragmentation can be successful under favorable conditions.

A type of polyp bailout has also been reported for *Antipathella fiordensis* in aquaria under stressful conditions, where parts of polyps (presumably tentacles) separate from colonies, and then form highly mobile and ciliated planulae (Miller & Grange 1995; Parker et al. 1997), a strategy also known from various other hexacorals (Sammarco 1982; Harrison & Wallace 1990; Richmond & Hunter 1990). This phenomenon has never been observed in the field, and it is therefore unknown whether it occurs naturally. However, molecular studies on the population genetic structure of *A. fiordensis* in New Zealand suggest that asexual reproduction is both common and geographically widespread within this species, because genetic clones have been reported to occur frequently and over long geographic distances (Miller & Grange 1995; Miller 1997; Miller 1998).

Growth rates and longevity

Several methodologies have been used to estimate growth rates and longevities of antipatharians, including (1) time-series measurements of colony fragments in aquaria, (2) time-series measurements of tagged colonies in the field, (3) measurements of colonies on artificial structures of known age, (4) growth ring counts, (5) analysis of size-frequency distributions, and (6) radioisotope dating techniques (**Table 2.4**). Studies that have tracked black coral growth report either changes in colony height over time (i.e., vertical growth rate) or changes in the diameter of the main stem over time (i.e., radial growth rate). The latter is particularly useful when colony height is difficult to estimate due to the flexibility of branches (Olsen & Wood 1980), however, it requires more precise measurements because radial growth is much smaller than vertical growth (**Table**

2.4). Most of the studies that have validated the periodicity of growth rings via other methods, report that the formation of rings is roughly annual (Grigg 1976; Grange & Goldberg 1993; Williams et al. 2006; Love et al. 2007; Risk et al. 2009; Prouty et al. 2011). In contrast, Noome & Kristensen (1976) counted ~2000 growth rings within a *Stichopathes gracilis* colony that had settled on an artificial structure that was 6 years old, and concluded that growth rings are formed daily by this species.

The fastest growing antipatharians are shallow-water (10-36 m), tropical wire corals, with vertical growth rates ranging between 3-7 cm/yr for *Stichopathes* spp. from Puerto Rico (Goenaga 1977), to up to 159 cm/yr for *Stichopathes* cf. *maldivensis* from Indonesia (Bo et al. 2009c). Longevities have not been reported for these wire coral species (**Table 2.4**); however, individual colonies have been monitored for over 2-3 years with no signs of senescence, suggesting lifespans exceeding these time periods (Goenaga 1977; Bo 2008). Slightly slower growth rates have been reported for various species with the genus *Antipathes* (**Table 2.4**). Grigg (1964) monitored growth of fragments of the Hawaiian species *Antipathes griggi* (as *A. grandis*) kept in aquaria, and reported vertical extensions of 1.2 cm/yr. Subsequent studies using time-series measurements of tagged colonies in the field, yielded faster vertical growth rates ranging between 4.0-11.6 cm/yr for *Antipathes griggi*, and between 2.92-6.12 cm/yr for its sympatric congener *A. grandis* (Grigg 1974; Grigg 1976; Montgomery 2006). Assuming constant growth rates throughout the lifespan of corals, Grigg (1974) estimated longevities of 40 and 100 yr for these two species, respectively. These ages are consistent with those obtained for *A. griggi* using radiocarbon dating techniques (12-32 yr; Roark et al. 2006). Longevities on

Table 2.4. Previously published growth rate and longevity data for various antipatharian species (– = values not reported).

Species	Family	Study location	Study depth (m)	Vertical growth rate (cm/yr)	Radial growth rate (mm/yr)	Longevity (yrs)	Method	Reference
<i>Antipathes dendrochristos</i>	Antipathidae	California	106	1.5	0.121	140	Growth ring counts, ²¹⁰ Pb and ¹⁴ C dating	(Love et al. 2007)
<i>Antipathes grandis</i>	Antipathidae	Hawai'i	–	2.92	–	100	Time-series measurements of tagged colonies	(Grigg 1974)
<i>Antipathes grandis</i>	Antipathidae	Hawai'i	45-58	6.12	–	–	Time-series measurements of tagged colonies and growth ring counts	(Grigg 1976)
<i>Antipathes griggi</i>	Antipathidae	Hawai'i	–	5.86	–	40	Time-series measurements of tagged colonies	(Grigg 1974)
<i>Antipathes griggi</i>	Antipathidae	Hawai'i	45-58	6.42	–	–	Time-series measurements of tagged colonies	(Grigg 1976)
<i>Antipathes griggi</i> (as <i>A. grandis</i>)	Antipathidae	Hawai'i	Laboratory	1.2	–	–	Time-series measurements of branches in the aquaria	(Grigg 1964)
<i>Antipathes griggi</i>	Antipathidae	Hawai'i	50	–	0.13-1.14	12-32	¹⁴ C dating	(Roark et al. 2006)
<i>Antipathes griggi</i>	Antipathidae	Hawai'i	–	4.0-11.6	N/A	–	Time-series measurements of tagged colonies	(Montgomery 2006)
<i>Antipathes</i> sp.	Antipathidae	Red Sea	2-8	–	0.05	81	Growth ring counts verified by bomb ¹⁴ C	(Risk et al. 2009)
<i>Antipathes</i> sp. (as <i>A. dichotoma</i>)	Antipathidae	Palau	24-34	4.52-9.32	–	–	Measurements of colonies on artificial structure of known age	(Grigg 1975)
<i>Cirripathes</i> cf. <i>anguina</i>	Antipathidae	Indonesia	20	≤ 159	–	–	Time-series measurements of tagged colonies	(Bo et al. 2009c)
<i>Stichopathes</i> cf. <i>maldivensis</i>	Antipathidae	Indonesia	20	≤ 15.6	–	–	Time-series measurements of tagged colonies	(Bo et al. 2009c)
<i>Stichopathes lutkeni</i>	Antipathidae	Jamaica	18	76.65	–	–	Measurements of colonies on artificial structure of known age	(Warner 2005)
<i>Stichopathes</i> spp. (n=2)	Antipathidae	Puerto Rico	22-36	3-7	–	–	Time-series measurements of tagged colonies	(Goenaga 1977)
<i>Stichopathes gracilis</i>	Antipathidae	Curacao	> 10	46.8-84.76	–	–	Time-series measurements of tagged colonies, measurements of colonies on artificial structures of known age and growth ring counts	(Noome & Kristensen 1976)
<i>Aphanipathes salix</i>	Aphanipathidae	St. Croix	15-46	–	0.7	–	Time-series measurements of tagged colonies	(Olsen & Wood 1980)
<i>Leiopathes</i> sp. (as <i>L. glaberrima</i>)	Leiopathidae	Hawai'i	450	–	0.005	2377	¹⁴ C dating	(Roark et al. 2006)
<i>Leiopathes</i> sp.	Leiopathidae	Hawai'i	400-500	–	0.005-0.013	350-4250	¹⁴ C dating	(Roark et al. 2009)
<i>Leiopathes</i> sp.	Leiopathidae	SE United States	304-317	–	0.008-0.022	530-2100	¹⁴ C dating and growth rings counts	(Prouty et al. 2011)
<i>Leiopathes glaberrima</i>	Leiopathidae	SE United States	307-697	–	0.014-0.015	198-483	²¹⁰ Pb dating and growth ring counts	(Williams et al. 2006; Williams et al. 2007)
<i>Antipathella fiordensis</i> (as <i>Antipathes aperta</i>)	Myriopathidae	New Zealand	5-25	3.9	–	–	Colony size-frequency distributions	(Grange & Singleton 1988)
<i>Antipathella fiordensis</i>	Myriopathidae	New Zealand	–	1.3-1.8	0.0984	300	Growth ring counts and time series measurements of tagged colonies	(Grange & Goldberg 1993)
<i>Antipathella fiordensis</i> (as undescribed sp.)	Myriopathidae	New Zealand	5-35	2.9	–	–	Growth ring counts	(Grange 1985)
<i>Plumapathes pennacea</i>	Myriopathidae	Gulf of Mexico	38	2.92	–	–	Measurements of colonies on artificial structure of known age	(Boland & Sammarco 2005)
<i>Plumapathes pennacea</i>	Myriopathidae	Jamaica	30	5.7	0.92	35	Measurements of colonies on artificial structure of known age	(Oakley 1988)
<i>Plumapathes pennacea</i>	Myriopathidae	St. Croix	15-46	–	0.81	–	Time-series measurements of tagged colonies	(Olsen & Wood 1980)
<i>Stauropathes arctica</i>	Schizopathidae	Newfoundland & Labrador	812-876	1.22-1.36	0.033-0.066	33-66	Bomb ¹⁴ C	(Sherwood & Edinger 2009)

a similar order have also been reported for *Stauropathes arctica* from the Newfoundland and Labrador region (33-66 yr; Sherwood & Edinger 2009), *Plumapathes pennacea* from Jamaica (35 yr; Oakley 1988), *Antipathes* sp. from the Red Sea (81 yr; Risk et al. 2009), and *Antipathes dendrochristos* from California (140 yr; Love et al. 2007) (**Table 2.4**). Slightly longer lifespan estimates have been reported for *Antipathella fiordensis* from New Zealand, with maximum longevities of up to 300 yr (Grange & Goldberg 1993), and vertical growth rates ranging between 1.3-3.9 cm/yr (Grange 1985; Grange & Singleton 1988; Grange & Goldberg 1993) (**Table 2.4**).

The slowest growing antipatharians belong to the genus *Leiopathes*, with radial growth rates ranging between 0.005-0.022 mm/yr (Roark et al. 2006; Williams et al. 2006; Williams et al. 2007; Roark et al. 2009; Prouty et al. 2011). Radioisotope techniques have been used to date various colonies within this genus, with estimates ranging from centuries to millennia (**Table 2.4**). In particular, *Leiopathes* sp. samples from off Hawai'i (Roark et al. 2006; Roark et al. 2009) and the Southwestern United States (Prouty et al. 2011) have yielded maximum longevity estimates ranging between 2377-4250 yr (**Table 4**), thus making these the longest living colonial organisms examined to date. Collectively, the available information suggests that antipatharians are generally slow-growing and long-lived organisms, with longevities varying on the order of decades to millennia (**Table 4**).

Competition

Most of the published notes on competitive interactions involving antipatharians, are limited to descriptions of the physical habitats that black corals occupy and are avoided by other organisms. Coral reef ecosystems exhibit a similar pattern of dominant organisms with depth, that is dominated by obligate photosynthetic fauna (e.g. algae and zooxanthellate corals) in shallow-water (<50 m), and then gives rise to non-photosynthetic or facultatively photosynthetic fauna in deeper waters (reviewed by Kahng et al. 2010). Antipatharians start becoming dominant in this transition zone (~50 m) in many regions around the globe, suggesting that black corals escape competition with obligate photosynthetic fauna by being more abundant at depth (Grigg & Opresko 1977; Kuehlmann 1983; Rezak et al. 1990; Sanchez et al. 1998; Sanchez 1999; Vega et al. 2002; Paulay et al. 2003; Singh et al. 2004; Armstrong et al. 2006; Kahng & Kelley 2007; Tazioli et al. 2007; Bo 2008). As sessile organisms, black corals have limited abilities to dynamically interact with organisms in order to compete for resources. The only exception to this trend, is the formation of sweeper tentacles, a defensive adaptation well known among anthozoans (Fautin & Mariscal 1991; Williams 1991). Sweeper tentacles are exceptionally long and form in response to competitive interactions with nearby organisms, and have been reported for *Antipathella fiordensis* in New Zealand (Goldberg et al. 1990; Grange 1990) and *Pseudocirripathes mapia* in Indonesia (Bo et al. 2009a). In *A. fiordensis*, sweeper tentacles form in response to encrusting fauna such as the octocoral *Alcyonium aurantiacum* and the red algae *Epymenia* sp. and *Lithothamnion* sp. (Goldberg et al. 1990; Grange 1990). Similarly, in *P. mapia* sweeper tentacles form on branches with settlement of tube polychaetes, and on portions of

colonies that are in contact with corals of the genus *Acropora* (Bo et al. 2009a). Another strategy to compete with nearby organisms is the use of secondary metabolites, a strategy well documented among anthozoans (Sammarco & Coll 1992; Rossi & Snyder 2001). Compounds with deterrent effects have been isolated from several black coral species (Morse et al. 1978; Guerriero et al. 1988; Aiello et al. 1991; Aiello et al. 1992; Wilsanand et al. 1999; Encarnacion et al. 2000; Qi et al. 2009; Al-Lihaibi et al. 2011; Bai et al. 2011), however, their ecological functions have not yet been investigated. Some field observations suggest that black corals may make use of allelopathy for space competition. In particular, Goenaga (1977) noted that scleractinian corals like *Mycetophyllia lamarkiana* avoid contact with *Stichopathes* spp. from Puerto Rico by growing around antipatharian colonies in a u-shape.

Predators and natural mortality

There is very limited information on any animals preying on antipatharians. While this is at least in part due to the remoteness of antipatharian habitats, which make direct observations challenging, it may also reflect that predation is less widespread among this taxonomic order. The limited studies that have monitored black coral populations over a prolonged time, note that predation is not an important ecological factor (Grigg 1964; Grigg 1965; Grigg 1976; Goenaga 1977; Grange & Singleton 1988; Tazioli et al. 2007; Bo 2008). Additionally, several studies on the chemical components of antipatharian tissues suggest that various species contain deterrent compounds (Morse et al. 1978; Guerriero et al. 1988; Aiello et al. 1991; Aiello et al. 1992; Wilsanand et al. 1999; Encarnacion et al. 2000; Qi et al. 2009; Al-Lihaibi et al. 2011; Bai et al. 2011).

Furthermore, the antipatharian skeleton is composed primarily of chitin and protein, and is nearly inert chemically (Goldberg 1976; Goldberg 1978; Goldberg 1991; Holl et al. 1992; Kim et al. 1992; Schwartzman & Opresko 1992; Goldberg et al. 1994; Nowak et al. 2005; Juarez-de la Rosa et al. 2007; Nowak et al. 2009). Multiple proteolytic enzymes, acids, bases and reducing agents have practically no effect in solubilizing the antipatharian skeleton, indicating that it is almost certainly of low nutritional value (Goldberg 1976).

There are few observations of fish occasionally biting on antipatharian colonies, including various parrotfishes on *Stichopathes* spp. in Puerto Rico (Goenaga 1977), the butterflyfish *Chaetodon aculeatus* on *Antipathes* sp. in St. Croix (Neudecker & Lobel 1982) and the butterflyfish *Chaetodon bennetti* on shallow-water (5-45 m) antipatharians in Indonesia (Tazioli et al. 2007). Additionally, in aquarium cultures the butterflyfish *Chaetodon tinker* occasionally bites on various shallow-water (< 50 m) black corals from Hawai'i (Montgomery & Crow 1998). There is also one report of the black coral *Bathypathes arctica* being recovered from the stomach of a shark (Lütken 1872). Collectively, the sporadic nature of these reports suggests that black corals are not regular components of the diet of these fishes. In contrast, the green sea turtle *Chelonia mydas* regularly consumes *Antipathes galapagensis* in the Gulf of California (Seminoff et al. 2002; Seminoff et al. 2006). Green sea turtles have repeatedly been observed feeding on black corals (Seminoff et al. 2006), and fragments of the black coral are regularly found in fecal and esophageal samples of turtles (Seminoff et al. 2002).

In contrast to the sporadic nature and scarcity of records of vertebrate predation on antipatharians, numerous invertebrates appear to be specialized predators of black corals, including various species within the molluscan families Muricidae and Ovulidae. The muricids *Rhizochilus* sp., *R. antipathum* and *R. teramachii* all been reported to feed on antipatharians throughout the Indo-Pacific and Red Sea (Totton 1923; Rees 1969; Okamura & Habe 1976; Poorman 1981; Vega et al. 2002). Additionally, the muricid *Coralliophila kaofitorum* lives in strict association with *Antipathes wollastoni* in the Canary Islands, suggesting that it likely feeds on its black coral host (Vega et al. 2002; Brito & Ocaña 2004). The ovullid *Phenacovolva weaveri* is a specialized predator of *Cirrhopathes* spp. and *Antipathes* spp. in Indonesia, and mimics the color and shape of the polyps of its antipatharian prey (Schiaparelli et al. 2005; Tazioli et al. 2007). Another ovullid, *Phenacovolva carnepecta* lives in association with *Antipathes* sp. throughout the Pacific, and likely preys on the tissues of its antipatharian host (Rehder & Wilson 1975). A number of different decapods occasionally feed on shallow-water (<40 m) antipatharians in the Cape Verde Islands, especially when other food sources are scarce (Wirtz & d'Udekem-d'Acoz 2001). In Indonesia, Tazioli et al. (2007) observed thousands of unidentified caprellid amphipods feeding on *Antipathes* sp., which eventually lead to the death of an entire colony. This phenomenon was only observed on a single occasion and it was not clear whether the *Antipathes* sp. colony had been previously stressed, suggesting that such massive predation events are not common occurrences among shallow-water (5-45 m) black coral populations in Indonesia (Tazioli et al. 2007).

A number of other sources of natural mortality besides predation have been reported for black corals. In species that grow to large heights, mortality commonly occurs as colonies become too massive for the holdfast to support and consequently topple over (Grigg 1976; Grange & Singleton 1988; Chave & Jones 1991). This process may be aided by boring organisms such as sponges that weaken the holdfasts (Grigg 1984). Based on size frequency distributions of colonies, natural rates of mortality have been calculated for *Antipathes griggi* in Hawai'i (Grigg 1976; Grigg 1984) and *Aphanipathes salix* in St. Croix (Olsen & Wood 1980), with annual mortality rates of 7% and 4.13%, respectively. Only a few reports note black coral mortality as a result of natural disturbances (Olsen & Wood 1980; Grange & Singleton 1988). Olsen & Wood (1980) observed substantial damages to shallow-water (15-46 m) populations of *Aphanipathes salix* and *Plumapathes pennacea* in St. Croix, which they attributed to a hurricane. Also in shallow-water (5-25 m), Grange & Singleton (1988) noted that black coral populations in the fiords of New Zealand are frequently impacted by terrestrial landslides that bring down boulders and trees onto the submarine habitats where black corals grow. These landslides can directly tear submarine fauna from the substrate, or produce sediment clouds that settle over delicate organisms such as black corals (Grange & Singleton 1988).

Associated fauna

Like other corals, antipatharians represent important habitats for a myriad of associated organisms including polychaetes, barnacles, ophiuroids, copepods, crabs, shrimp, anemones, zoanthids, hydroids, crinoids, bryozoans, snails, bivalves, tunicates

and fish (**Table 2.5**). Associated species can inhabit four different microhabitats within black corals, including (1) surfaces of living branches, (2) surfaces of dead branches or colonies, (3) cavities inside tissues or skeletons, or (4) free spaces between branches (Buhl-Mortensen & Mortensen 2004). Many organisms use black corals opportunistically or transiently, and therefore are not true symbionts. In particular, numerous mobile organisms like fish occasionally hide behind branches of antipatharians (Grigg 1964; Aburto-Oropeza & Balart 2001; Boland & Parrish 2005; Parrish 2006; Sink et al. 2006; Tissot et al. 2006; Tazioli et al. 2007). Additionally, many organisms like sponges, bryozoans, amphipods, hydroids and algae opportunistically overgrow already dead colonies (Grigg 1964; Chave & Jones 1991; Love et al. 2007; Bo et al. 2009b), and are therefore also not true symbionts. However, defining symbioses involving black corals is often difficult, because many antipatharian associates are only known from limited observations (**Table 2.5**). Consequently, the term symbiont is exclusively used here for those organisms where a long-term association with living black coral colonies has been documented. In these cases, the symbiosis is further categorized in terms of the dependence (i.e., obligate or facultative) and relation (i.e., commensal, mutualistic or parasitic), where possible (Buhl-Mortensen & Mortensen 2004).

Arthropods are the most common symbionts of antipatharians in terms of the number of species, and generally form commensal associations with black corals (**Table 2.5**). Among arthropod symbionts, barnacles, crabs, shrimp and copepods are particularly widespread (**Table 2.5**). Barnacles are frequently firmly attached to the skeleton of black corals, and in some cases the coenenchyme of the host even covers the stalk and valves of

barnacle symbionts (Ellis & Solander 1786; Warner 1981; Jones et al. 2000; Yoklavich & Love 2005; Bo 2008). Furthermore, in some symbioses the spines that cover the peduncle of barnacles are produced by both the symbiont and the antipatharian host, indicating an intimate association (Newman 1972; Bo 2008). While many barnacles exhibit some degree of facultative dependence on their hosts, the family Oxynaspididae, and in particular the genus *Oxinaspis*, contains members that are almost exclusively found on black corals (Newman 1972; Rosell 1981; Jones et al. 2000). Decapod shrimps and crabs are also commonly associated with black corals (**Table 2.5**). Several reports note decapods crawling on the branches of colonies, where they feed on material trapped by the mucus secreted by black corals, or perch on the top of colonies facing into the current to feed (Wirtz & d'Udekem-d'Acoz 2001; Bright 2007; Tazioli et al. 2007; Le Guilloux et al. 2010). These associations therefore benefit the decapods involved, because symbionts obtain protection from predators, feed on particles collected by their hosts and get off the benthic boundary layer where catching prey is more difficult (Angel & Boxhall 1990). However, in most cases it is unknown whether antipatharians experience any fitness benefits or detriments from hosting decapods. Symbiotic decapods occasionally feed on antipatharian tissues, and some of these associations might therefore be parasitic (Wirtz & d'Udekem-d'Acoz 2001). On the contrary, decapods may help their antipatharian hosts by cleaning them from encrusting fauna (Le Guilloux et al. 2010), or by protecting them from predators, as has been documented in symbioses between decapods and shallow-water corals (Glynn 1980; Zann 1987; Pratchett 2001). Many symbiotic decapods of antipatharians also inhabit other hosts and substrates, however, some groups may be specialized to antipatharians (**Table 2.5**). In particular, the decapods *Chirostylus*

dolichopus, *Dasycaris zanzibarica*, *Nematopagurus longicornis*, *Periclimenes wirtzi*, *Pontonides unciger* as well as several species within the genus *Quadrella* apparently are obligate associates of antipatharians (**Table 2.5**).

Copepods are also commonly associated with black corals, where they inhabit either the external surfaces of living branches, or cavities within tissues (**Table 2.5**). In the latter case, copepods may subsist within antipatharians by ingesting mucus or tissues of their hosts (Goenaga 1977; Humes & Goenaga 1978). However, this may not necessarily imply a parasitic association. For instance, *Calonastes imparipes* lives within *Stichopathes* spp. from Puerto Rico, without inflicting damages to its black coral host even in the most heavily infested colonies (Goenaga 1977; Humes & Goenaga 1978). Similarly, endosymbiotic copepod nauplii develop within mesenterial filaments of *Cirrhopathes* cf. *anguina* from Indonesia, without inflicting any apparent damages to the antipatharian host (Scoccia & Gaino 2010). Like copepods, polychaete symbionts also inhabit either external surfaces of living branches, or are found within the tissues or skeletons where they typically build worm runs (Pourtales 1874; Silberfeld 1909; Totton 1923; Pettibone 1989; Molodtsova & Budaeva 2007; Bo 2008). In many polychaete symbioses there are no apparent visible damages to black corals, suggesting a commensal relationship (Brook 1889; Van Pesch 1914; Pettibone 1989; Pettibone 1991). However, some polychaete associates cause substantial growth anomalies to their black coral hosts (Pourtales 1874; Pax 1918; Totton 1923; Molodtsova & Budaeva 2007). In most cases the degree of dependence of polychaete symbioses with black corals is unknown,

although the species *Bayerpolynoe floridensis*, *Benhamipolynae antipathicola* and *Brychionoe karenae* all appear to be obligate associates of black corals (**Table 2.5**).

Molluscan associates of black corals include both bivalves within the genus *Pteria*, as well as several ovullid and muricid gastropods (**Table 2.5**). The former are commonly attached to either living or dead branches of various black coral species, and use the black corals to position themselves for more effective filter feeding in the water column (Weaver 1961; Grigg 1964; Rees 1969; Opresko 1976; Tazioli et al. 2007; Bo 2008; Bo et al. 2008). Gastropod symbionts are generally predators of antipatharians, some of which exhibit specialized adaptations to live on black corals, such as camouflage or mimicry (Grigg 1964; Schiaparelli et al. 2005; Tazioli et al. 2007). Within cnidarian associates of black corals, hydroids and zoanths are most abundant (**Table 2.5**). Hydroids are frequently found on the main stem of living colonies, or covering dead branches or colonies (Ralph 1958; Grigg 1964; Chave & Jones 1991; Yoklavich & Love 2005; Tazioli et al. 2007; Bo 2008; Di Camillo et al. 2008; Henry et al. 2008). In many cases, epibiotic hydroids settle after antipatharian colonies are already dead (Chave & Jones 1991; Henry et al. 2008). On the contrary, Bo et al. (in press) described a commensal association between *Antipathella subpinnata* and the hydroid *Ectopleura* sp., in which the epibiont is covered by the tissues and skeleton of its host, indicating that there are intimate associations between antipatharians and hydroids. Epizoism on antipatharians is also a common trait of zoanthid cnidarians, although zoanths generally parasitize black corals by progressively overgrowing and smothering living tissues (Chave & Malahoff 1998; Sinninger et al. 2005; Reimer et al. 2008; Sinninger et al.

2008; Mastrototaro et al. 2010). Parasitic zoanthids are generally facultative symbionts on antipatharians (**Table 2.5**), although *Savalia* sp. exclusively parasitizes *Tanacetipathes cavernicola* in the Cape Verde Islands (Sinninger et al. 2005).

A number of different fish use black corals as habitat (Grigg 1964; Davis & Cohen 1968; Donaldson & Colin 1989; Kerstitch 1989; Okiyama & Tsukamoto 1989; Colin & Arneson 1995; Aburto-Oropeza & Balart 2001; Greenfield & Randall 2004; Boland & Parrish 2005; Parrish 2006; Tissot et al. 2006; Herler 2007; Tazioli et al. 2007; Bo et al. 2009b). The level of usage ranges from fish occasionally hiding among black coral branches, to fish being residents of specific colonies but also using other habitats, to fish never leaving individual colonies. The latter is particularly common among various goby species within the genus *Bryaninops*, which live in association with *Antipathes* spp. and *Cirrhopathes* spp. throughout the Pacific and the Red Sea (Davis & Cohen 1968; Okiyama & Tsukamoto 1989; Colin & Arneson 1995; Greenfield & Randall 2004; Herler 2007; Tazioli et al. 2007). Additionally, some fish lay their eggs on black coral colonies, including *Amblyglyphidodon aureus* on shallow-water (5-45 m) antipatharians in Indonesia (Tazioli et al. 2007), and *Scyliorhinus* sp. on *Antipathella subpinnata* in the Mediterranean (Bo 2008; Bo et al. 2009b).

One of the best documented symbioses among black corals is the mutual association between the ophiuroid *Astrobrachion constrictum* and *Antipathella fiordensis* from New Zealand (Grange 1991; Stewart 1996; Stewart 1998). The ophiuroid gains protection and food, whilst enhancing the survival of its antipatharian host by removing

silt and debris that can smother polyps. Individual ophiuroids have been observed on the same antipatharian colony for over five years, indicating a long-lived and intimate relationship. Furthermore, *A. constrictum* has never been recorded from any other host or free-living, suggesting an obligate symbiosis (Grange 1991) .

Very little is known about microorganisms associated with black corals. Van Pesch (1914) reported unicellular parasites from the tissues of various black coral species, however, he did not provide any further descriptions. More recently, a few studies examined the bacterial communities associated with antipatharians (Park et al. 2002; Penn et al. 2006; Santiago-Vazquez et al. 2007). Park et al. (2002), studied the abundance of microorganisms on various marine invertebrates from South Korea, including an *Antipathes* sp. collected at 22 m. The bacterial abundance of *Antipathes* sp. was significantly higher than seawater, and similar to those of sympatric octocorals (Park et al. 2002). Penn et al. (2006) and Santiago-Vazquez et al. (2007) characterized the bacterial community of black corals. The microbiota of an unidentified black coral collected from deep-waters (1100-1950 m) off Alaska was dominated by alphaproteobacteria (Penn et al. 2006), whereas a shallow-water (45 m) wire coral sampled off Florida hosted mostly gammaproteobacteria, alphaproteobacteria and actinobacteria (Santiago-Vazquez et al. 2007). Additionally, in both cases the bacterial communities from black corals were substantially different from that of surrounding seawater, indicating a distinct microorganism community associated with black corals (Penn et al. 2006; Santiago-Vazquez et al. 2007).

Endosymbiotic dinoflagellates within the genus *Symbiodinium* provide photosynthetically derived nutrients to a diverse array of coral hosts (Baker 2003; Knowlton & Rowder 2003). Due to the predominant occurrence of black corals in low-light environments that do not support photosynthesis (Cairns 2007), the absence of *Symbiodinium* within black corals has generally been inferred rather than empirically demonstrated, and the whole taxonomic order has been considered azooxanthellate (see Wagner et al. 2011b). That said, Brook (1889) and Van Pesch (1914) both noted round bodies within the tissues of several black coral species, which they interpreted as symbiotic algae. However, these reports have been largely overlooked, or dismissed as questionable (Bo 2008). Supporting the questionable nature of these early reports, several more recent studies using histological techniques (Grigg 1964; Grigg 1976; Goenaga 1977), spectrophotometric chlorophyll measurements (Shick & Dykens 1985; Santiago-Vazquez et al. 2007) and molecular approaches (Santiago-Vazquez et al. 2007), have failed to detect *Symbiodinium* within black corals. In contrast, Wagner et al. (2011b) detected very low densities (0-92 cells/mm³) of endosymbiotic *Symbiodinium* within the majority of black coral species from Hawai'i. While the physiological role of the symbiont cells was not determined, their low densities coupled with the extreme depths at which they were recorded (≤ 396 m), argue that they do not provide their antipatharian hosts with photosynthetic products, and thus suggest an either parasitic or commensal association (Wagner et al. 2011b). Bo (2011) recorded endosymbiotic *Symbiodinium* in the shallow-water (40 m) *Cirrhipathes* sp. from Indonesia (Bo 2011). In contrast to other reports (Brook 1889; Van Pesch 1914; Wagner et al. 2011b), Bo (2011) noted very high densities of *Symbiodinium* cells within *Cirrhipathes* sp. ($\leq 10^6$ cells/mm³), and showed

Table 2.5. List of symbiotic organisms recorded from antipatharians (LB = surfaces of living branches; DB = surfaces of dead branches; IT = inside tissues; BB = spaces between branches; O = obligate, F = facultative; M = mutualistic; C = commensal; P = parasitic; – = values not reported).

Symbiont species	Host species	Symbiont microhabitat	Depen- dence	Relation	Locality	Depth (m)	Comments	Reference(s)
KINGDOM: ANIMALIA								
PHYLUM: ANNELIDA								
Class: Polychaeta								
<i>Aciculomarpysa comes</i>	Antipatharian	LB	–	–	–	–	–	(Molodtsova & Budaeva 2007)
<i>Antipathipolyeumoanuttingi</i>	<i>Tanacetipathes tanacetum</i>	LB, IT	–	C	Caribbean	70-91	Living on external surface of antipatharian and also found in hollow tubes along the main stem	(Pettibone 1991; Molodtsova & Budaeva 2007)
<i>Bayerpolynoe floridensis</i>	<i>Stylopathes columnaris</i>	LB	O	C	Florida	237	Obligate commensal on coral	(Pettibone 1991; Martin & Britayev 1998; Buhl-Mortensen & Mortensen 2004; Molodtsova & Budaeva 2007)
<i>Benhamipolynae antipathicola</i>	Antipathidae and Myriopathidae spp., <i>Parantipathes tenuispina</i>	LB, IT	O	C	Indo-Pacific, Florida	128-600	Lives in latticed tunnels	(Pettibone 1989; Pettibone 1991; Martin & Britayev 1998; Buhl-Mortensen & Mortensen 2004; Molodtsova & Budaeva 2007)
<i>Bollandiella antipathicola</i>	<i>Antipathes</i> sp.	LB	–	–	Okinawa	52-61	Species described from antipatharian associates	(Glasby 1994; Martin & Britayev 1998; Molodtsova & Budaeva 2007)
<i>Brychionoe karenae</i>	<i>Leiopathes</i> sp.	LB	O	C	Tasman Sea	–	–	(Martin & Britayev 1998; Buhl-Mortensen & Mortensen 2004)
<i>Eunice antipathum</i>	<i>Distichopathes filix</i> , <i>Elatopathes abietina</i>	LB	–	–	–	–	–	(Molodtsova & Budaeva 2007)
<i>Eunice kristiani</i>	Antipathidae and Myriopathidae spp.	IT	–	–	Indo-Pacific	300-600	Symbionts cause skeletal spine modifications in host	(Molodtsova & Budaeva 2007)
<i>Eunice marianae</i>	Antipathidae and Myriopathidae spp.	IT	–	–	Indo-Pacific	300-600	Symbionts cause skeletal spine modifications in host	(Molodtsova & Budaeva 2007)
<i>Filograna implexa</i>	<i>Antipathella subpinnata</i>	LB	–	–	Mediterranean	<100	Found on live colonies	(Bo 2008)
<i>Filograna</i> spp.	<i>Antipathella subpinnata</i>	LB	–	–	Mediterranean	<100	Found on live colonies	(Bo et al. 2009b)
<i>Marphysa antipathum</i>	<i>Distichopathes filix</i>	IT	–	–	–	–	Polychaete builds tube along stem of antipatharian	(Totton 1923)
<i>Neohololepidella antipathicola</i>	<i>Elatopathes abietina</i>	LB	–	–	–	–	–	(Molodtsova & Budaeva 2007)
Pilargidae sp.	<i>Stichopathes</i> spp.	LB	–	–	Puerto Rico	15-70	Relation of polychaete to coral unknown	(Goenaga 1977; Humes & Goenaga 1978)
Polynoidae sp.	<i>Antipathes dendrochistos</i>	LB	–	–	California	106	Ubiquitous on live but not on dead colonies	(Love et al. 2007)
Polynoidae sp.	<i>Hexapathes hivaensis</i>	LB	–	–	Marquesas	400-430	Found on antipatharian	(Molodtsova 2006)
Serpulidae sp.	<i>Antipathes griggi</i>	LB	–	–	Hawai'i	<50	Common epibiont	(Grigg 1964)
Spionidae sp.	<i>Antipathes griggi</i>	LB	–	–	Hawai'i	<50	Common epibiont	(Grigg 1964)
<i>Tottonpolynoe symantipatharia</i>	<i>Parantipathes</i> sp.	LB	F	C	New Zealand	787-1684	Found in groove along main stem of antipatharian and on gorgonian	(Pettibone 1991)
PHYLUM: ARTHROPODA								
Class: Malacostraca								
Subclass: Eumalacostraca								

Symbiont species	Host species	Symbiont microhabitat	Depen- dence	Relation	Locality	Depth (m)	Comments	Reference(s)
<i>Anachlorocurtis commensalis</i>	<i>Myriopathes japonica</i> , <i>Antipathes</i> spp.	LB	–	C	Japan	8-15	Commensal on coral	(Hayashi 1975)
<i>Balssia gastii</i>	<i>Antipathella wollastoni</i> , <i>A. subpinnata</i> , <i>Tanacetipathes spinescens</i>	LB	F	–	Azores, Cape Verde	38-41	Collected on antipatharians and other hosts	(d'Udekem-d'Acoz 2001; Wirtz & d'Udekem-d'Acoz 2001)
<i>Calappa granulata</i>	<i>Stichopathes gracilis</i>	LB	F	–	Canary Islands	130-300	Crab lives in bottoms dominated by <i>S. gracilis</i> and urchins	(Gonzalez et al. 2000)
<i>Calcinus tubularis</i>	<i>Antipathella wollastoni</i>	LB	F	–	Azores	–	Facultative relationship with antipatharians	(d'Udekem-d'Acoz & Wirtz 2002)
<i>Calocarcinus africanus</i>	<i>Antipathes</i> sp.	LB	F	–	Norfolk Ridge	400-460	Also collected on gorgonians and scleractinians	(Castro 1997b)
<i>Chirostylus affinis</i>	<i>Parantipathes</i> sp., <i>Antipathes</i> sp.	LB	–	M	Ireland	620-700	Antipatharians often associated with large numbers of spider crabs	(Wienberg et al. 2008)
<i>Chirostylus dolichopus</i>	<i>Rhipidipathes</i> sp.	LB	O	C	Indonesia	5-45	Always observed on <i>Rhipidipathes</i> sp.	(Tazioli et al. 2007)
<i>Chirostylus ortmanni</i>	Antipatharian	LB	F	–	NR	–	Found within antipatharian but also on gorgonian	(Tirmizi & Khan 1979; Osawa 2007)
<i>Chirostylus stellaris</i>	Antipatharian	LB	F	–	Japan	15-30	Found on antipatharians and octocorals, mostly at night	(Osawa 2007)
<i>Chirostyruis dolichopus</i>	<i>Antipathes</i> spp.	LB	–	–	Japan	–	–	(Hayashi 1975)
<i>Dasycares ceratops</i>	Antipatharian	LB	–	–	Australia	35	–	(Bruce 1982; Spotte et al. 1994)
<i>Dasycares zanzibarica</i>	<i>Cirripathes</i> spp., <i>C. anguina</i> ,	LB	O	C	Indo-West Pacific	5-45	Associated with antipatharian	(Bruce 1982; Bruce 1983; Spotte et al. 1994; Tazioli et al. 2007)
<i>Eualus occultus</i>	<i>Antipathella wollastoni</i>	LB	–	–	Azores	40	–	(d'Udekem-d'Acoz & Wirtz 2002)
<i>Galathea intermedia</i>	<i>Antipathella subpinnata</i> , <i>Tanacetipathes spinescens</i>	LB	–	–	Cape Verde	–	–	(Wirtz & d'Udekem-d'Acoz 2001)
<i>Gastrotychus formosus</i>	<i>Bathypathes</i> sp., <i>Leiopathes</i> sp.	LB	F	–	Ireland	600-1200	Adults also found on gorgonians. Lobsters possibly feed on mucus of antipatharian thereby cleaning it	(Le Guilloux et al. 2010)
<i>Hippolyte varians</i>	<i>Antipathella wollastoni</i>	LB	–	–	Azores	32-41	Not clear if living on black coral or algae covering coral	(Fransen & Wirtz 1997; d'Udekem-d'Acoz & Wirtz 2002)
<i>Macropodia</i> sp.	<i>Antipathella wollastoni</i>	LB	–	–	Azores	40-41	–	(d'Udekem-d'Acoz & Wirtz 2002)
<i>Micropisa ovata</i>	<i>Antipathella subpinnata</i> , <i>Tanacetipathes spinescens</i>	LB	–	–	Cape Verde	–	–	(Wirtz & d'Udekem-d'Acoz 2001)
<i>Miopontonia yongei</i>	<i>Cirripathes anguina</i>	LB	F	–	Japan	20	Also found on gorgonian	(Okuno 1998)
<i>Miopandalus hardingi</i>	<i>Cirripathes</i> sp. <i>C. anguina</i>	LB	–	–	Indo-West Pacific	–	–	(Bruce 1983; Okuno 1998)
<i>Naxiodes taurus</i>	<i>Antipathes</i> sp., <i>Rhipidipathes</i> sp.	LB	F	C	Indonesia	5-45	Walk on antipatharian, especially at night	(Tazioli et al. 2007)
<i>Nematopagurus longicornis</i>	<i>Antipathella wollastoni</i>	LB	O	–	Azores	40-41	Only found on antipatharians	(d'Udekem-d'Acoz & Wirtz 2002)
<i>Neopericlimenes thornei</i>	<i>Cirripathes</i> sp., <i>Stichopathes</i> sp.	LB	–	–	Turks & Caicos Islands	40	Associated with antipatharian	(Heard et al. 1993; Spotte et al. 1994)
<i>Neopontonides beaufortensis</i>	<i>Stichopathes gracilis</i>	LB	–	–	Caribbean	3-25	–	(Criales 1984)
<i>Neopontonides principis</i>	<i>Stichopathes gracilis</i>	LB	–	–	Caribbean	3-25	–	(Criales 1984)
<i>Pagurus</i> sp.	<i>Parantipathes</i> sp., <i>Antipathes</i> sp.	LB	–	M	Ireland	620-700	Antipatharians often associated with large numbers of crabs	(Wienberg et al. 2008)
<i>Palaemonella atlantica</i>	<i>Antipathes</i> sp., <i>Antipathella subpinnata</i> , <i>Tanacetipathes spinescens</i>	LB	F	–	Cape Verde	<60	Also found on anemone	(Fransen & Wirtz 1997; Wirtz & d'Udekem-d'Acoz 2001)
Palaemonidae sp.	<i>Stichopathes lutkeni</i> , <i>Stichopathes</i> sp.	LB	–	–	Puerto Rico	25-75	External symbiont	(Humes & Goenaga 1978)

Symbiont species	Host species	Symbiont microhabitat	Depen- dence	Relation	Locality	Depth (m)	Comments	Reference(s)
<i>Periclimeses antipathophilus</i>	<i>Antipathes gracilis</i> , <i>Plumapathes pennacea</i> , <i>Antipathes</i> spp.	LB	–	–	Caribbean	17-45	Associated with antipatharian	(Spotte et al. 1994; De Grave & Anker 2009)
<i>Periclimeses arabicus</i>	<i>Antipathes</i> sp.	LB	–	–	Maldives	50	Associated with antipatharian	(Duris 1990)
<i>Periclimeses granulimanus</i>	Antipatharian	LB	F	–	Madagascar	24	Associated with antipatharian, also found on hydroids	(Bruce 1982; Spotte et al. 1994)
<i>Periclimeses infraspinis</i>	<i>Antipathes galapagensis</i>	LB	–	–	Eastern Pacific	3-76	Lives on branches of coral	(Kerstitch 1989)
<i>Periclimeses iridescens</i>	<i>Stichopathes gracilis</i> , <i>S. lutkeni</i>	LB	F	–	Caribbean	3-183	Also found on sand, algae and anemones	(Criales 1984; Spotte et al. 1994; De Grave & Anker 2009)
<i>Periclimeses lepidus</i>	Antipatharian	LB	–	–	Kenya, Madagascar	–	Associated with antipatharian	(Spotte et al. 1994)
<i>Periclimeses murcielagensis</i>	<i>Myriopathes panamensis</i>	LB	–	–	Caribbean	25	Associated with antipatharian	(Vargas 2000)
<i>Periclimeses nevillei</i>	<i>Cirripathes</i> sp.	LB	–	–	Vanuatu	8	Shrimp described from antipatharian associates	(Bruce 2010)
<i>Periclimeses nilandensis</i>	Antipatharian	LB	–	–	Kenya, Maldives, Madagascar, Indonesia	–	Associated with antipatharian	(Spotte et al. 1994)
<i>Periclimeses pedersoni</i>	<i>Plumapathes pennacea</i>	LB	–	–	Netherlands Antilles	12	Associated with various cnidarians	(Spotte 1996)
<i>Periclimeses platalea</i>	<i>Antipathella subpinnata</i> , <i>Tanacetipathes spinescens</i>	LB	–	–	Cape Verde	15-30	Collected on antipatharian	(Wirtz & d'Udekem-d'Acoz 2001)
<i>Periclimeses psamanthe</i>	<i>Antipathes</i> cf. <i>plana</i> , Antipatharians	LB	F	C	Indo-Pacific	5-45	Occasional associate of antipatharians	(Spotte et al. 1994; De Grave 2000; Tazioli et al. 2007)
<i>Periclimeses sagittifer</i>	<i>Antipathella wollastoni</i>	LB	–	–	Azores	29-40		(d'Udekem-d'Acoz & Wirtz 2002)
<i>Periclimeses</i> sp.	Antipatharian	LB	–	–	Madagascar, Australia	–	Associated with antipatharian	(Spotte et al. 1994)
<i>Periclimeses wirtzi</i>	<i>Antipathella subpinnata</i> , <i>A. wollastoni</i> , <i>Tanacetipathes spinescens</i>	LB	O	C	Cape Verde, Azores and Canary Islands	29-54	Obligatory commensal	(Fransen & Wirtz 1997; Wirtz & d'Udekem-d'Acoz 2001; d'Udekem-d'Acoz & Wirtz 2002)
Pontonidae sp.	<i>Antipathes griggi</i>	LB	–	–	Hawai'i	<50	–	(Grigg 1964)
<i>Pontonides</i> aff. <i>unciger</i>	<i>Cirripathes</i> sp., <i>Cirripathes anguina</i>	LB	–	–	Australia, Hawai'i	23	Associated with antipatharian	(Bruce 1982; Heard 1986; Spotte et al. 1994)
<i>Pontonides asperulatus</i>	<i>Cirripathes</i> sp.	LB	–	–	Papua New Guinea	16	–	(Marin 2006)
<i>Pontonides</i> cf. <i>maldivensis</i>	<i>Cirripathes</i> sp.	LB	–	–	Hawai'i	–	–	(Heard 1986)
<i>Pontonides loloata</i>	<i>Cirripathes</i> sp.	LB	–	–	Papua New Guinea	5	–	(Marin 2006)
<i>Pontonides</i> sp.	<i>Cirripathes</i> sp., <i>Antipathes griggi</i> , <i>A. grandis</i>	LB	–	–	Indo-West Pacific	20	Shrimp species needs redescription	(Grigg 1964; Castro 1971; Okuno 1998)
<i>Pontonides sympathes</i>	<i>Antipathes galapagensis</i>	LB	–	–	Galapagos	–	Associated with antipatharian	(Spotte et al. 1994) Heard 196
<i>Pontonides unciger</i>	<i>Cirripathes</i> spp., <i>C. cf. anguina</i> , <i>Pseudocirripathes mapia</i>	LB	O	C	Indo-West Pacific	5-45	Shrimps coloration pattern matches host	(Davis & Cohen 1968; Heard 1986; Spotte et al. 1994; De Grave 2000; Tazioli et al. 2007; Bo et al. 2009a; Bo et al. 2009c)
<i>Pseudocoutierea conchae</i>	<i>Stichopathes gracilis</i>	LB	–	–	Caribbean	15-25	Associated with antipatharian	(Criales 1984; Spotte et al. 1994)
<i>Pseudocoutierea edentata</i>	<i>Stichopathes gracilis</i>	LB	–	–	Caribbean	–	Associated with antipatharian	(Spotte et al. 1994)
<i>Pseudocoutierea wirtzi</i>	<i>Stichopathes lutkeni</i>	LB	–	–	Cape Verde Islands, Azores	29-54	Associated with antipatharian	(Wirtz & d'Udekem-d'Acoz 2001; Marin 2006)

Symbiont species	Host species	Symbiont microhabitat	Depen- dence	Relation	Locality	Depth (m)	Comments	Reference(s)
<i>Pseudopontonides plumosus</i>	<i>Antipathes</i> sp.	LB	–	–	Curacao	29	Species described from antipatharian associates	(Snijders & Fransen 2010)
<i>Pseudopontonides principis</i>	<i>Stichopathes</i> spp., <i>S. gracilis</i> , <i>Cirripathes</i> spp., <i>Antipathes gracilis</i> , <i>Plumapathes pennacea</i>	LB	F	–	Caribbean	–	Also found with <i>Virgularia</i> sp.	(Heard 1986; Spotte et al. 1994)
<i>Quadrella lewinoehni</i>	Antipatharian	LB	–	–	Marquesas	10-15	Found on antipatharian	(Castro 1997a)
<i>Quadrella maculosa</i>	<i>Antipathes</i> sp., <i>A. abies</i> , <i>Parantipathes</i> sp., Antipatharian	LB	O	C	Indo-West Pacific	5-45	Associations in genus <i>Quadrella</i> are almost obligate with antipatharians	(Colin & Arneson 1995; Shih & Mok 1996; Castro 1997b; Tazioli et al. 2007)
<i>Quadrella reticulata</i>	<i>Antipathes</i> sp.	LB	–	–	Moluccas	18-25	Collected on antipatharian	(Castro 1999)
<i>Quadrella</i> spp.	<i>Cirripathes abies</i> , <i>Antipathes</i> spp.	LB	O	C	Indonesia	5-45	Associations in genus <i>Quadrella</i> are almost obligate with antipatharians	(Tazioli et al. 2007)
<i>Rapipontonia platalea</i>	Antipatharians	LB	F	–	–	–	Also found on gorgonian	(De Grave & Anker 2009)
<i>Tozeuma armatum</i>	<i>Antipathes</i> spp.	LB	–	C	Indonesia	5-45	Lives on antipatharian	(Tazioli et al. 2007)
<i>Waldola schmitti</i>	<i>Myriopathes panamensis</i>	IT	–	–	Caribbean	–	found within the colony	(Vargas 2000)
<i>Xenocarcinus</i> spp.	<i>Antipathes</i> spp.	LB	–	C	Japan	–	Color matches that of host. No apparent damage to host	(Hayashi 1975)
<i>Xenocarcinus tuberculatus</i>	<i>Cirripathes</i> spp.	LB	–	C	Indonesia	5-45	Firmly attached to antipatharian	(Tazioli et al. 2007)
Class: Maxillopoda								
Subclass: Copepoda								
<i>Asteropontius bandicola</i>	<i>Cupressopathes abies</i> , <i>Tanacetipathes</i> cf. <i>spinescens</i>	LB	–	–	Moluccas, Madagascar	–	Collected on antipatharian	(Humes 1992)
<i>Asteropontius bifurcatus</i>	<i>Myriopathes japonica</i>	LB	–	–	Korea	–	Species described from antipatharian associates	(Kim & Je 2000)
<i>Asteropontius latus</i>	<i>Antipathes</i> sp.	LB	–	–	Philippines	–	Collected on antipatharian	(Humes 1992)
<i>Calonastes imparipes</i>	<i>Stichopathes lutkeni</i> , <i>Stichopathes</i> sp.	IT	–	C	Puerto Rico	25-75	No damage to host even in heavy infestations	(Goenaga 1977; Humes & Goenaga 1978)
<i>Camotesia bullifera</i>	<i>Antipathes</i> sp.	LB	–	–	Philippines	30	Collected on antipatharian	(Humes 1990)
<i>Lichomolgus insectus</i>	<i>Tanacetipathes</i> cf. <i>spinescens</i> , <i>Myriopathes myriophyllia</i> and <i>Cupressopathes abies</i>	LB	–	–	Madagascar	23-25	–	(Humes 1969)
<i>Orecturus grandisetiger</i>	<i>Antipathes</i> sp., <i>A. longibrachiata</i> , <i>Arachnopathes ericoides</i> , <i>Rhipidipathes reticulata</i>	LB	–	–	Madagascar, Moluccas, Philippines	–	Collected on antipatharian	(Humes 1992)
<i>Paramolgus constrictus</i>	<i>Cupressopathes abies</i> , <i>Arachnopathes ericoides</i>	LB	–	–	Madagascar	24-35	Collected on antipatharian	(Humes 1969; Humes & Stock 1973; Humes 1979)
<i>Paramolgus delicatulus</i>	<i>Antipathes</i> sp.	LB	–	–	Philippines	–	Collected on antipatharian	(Humes 1992)
<i>Paramolgus insectus</i>	<i>Antipathes</i> sp., <i>Tanacetipathes</i> cf. <i>spinescens</i> , <i>A. abies</i> , <i>Myriopathes myriophylla</i> , <i>Cirripathes anguina</i>	LB	–	–	Madagascar, Moluccas, Philippines	–	Collected on antipatharian	(Humes 1969; Humes & Stock 1973; Humes 1979; Humes 1992)
Saphellidae sp.	<i>Antipathes</i> sp.	LB	–	–	Philippines	30	Collected on antipatharian	(Humes 1990)
<i>Thamnomolgus nodulus</i>	<i>Antipathes</i> sp.	LB	–	–	Philippines	30	Collected on antipatharian	(Humes 1990)

Symbiont species	Host species	Symbiont microhabitat	Dependence	Relation	Locality	Depth (m)	Comments	Reference(s)
<i>Thamnomolgus robustus</i>	<i>Antipathes</i> sp., <i>Cupressopathes abies</i> , <i>Myriopathes myriophylla</i> , <i>Tanacetipathes</i> cf. <i>spinescens</i> , <i>Arachnopathes</i> <i>ericoides</i>	LB	–	–	Madagascar, Philippines	20-30	Collected on antipatharian	(Humes 1969; Humes 1979; Humes 1990; Humes 1992)
<i>Vahinius petax</i>	<i>Stichopathes echinulata</i> and <i>Antipathes longibrachiata</i>	IT	–	P	Madagascar	30	Copepods recovered after thoroughly washing antipatharian with preservative, suggesting that they live internally within antipatharian	(Humes 1967; Humes 1969; Humes 1979; Humes 1992)
<i>Vahinius verbericolus</i>	<i>Cupressopathes abies</i>	LB	–	P	Moluccas	–	Collected on antipatharian	(Humes 1979)
<i>Visayasias lobura</i>	<i>Antipathes</i> sp.	LB	–	–	Philippines	–	Collected on antipatharian	(Humes 1992)
<i>Visayasias subterna</i>	<i>Antipathes</i> sp.	LB	–	–	Philippines	–	Collected on antipatharian	(Humes 1992)
Class: Maxillopoda								
Subclass: Thecostraca								
Infraclass: Ascothoracida								
<i>Synagoga mira</i>	<i>Parantipathes larix</i>	LB	F	P	Naples harbor	–	Ascothoracida crustaceans commonly parasitize echinoderms and cnidarians. Not host specific.	(Grygier 1983)
Class: Maxillopoda								
Subclass: Thecostraca								
Infraclass: Cirripedia								
<i>Calantica graphica</i>	Antipatharians	LB	–	–	Philippines	193-205	Attached to antipatharian	(Jones et al. 2000)
<i>Conopea cymbiformis</i>	Antipatharians	LB	F	–	Indo-West Pacific	<403	Attached to coenosarc of antipatharians and gorgonians	(Jones et al. 2000)
<i>Conopea dentifer</i>	Antipatharians	LB	F	–	Indonesia, Philippines, Japan, Tonga	26-266	Embedded in coenosarc of antipatharians and gorgonians	(Jones et al. 2000)
<i>Conopea granulatus</i>	Antipatharians	LB	F	–	Japan, China, Taiwan, Philippines	90-200	Embedded in coenosarc of antipatharians and gorgonians	(Jones et al. 2000)
<i>Conopea sinensis</i>	Antipatharians	LB	–	–	South China Sea	–	–	(Jones et al. 2000)
<i>Heteralepas cornuta</i>	<i>Antipathes</i> sp.	LB	–	–	St. Vincent, West Indies	–	–	(Rosell 1981)
<i>Heteralepas smilius</i>	Antipatharians	LB	–	–	South and East China Sea	167-217	Attached to antipatharian	(Jones et al. 2000)
<i>Lepas minima</i>	<i>Antipathes</i> sp.	LB	–	–	NR	NR	Attached to antipatharian	(Thompson 1835)
<i>Megalasma minus</i>	<i>Antipathes</i> sp.	LB	F	–	Philippines	484-448	Also found on sea urchin spines	(Rosell 1981)
<i>Megalasma striatum</i>	<i>Antipathes</i> sp.	LB	–	–	Indo-West Pacific	125-984	Attached to antipatharian	(Jones et al. 2000)
<i>Octolasmis warwickii</i>	Antipatharians	LB	F	–	Indo-West Pacific	14-100	Also attached to mollusks, decapods, sea snakes and fishes	(Jones et al. 2000)
<i>Octolasmis weberi</i>	<i>Antipathes</i> sp.	LB	–	–	Philippines	448-484	Attached to antipatharian	(Rosell 1981; Jones et al. 2000)
<i>Oxynaspis aurivillii</i>	Antipatharians	LB	–	–	South China Sea	10-453	Attached to antipatharian	(Jones et al. 2000)
<i>Oxynaspis bocki</i>	Antipatharians	LB	–	–	Japan, China, Philippines	150-300	Attached to antipatharian	(Rosell 1981; Jones et al. 2000)

Symbiont species	Host species	Symbiont microhabitat	Dependence	Relation	Locality	Depth (m)	Comments	Reference(s)
<i>Oxynaspis celata</i>	<i>Antipathella wollastoni</i> , antipatharians	LB	–	C	Atlantic, Pacific and Indian	15-1425	Attached to antipatharian; coral host covers barnacle valves	(Johnson 1899; Totton 1923; Jones et al. 2000; Jones 2003; Brito & Ocaña 2004; Wirtz et al. 2006)
<i>Oxynaspis connectens</i>	<i>Antipathes</i> sp., Antipatharians	LB	–	–	Philippines, Indonesia	183-245	Attached to antipatharian	(Rosell 1981; Jones et al. 2000)
<i>Oxynaspis faroni</i>	<i>Antipathes lentipinna</i>	LB	–	–	Red Sea, China	20	Attached to antipatharian	(Jones et al. 2000)
<i>Oxynaspis granti</i>	Antipatharians	LB	–	–	South of Penang	NR	Attached to antipatharian	(Jones et al. 2000)
<i>Oxynaspis reducens</i>	<i>Myriopathes japonica</i> , <i>Cirripathes anguina</i>	LB	–	–	Hong Kong, China	12	Attached to antipatharian	(Jones et al. 2000)
<i>Oxynaspis rossi</i>	<i>Antipathes</i> sp., <i>A. dendrochistos</i> , antipatharian	LB	O	–	Southern and Baja California	55-183	Spines may be of dual origin of both host and symbiont	(Newman 1972; Love et al. 2007)
<i>Oxynaspis</i> sp.	<i>Antipathella aperta</i>	LB	–	–	New Zealand	128	Attached to antipatharian	(Totton 1923)
<i>Oxynaspis terrae-novae</i>	<i>Lillipathes lilliei</i>	LB	F	–	New Zealand	128	Chance association	(Totton 1923)
<i>Pachylasma scutistriata</i>	Antipatharians	LB	F	–	Indo-West Pacific	104-2050	Also attached to crinoids	(Jones et al. 2000)
<i>Solidobalanus ciliatus</i>	<i>Myriopathes japonica</i>	LB	F	–	Indo-West Pacific	13-220	Also attached to octocoral	(Jones et al. 2000)
<i>Solidobalanus hawaiiensis</i>	Antipatharians	LB	F	–	Philippines, Japan, Hawai'i	184-193	Also found on algae	(Rosell 1981; Jones et al. 2000)
PHYLUM: BRYOZOA								
Class: Gymnolaemata								
Smittinidae spp.	Antipatharians	LB	–	–	Hawai'i	–	Commonly attached to antipatharians	(Soule & Soule 1972)
PHYLUM: CHORDATA								
Class: Actinopterygii								
<i>Bryaninops</i> sp.	<i>Cirripathes</i> sp.	LB	O	C	Palau	20	Gobies live and lay eggs on antipatharian	(Colin & Arneson 1995)
<i>Bryaninops tigris</i>	<i>Antipathes</i> sp.	LB	O	C	Throughout Pacific	5-53	Gobies bite coenenchyme of host to prepare nest	(Greenfield & Randall 2004; Tazioli et al. 2007)
<i>Bryaninops yongei</i>	<i>Cirripathes</i> spp.	LB	O	C	Red Sea to Hawai'i	5-158	Coloration of gobies matches host	(Davis & Cohen 1968; Okiyama & Tsukamoto 1989; Greenfield & Randall 2004; Herler 2007; Tazioli et al. 2007)
<i>Centropyge potteri</i>	<i>Antipathes grandis</i> , <i>A. griggi</i> , <i>Myriopathes ulex</i>	BB	F	C	Hawai'i	50-73	Fish are residents of specific trees	(Boland & Parrish 2005)
<i>Dascyllus albisella</i>	<i>Antipathes grandis</i> , <i>A. griggi</i> , <i>Myriopathes ulex</i>	BB	F	C	Hawai'i	50-73	Fish are residents of specific trees	(Boland & Parrish 2005)
<i>Oxycirrhites typus</i>	<i>Antipathes grandis</i> , <i>A. griggi</i> , <i>Myriopathes ulex</i>	BB	F	C	Red Sea, throughout Pacific	3-100	Lives on antipatharian branches, but also on gorgonians	(Donaldson & Colin 1989; Kerstitch 1989; Aburto-Oropeza & Balart 2001; Boland & Parrish 2005; Tazioli et al. 2007)
Class: Ascidiacea								
<i>Clavellia dellavallei</i>	<i>Antipathella subpinnata</i>	LB	–	–	Mediterranean	<100	–	(Bo 2008; Bo et al. 2009b)
PHYLUM: CNIDARIA								
Class: Anthozoa								

Symbiont species	Host species	Symbiont microhabitat	Depen- dence	Relation	Locality	Depth (m)	Comments	Reference(s)
<i>Carijoa</i> sp.	<i>Antipathes griggi</i> , <i>A. grandis</i>	LB, DB	F	P	Hawai'i	50-110	Octocoral overgrows tissues and skeleton of antipatharians	(Grigg 2003; Grigg 2004; Boland & Parrish 2005; Kahng & Grigg 2005)
<i>Epizoanthus</i> sp.	<i>Leiopathes glaberrima</i>	LB, DB	F	P	Mediterranean	671-790	Zoanthid parasite found on antipatharian colonies and on scleractinian <i>Madrepora oculata</i>	(Mastrototaro et al. 2010)
<i>Gerardia savaglia</i>	<i>Antipathes</i> sp.	LB	F	P	Madeira	<60	Zoanthid overgrows tissues and skeleton of antipatharians	(Wirtz 1998)
<i>Nemanthus</i> sp.	<i>Antipathes</i> sp.	LB	F	P	Indonesia	5-45	Frequently observed on dead colonies	(Tazioli et al. 2007)
<i>Parazoanthus</i> sp.	Antipatharian	LB	–	P	Cape Verde	–	Associated with antipatharians	(Sinninger et al. 2008)
<i>Parazoanthus</i> sp.	<i>Antipathes galapagensis</i>	LB	–	P	Galapagos	12-35	Zoanthids may overgrow and kill host	(Reimer et al. 2008)
<i>Savalia</i> sp.	<i>Tanacetipathes cavernicola</i>	LB	O	P	Cape Verde	–	Exclusively found on black corals	(Sinninger et al. 2005)
<i>Zoanthus</i> sp.	<i>Antipathes</i> spp., <i>Cirripathes</i> spp.	LB	–	P	Indonesia	5-45	Settle on bare parts of skeleton	(Tazioli et al. 2007)
Class: Hydrozoa								
<i>Bougainvillia</i> sp.	–	–	–	–	Mediterranean	<100	Common epibiont	(Bo 2008)
<i>Ectopleura</i> sp.	<i>Antipathella subpinnata</i>	LB, DB	F	C	Mediterranean	<100	Causes no apparent damage to host, also found on gorgonians	(Bo et al. in press)
<i>Lafoea gracillima</i>	<i>Antipathella aperta</i>	–	–	–	New Zealand	55	Commonly found on antipatharian	(Ralph 1958)
<i>Obelia</i> sp.	<i>Antipathella subpinnata</i>	–	–	–	Mediterranean	<100	Common epibiont	(Bo 2008)
PHYLUM: ECHINODERMATA								
Class: Crinoidea								
<i>Cenometra bella</i>	Various antipatharians	LB	F	C	Guam	30-45	Species clings to antipatharians and gorgonians	(Kirkendale & Messing 2003)
Class: Ophiuroidea								
<i>Asterogordius cacaoitica</i>	<i>Antipathes</i> sp.	LB	F	C	Jamaica	–	–	(Buhl-Mortensen & Mortensen 2004)
<i>Asteropora annulata</i>	<i>Elatopathes abietina</i> , <i>Antipathes</i> sp.	LB	F	C	Jamaica	–	–	(Buhl-Mortensen & Mortensen 2004)
<i>Astrobrachion constrictum</i>	<i>Antipathella fiordensis</i>	LB	O	M	New Zealand	10-30	Ophioroid cleans host and gets protection and food. Symbiont never found on any other host or free living	(Grange 1991; Stewart 1996; Stewart & Mladenov 1997; Stewart 1998)
<i>Ophiothrix</i> sp.	<i>Antipathes griggi</i>	LB	–	C	Hawai'i	<50	Holds on to black coral to feed on plankton	(Grigg 1964)
PHYLUM: MOLLUSCA								
Class: Bivalvia								
<i>Pteria</i> sp.	<i>Antipathes griggi</i>	LB, DB	F	C	Hawai'i	<50	–	(Weaver 1961; Grigg 1964)
<i>Pteria</i> spp.	<i>Antipathes griggi</i>	LB, DB	F	C	Indonesia	5-45	Settle on bare parts of skeleton	(Rees 1969; Tazioli et al. 2007)
<i>Pteria hirundo</i>	<i>Antipathella subpinnata</i>	LB, DB	F	C	Mediterranean	<100	Common epibiont	(Bo 2008; Bo et al. 2008)
<i>Pteria sterna</i>	<i>Myriopathes panamensis</i> , <i>Arachnopathes ericoides</i>	LB, DB	F	–	Gulf of Panama	10-25	Coral branches provide substrate for bivalves	(Opresko 1976)
Class: Gastropoda								
<i>Coralliophila kaofitorum</i>	<i>Antipathella wollastoni</i>	LB	O	P	Canary Islands	15-520	Preys on black coral host	(Vega et al. 2002; Brito & Ocaña 2004)
<i>Cypraea helvola</i>	<i>Antipathes griggi</i>	LB	F	C	Hawai'i	<50	Live at the bases of colonies	(Grigg 1964)

Symbiont species	Host species	Symbiont microhabitat	Dependence	Relation	Locality	Depth (m)	Comments	Reference(s)
<i>Cypraea sulcidentata</i>	<i>Antipathes griggi</i>	LB	F	C	Hawai'i	<50	Live at the bases of colonies	(Grigg 1964)
<i>Cypraea tessellata</i>	<i>Antipathes griggi</i>	LB	F	C	Hawai'i	<50	Live at the bases of colonies	(Grigg 1964)
<i>Neosimnia sp.</i>	<i>Antipathes griggi</i>	LB	F	C	Hawai'i	<50	Color of gastropod matches antipatharian host	(Grigg 1964)
<i>Phenacovolva carnepicta</i>	<i>Antipathes sp.</i>	LB	–	P	Marquesas	59	Likely preys on antipatharian host	(Rehder & Wilson 1975)
<i>Phenacovolva weaveri</i>	<i>Antipathes spp.</i> , <i>Cirripathes spp.</i>	LB	O	P	Indonesia	5-45	Mimics its antipatharian host on which it preys	(Schiaparelli et al. 2005; Tazioli et al. 2007)
<i>Rhizochilus antipathum</i>	<i>Arachnopathes ericoides</i> , <i>Antipathes griggi</i>	LB	O	P	Red Sea, Hawai'i	<50	Preys on antipatharian host	(Totton 1923; Grigg 1964; Rees 1969; Okamura & Habe 1976)
<i>Rhizochilus teramachii</i>	<i>Myriopathes japonica</i>	LB	–	P	Japan	30-50	Likely preys on antipatharian host	(Okamura & Habe 1976)
<i>Rhizochilus sp.</i>	Antipatharian	LB	–	P	Mexico	–	Preys on antipatharian host	(Poorman 1981)
<i>Vermetus enderi</i>	<i>Antipathes spp.</i>	LB	F	P	Maldives, Philippines, Indonesia	15-20	Forms dense aggregation on antipatharian host, also found on gorgonians	(Schiaparelli & Metivier 2000)
KINGDOM: PROTOZOA								
PHYLUM: MYZOOZOA								
Class: Dinophyceae								
<i>Symbiodinium spp.</i>	<i>Cirripathes sp.</i>	IT	–	M	Indonesia	15-40	Symbionts enclosed by symbiosome	(Bo 2008; Bo et al. 2011)
<i>Symbiodinium spp.</i>	Various antipatharians	IT	F	C/P?	Hawai'i	10-396	Low densities exclude mutualism	(Wagner et al. 2011b)

that symbionts were enclosed by a symbiosome, a specialized structure that allows for mutualistic interactions between endosymbiont and host cells (Wakefield et al. 2000; Wakefield & Kempf 2001). Together, these observations provide strong evidence for a mutualistic relationship between *Symbiodinium* and *Cirrhopathes* sp. (Bo 2011). To date, this remains the only report of a mutualistic relationship between *Symbiodinium* and a black coral (**Table 2.5**).

Conclusion

Antipatharians are of great cultural and economic importance to many societies, however, because most species inhabit deep environments (> 50 m), very little is known about their basic biology and ecology. The literature review presented here reveals several generalities in the biology and ecology among the order Antipatharia. Black corals occur throughout all oceans and from subtidal to abyssal depths, however, they are particularly common in tropical and subtropical regions at depths below 50 m. Antipatharians are generally found on hard substrates, in areas with low-light intensities and strong currents. Under favorable conditions, black corals can form dense aggregations to the point of being ecologically dominant. Zooplankton appears to be a major component of the diet of black corals, which feed as suspension feeders and use mucus and nematocysts to capture their prey. Unlike other corals, zooxanthellae are generally not important to the nutrition of antipatharians. Reproduction occurs through both sexual and asexual processes, which have mostly been studied for a few shallow-water species (< 50 m). In general, polyps and colonies are strictly gonochoric, and fertilization and larval development likely occurs externally; however, to date

antipatharian larvae have only been observed for a single species. Antipatharians are generally slow-growing and long-lived organisms with maximum longevities ranging from decades to millennia, and contain the longest living colonial organism known on the planet (≤ 4250 yr). Black corals avoid competition with obligate photosynthetic fauna by being more abundant with depth, and may compete for space by using sweeper tentacles and secondary metabolites. With the exception of a few specialized gastropod predators and green sea turtles, antipatharians appear to be little impacted by predation. Like other corals, antipatharians are of great importance to a myriad of associated species, several of which are adapted to exclusively live on black corals.

One of the main conclusions of this review is that studies dedicated to the biology and ecology of antipatharians have traditionally been very scarce, and have for the most part been conducted in shallow water (< 50 m). Consequently, future studies targeting deeper black coral populations will be needed to verify whether the same patterns observed in shallow-water (< 50 m), also hold true in deeper water (> 50 m). In particular, future deep-water collections will be needed to determine whether antipatharian species have limited biogeographical distributions, or whether this has simply been an artifact of low sampling efforts and/or taxonomic uncertainties. Additionally, studies on reproductive processes, feeding preferences and associated organisms will have to increase sample sizes, because at present most information is derived from the examination of a limited amount of specimens. Given the remoteness of the environments that most black corals inhabit, our understanding of these organisms will certainly depend on our ability to effectively sample them. Many important

biological observations have already been made using aquarium cultures of black corals. Given the inaccessibility of antipatharian habitats, our understanding of their biology and ecology may well depend on our ability to successfully maintain them in laboratory cultures.

CHAPTER 3. TAXONOMIC STUDY

Historical background

In 1725, Marsilli produced the first description and illustration of an antipatharian coral. Even though Marsilli (1725) believed that the organism he was illustrating was a plant, he highlighted its skeletal spines, one of the key features that characterizes antipatharians. Linnaeus (1758) recognized that antipatharians were actually animals, and grouped them with gorgonians based on the fact that both groups possess a skeletal axis that is surrounded by a layer of tissue. Later, Pallas (1766) separated these two taxa, because unlike gorgonians, antipatharians possess skeletal spines and lack calcareous spicules in their tissues. Dana (1846) recognized further differences in the morphology of the tentacles between these two groups, which are branched in gorgonians and unbranched in antipatharians. As a result, Dana (1846) grouped antipatharians with anemones, which also possess unbranched tentacles. Milne-Edwards and Haime (1857) were the first to recognize the Antipatharia as a distinct taxonomic order, and proposed an antipatharian classification scheme based entirely on skeletal features. Brook (1889) revised the antipatharian order by adding features of polyps as classifying characters, in particular the number of mesenteries, the size and position of tentacles around the mouth, and the arrangement of polyps around the axis. Schultze (1896a; 1896b) used the number of mesenteries to separate antipatharian families, a classification system that was expanded by Van Pesch (1914), who added polyp morphology as the main character to distinguish amongst genera, and skeletal spine morphology as the main character to differentiate amongst species.

Complicating the classification of the Antipatharia at the time, were different interpretations on the systematic placement of *Gerardia* and *Dendrobranchia* (see below), two genera that were originally grouped with antipatharians despite notable morphological differences (Verrill 1869; Brook 1889; Bell 1891; Schultze 1896a; Schultze 1896b; Van Pesch 1914). *Gerardia* polyps possess 24 unbranched tentacles and *Dendrobranchia* polyps have eight branched tentacles, whereas all other antipatharians have polyps with six branched tentacles. Pourtales (1871), Schultze (1896b) and Pax (1918) all recognized that these two groups should be removed from the Antipatharia to homogenize the order. However, this was not completed until Carlgren (1895) identified *Gerardia* as a zoanthid, and Opresko and Bayer (1991) recognized *Dendrobranchia* as a gorgonian octocoral. The latter identification proved to be particularly difficult because species within the genus *Dendrobranchia* lack calcareous spicules, one of the main octocoral features, but possess a spiny proteinaceous axis like antipatharians (Opresko & Bayer 1991; Lopez-Gonzalez & Cunha 2010). The number and morphology of the tentacles was the key characteristic to separating *Dendrobranchia* from antipatharians and grouping them with gorgonian octocorals (Opresko & Bayer 1991), a systematic placement which has since been corroborated by molecular analyses (Berntson et al. 1999; Strychar et al. 2007). With the removal of *Gerardia* and *Dendrobranchia* from the Antipatharia, the order is now considered a morphologically homogenous group within the anthozoan subclass Hexacorallia that encompasses 7 families, 43 genera and over 235 species (Daly et al. 2007; Bo 2008). The order is characterized by (1) a spiny, proteinaceous skeleton, (2) polyps with six unbranched, non-retractile tentacles, (3) six

primary mesenteries, and (4) exclusively colonial organisms (Opresko & Baron-Szabo 2001; Daly et al. 2003; Opresko & Sanchez 2005; Daly et al. 2007; Bo 2008).

Taxonomic history of Hawaiian black corals

The taxonomic study of Hawaiian antipatharians began in 1928 when Verrill described *Antipathes grandis* and *Antipathes irregularis*. However, only the *A. grandis* *nomen* remains valid, because Grigg and Opresko (1977) later identified *A. irregularis* as a gorgonian. In 1958, large black coral beds of *A. grandis* and a second antipatharian species (see below) were discovered off West Maui at depths between 30-90 m, a discovery that eventually led to the establishment of local black coral fishery (Weaver 1961; Gage 1962; Grigg 1964; Grigg 1965). In 1961, specimens of this second antipatharian species collected off Lahaina, Maui, were tentatively identified as *Antipathes dichotoma* Pallas, 1766 (Bayer 1961), a species originally described from off Marseilles in the Mediterranean Sea (Opresko 2003a). In 1977, Grigg and Opresko published a taxonomic study of Hawaiian black corals based on colony branching pattern that included species descriptions and a taxonomic key to 14 species found in 30-570 m. Since the study of Grigg and Opresko (1977), skeletal spine morphology has become an increasingly important character in antipatharian taxonomy (Opresko 1972; Opresko 2001; Opresko 2002; Opresko 2003b; Opresko 2004; Opresko 2005a; Opresko 2006; and references therein), because this character is thought to be largely independent of environmental cues, as compared to other morphological characters (Lapian et al. 2007; Wagner et al. 2010). However, Molodtsova and Budaeva (2007) examined the morphology of antipatharians within the families Antipathidae and Myriopathidae, and

found that the morphology of both the skeletal spines and the corallum is influenced by the presence of symbiotic polychaetes. Despite these exceptions, the high-resolution capability of scanning electron microscopy (SEM) has aided in the use of skeletal spine morphology as a taxonomic character for antipatharians by allowing visualization of minute spine features that may be diagnostic of individual families, genera and species (Opresko 1972; Opresko 1998; Opresko 2001; Opresko 2002; Opresko 2003b; Opresko 2004; Opresko 2005a; Opresko 2006; Lapian et al. 2007; Wagner et al. 2010). As a result of this technological advance, type specimens of numerous antipatharian species throughout the world have recently been reevaluated and redescribed (Grange 1988; Opresko & Genin 1990; Opresko & Cairns 1994; Opresko & Baron-Szabo 2001; Opresko 2003a; Molodtsova & Pasternak 2005; Opresko & Sanchez 2005; Ocaña et al. 2006), including two species from Hawaiian waters (Opresko 2009b; Wagner et al. 2010).

Unlike many other parts of the world, antipatharian populations have been well documented in Hawai'i (Grigg 1976; Grigg & Opresko 1977; Grigg 1984; Grigg 1988b; Grigg 1993; Montgomery & Crow 1998; Grigg 2001; Grigg 2002; Montgomery 2002; Grigg 2003; Grigg 2004; Boland & Parrish 2005; Etnoyer & Morgan 2005; Kahng & Grigg 2005; Kahng & Kelley 2007; Parrish & Baco 2007; Grigg 2010; Wagner et al. 2010; Wagner et al. 2011a). This is in large part due to a black coral fishery that has operated in Hawai'i since the late 1950's (Gage 1962; Grigg 1965; Grigg 2001), and has led to many black coral surveys in Hawaiian waters. However, many previous surveys in Hawai'i did not identify black corals to the species level, in large part due to the absence of detailed taxonomic studies until recently, as well as difficulties in differentiating

species *in situ* or from video data alone (Opresko 2009b; Wagner et al. 2010). The purpose of this chapter is to provide a taxonomic guide to the shallow-water black coral fauna from the Hawaiian Islands using (1) skeletal spine morphology, (2) polyp morphology, (3) branching pattern, and (4) *in situ* photographs. For this purpose, type material of species previously reported from Hawai‘i were reexamined where available, and compared to specimens collected from Hawaiian waters. This study is mostly limited to those species found at depths shallower than the top of the thermocline in the Main Hawaiian Islands (~120 m; Grigg 1984; Grigg 1993; Kahng & Grigg 2005; Kahng & Kelley 2007), because of the scarcity of specimens available from deeper waters. Additionally, this depth also represents the lower limit for several Hawaiian antipatharian and thus serves as a logical cutoff point for this study (Grigg 1984; Grigg 1993; Kahng & Kelley 2007; Wagner et al. 2010).

Materials and methods

A total of 161 antipatharian samples were examined as part of this study, and included museum specimens deposited at (1) the Bernice P. Bishop Museum in Honolulu, Hawai‘i (BPBM), (2) the National Museum of Natural History, Smithsonian Institution in Washington, D.C. (USNM), (3) the Museum of Comparative Zoology in Cambridge, Massachusetts (MCZ), and (4) specimens recently collected using conventional SCUBA, mixed-gas technical diving and the Hawai‘i Undersea Research Laboratory (HURL) manned submersibles *Pisces IV* and *V* (**Table 3.1**). Museum samples ranged from whole colonies to colony fragments of various sizes, and included type material of *Antipathes grandis*, *A. griggi*, *Stichopathes echinulata*, *Aphanipathes verticillata* and *Acanthopathes*

Table 3.1. Antipatharian samples examined as part of this study. Samples listed in bold represent holotypes (BPBM = Bernice P. Bishop Museum; F = Personal collection of D. Wagner; USNM = National Museum of Natural History; MCZ = Museum of Comparative Zoology at Harvard University; HURL = Hawai‘i Undersea Research Laboratory submersible dive; – = data not available).

Species	Family	Sample number	Date	Collector	Depth (m)	Locality	Latitude	Longitude
<i>Antipathes grandis</i>	Antipathidae	BPBM 102	–	–	–	Maui	–	–
<i>Antipathes grandis</i>	Antipathidae	F-027	12/8/2007	HURL P4-200	92	Maui	20.942	-156.759
<i>Antipathes grandis</i>	Antipathidae	F-030	12/8/2007	HURL P4-200	97	Maui	20.943	-156.758
<i>Antipathes grandis</i>	Antipathidae	F-031	12/8/2007	HURL P4-200	96	Maui	20.943	-156.758
<i>Antipathes grandis</i>	Antipathidae	F-032	12/8/2007	HURL P4-200	96	Maui	20.943	-156.758
<i>Antipathes grandis</i>	Antipathidae	F-033	12/8/2007	HURL P4-200	91	Maui	20.943	-156.758
<i>Antipathes grandis</i>	Antipathidae	F-035	12/11/2007	HURL P4-202	62	Kauai	21.856	-159.433
<i>Antipathes grandis</i>	Antipathidae	F-046	4/3/2008	HURL P4-204	95	Maui	20.936	-156.767
<i>Antipathes grandis</i>	Antipathidae	F-047	4/3/2008	HURL P4-204	95	Maui	20.936	-156.768
<i>Antipathes grandis</i>	Antipathidae	F-049	4/3/2008	HURL P4-204	96	Maui	20.936	-156.768
<i>Antipathes grandis</i>	Antipathidae	F-051	4/3/2008	HURL P4-204	96	Maui	20.936	-156.770
<i>Antipathes grandis</i>	Antipathidae	F-058	4/4/2008	HURL P4-205	95	Maui	20.951	-156.753
<i>Antipathes grandis</i>	Antipathidae	F-059	4/4/2008	HURL P4-205	88	Maui	–	–
<i>Antipathes grandis</i>	Antipathidae	F-060	4/4/2008	HURL P4-205	91	Maui	20.951	-156.753
<i>Antipathes grandis</i>	Antipathidae	F-061	4/4/2008	HURL P4-205	90	Maui	20.951	-156.753
<i>Antipathes grandis</i>	Antipathidae	F-067	4/5/2008	HURL P4-206	91	Maui	20.942	-156.757
<i>Antipathes grandis</i>	Antipathidae	F-068	4/5/2008	HURL P4-206	96	Maui	20.943	-156.758
<i>Antipathes grandis</i>	Antipathidae	F-070	4/5/2008	HURL P4-206	90	Maui	20.943	-156.756
<i>Antipathes grandis</i>	Antipathidae	F-071	4/5/2008	HURL P4-206	94	Maui	20.942	-156.757
<i>Antipathes grandis</i>	Antipathidae	F-072	4/5/2008	HURL P4-206	102	Maui	20.943	-156.757
<i>Antipathes grandis</i>	Antipathidae	F-197	4/4/2008	HURL P4-206	90	Maui	20.951	-156.753
<i>Antipathes grandis</i>	Antipathidae	F-199	5/28/2008	T. Montgomery	52	Maui	20.879	-156.747
<i>Antipathes grandis</i>	Antipathidae	F-200	5/28/2008	T. Montgomery	52	Maui	20.879	-156.746
<i>Antipathes grandis</i>	Antipathidae	F-201	5/28/2008	T. Montgomery	52	Maui	20.879	-156.747
<i>Antipathes grandis</i>	Antipathidae	F-204	5/28/2008	T. Montgomery	54	Maui	20.879	-156.747
<i>Antipathes grandis</i>	Antipathidae	F-205	5/29/2008	T. Montgomery	58	Maui	20.884	-156.724
<i>Antipathes grandis</i>	Antipathidae	F-249	10/31/2009	D. Wagner	28	Kaua‘i	21.928	-159.661
<i>Antipathes grandis</i>	Antipathidae	F-365	2/22/2009	HURL P5-716	100	Maui	20.941	-156.761
<i>Antipathes grandis</i>	Antipathidae	F-442	4/7/2009	HURL P5-739	127	Maui	20.941	-156.761
<i>Antipathes grandis</i>	Antipathidae	F-445	4/7/2009	HURL P5-739	102	Maui	20.941	-156.761
<i>Antipathes grandis</i>	Antipathidae	F-446	4/7/2009	HURL P5-739	102	Maui	20.941	-156.761
<i>Antipathes grandis</i>	Antipathidae	USNM 99812	7/16/1902	R/V Albatross	48-91	Hawai‘i	19.783	-155.074
<i>Antipathes griggi</i>	Antipathidae	USNM 52436	July 1961	H. Hall	45	Maui	–	–
<i>Antipathes griggi</i>	Antipathidae	F-019	7/17/2007	T. Montgomery	37	Ni‘ihau	22.030	-160.102
<i>Antipathes griggi</i>	Antipathidae	F-028	12/8/2007	HURL P4-200	95	Maui	20.943	-156.761
<i>Antipathes griggi</i>	Antipathidae	F-029	12/8/2007	HURL P4-200	93	Maui	20.943	-156.761
<i>Antipathes griggi</i>	Antipathidae	F-034	12/11/2007	HURL P4-202	62	Kaua‘i	21.856	-159.433
<i>Antipathes griggi</i>	Antipathidae	F-036	12/11/2007	HURL P4-202	62	Kaua‘i	21.856	-159.433
<i>Antipathes griggi</i>	Antipathidae	F-037	12/11/2007	HURL P4-202	62	Kaua‘i	21.856	-159.433
<i>Antipathes griggi</i>	Antipathidae	F-038	12/11/2007	HURL P4-202	62	Kaua‘i	21.856	-159.433
<i>Antipathes griggi</i>	Antipathidae	F-039	12/11/2007	HURL P4-202	62	Kaua‘i	21.856	-159.433
<i>Antipathes griggi</i>	Antipathidae	F-040	12/11/2007	HURL P4-202	62	Kaua‘i	21.856	-159.433
<i>Antipathes griggi</i>	Antipathidae	F-041	12/11/2007	HURL P4-202	62	Kaua‘i	21.856	-159.433
<i>Antipathes griggi</i>	Antipathidae	F-042	12/11/2007	HURL P4-202	62	Kaua‘i	21.856	-159.433
<i>Antipathes griggi</i>	Antipathidae	F-053	4/4/2008	HURL P4-205	90	Maui	20.952	-156.749
<i>Antipathes griggi</i>	Antipathidae	F-055	4/4/2008	HURL P4-205	99	Maui	20.950	-156.753
<i>Antipathes griggi</i>	Antipathidae	F-352	2/4/2009	D. Wagner	30	Kaua‘i	21.889	-159.583
<i>Antipathes griggi</i>	Antipathidae	F-448	4/7/2009	HURL P5-739	93	Maui	20.942	-156.759
<i>Antipathes griggi</i>	Antipathidae	F-526	6/13/2009	T. Montgomery	58	Kaua‘i	22.173	-159.755
<i>Antipathes griggi</i>	Antipathidae	F-530	6/15/2009	T. Montgomery	52	Kaua‘i	21.857	-159.433
<i>Antipathes griggi</i>	Antipathidae	F-561	8/1/2009	D. Wagner	35	Maui	20.885	-156.730
<i>Antipathes griggi</i>	Antipathidae	F-571	8/1/2009	D. Wagner	56	Maui	20.777	-156.620

Species	Family	Sample number	Date	Collector	Depth (m)	Locality	Latitude	Longitude
<i>Antipathes griggi</i>	Antipathidae	F-589	8/15/2009	D. Wagner	58	Laysan	25.726	-171.824
<i>Antipathes griggi</i>	Antipathidae	F-606	8/27/2009	D. Wagner	70	Laysan	25.711	-171.810
<i>Antipathes griggi</i>	Antipathidae	F-610	8/30/2009	D. Wagner	58	Necker	23.634	-164.742
<i>Antipathes griggi</i>	Antipathidae	F-611	8/30/2009	D. Wagner	58	Necker	23.634	-164.741
<i>Antipathes griggi</i>	Antipathidae	F-072b	8/28/2008	D. Wagner	23	O'ahu	21.593	-158.111
<i>Antipathes griggi</i>	Antipathidae	F-029b	11/22/2006	D. Wagner	10	O'ahu	21.260	-157.709
<i>Cirripathes cf. anguina</i>	Antipathidae	F-045	1/1/2006	D. Wagner	30	O'ahu	21.280	-157.860
<i>Cirripathes cf. anguina</i>	Antipathidae	F-212	10/29/2008	D. Wagner	10	O'ahu	21.260	-157.709
<i>Cirripathes cf. anguina</i>	Antipathidae	F-213	10/29/2008	D. Wagner	10	O'ahu	21.260	-157.709
<i>Cirripathes cf. anguina</i>	Antipathidae	F-250	10/31/2008	D. Wagner	24	Kaua'i	21.928	-159.661
<i>Cirripathes cf. anguina</i>	Antipathidae	F-252	11/6/2008	D. Wagner	10	O'ahu	21.282	-157.678
<i>Cirripathes cf. anguina</i>	Antipathidae	F-353	2/4/2009	D. Wagner	30	Kaua'i	21.889	-159.583
<i>Cirripathes cf. anguina</i>	Antipathidae	F-354	2/4/2009	D. Wagner	30	Kaua'i	21.889	-159.583
<i>Cirripathes cf. anguina</i>	Antipathidae	F-403	3/4/2009	D. Wagner	23	Kaua'i	21.887	-159.602
<i>Cirripathes cf. anguina</i>	Antipathidae	F-404	3/4/2009	D. Wagner	23	Kaua'i	21.887	-159.602
<i>Cirripathes cf. anguina</i>	Antipathidae	F-405	3/4/2009	D. Wagner	23	Kaua'i	21.887	-159.602
<i>Cirripathes cf. anguina</i>	Antipathidae	F-410	3/4/2009	D. Wagner	30	Kaua'i	21.889	-159.583
<i>Cirripathes cf. anguina</i>	Antipathidae	F-483	5/4/2009	D. Wagner	30	Kaua'i	21.889	-159.583
<i>Cirripathes cf. anguina</i>	Antipathidae	F-484	5/4/2009	D. Wagner	30	Kaua'i	21.889	-159.583
<i>Cirripathes cf. anguina</i>	Antipathidae	F-490	5/4/2009	D. Wagner	15	Kaua'i	21.881	-159.492
<i>Cirripathes cf. anguina</i>	Antipathidae	F-523	6/2/2009	D. Wagner	12	Kaua'i	21.907	-159.629
<i>Cirripathes cf. anguina</i>	Antipathidae	F-524	6/2/2009	D. Wagner	12	Kaua'i	21.907	-159.629
<i>Cirripathes cf. anguina</i>	Antipathidae	F-525	6/2/2009	D. Wagner	12	Kaua'i	21.907	-159.629
<i>Cirripathes cf. anguina</i>	Antipathidae	F-569	8/1/2009	D. Wagner	35	Maui	20.885	-156.730
<i>Cirripathes cf. anguina</i>	Antipathidae	F-583	8/1/2009	D. Wagner	56	Maui	20.777	-156.620
<i>Cirripathes cf. anguina</i>	Antipathidae	F-619	9/5/2009	D. Wagner	82	Lehua	22.018	160.102
<i>Cirripathes cf. anguina</i>	Antipathidae	F-620	9/5/2009	D. Wagner	82	Lehua	22.018	160.102
<i>Cirripathes cf. anguina</i>	Antipathidae	F-621	9/5/2009	D. Wagner	82	Lehua	22.018	160.102
<i>Cirripathes cf. anguina</i>	Antipathidae	F-622	9/5/2009	D. Wagner	82	Lehua	22.018	160.102
<i>Cirripathes cf. anguina</i>	Antipathidae	F-636	7/2/2010	D. Wagner	10	Oahu	21.260	-157.709
<i>Cirripathes cf. anguina</i>	Antipathidae	BPBM 361	August 1961	–	11	Hawai'i	–	–
<i>Cirripathes cf. anguina</i>	Antipathidae	USNM 91845	7/18/1902	–	44-152	Hawai'i	–	–
<i>Cirripathes cf. anguina</i>	Antipathidae	USNM 99918	–	R.A. Kinzie	9	–	–	–
<i>Cirripathes cf. anguina</i>	Antipathidae	F-235a	4/24/2010	D. Wagner	43	Palmyra	5.864	-162.137
<i>Cirripathes cf. anguina</i>	Antipathidae	F-269a	8/17/2010	D. Wagner	30	French Frigate Shoals	23.635	-166.186
<i>Cirripathes cf. anguina</i>	Antipathidae	F-166a	8/14/2009	D. Wagner	59	Laysan	25.710	-171.806
<i>Cirripathes cf. anguina</i>	Antipathidae	F-209b	9/4/2009	D. Wagner	27	Ni'ihau	22.022	-160.097
<i>Stichopathes echinulata</i>	Antipathidae	USNM 100371	–	R/V Challenger	–	Mauritius	–	–
<i>Stichopathes echinulata</i>	Antipathidae	F-001	10/23/2006	HURL P4-173	129	Maui	–	–
<i>Stichopathes echinulata</i>	Antipathidae	F-362	2/22/2009	HURL P5-716	130	Maui	20.941	-156.761
<i>Stichopathes echinulata</i>	Antipathidae	F-441	4/6/2009	HURL P5-738	129	Maui	20.735	-156.655
<i>Stichopathes echinulata</i>	Antipathidae	USNM 99705	10/23/1970	R/V Cromwell	108-198	Hawai'i	19.772	-156.109
<i>Stichopathes echinulata</i>	Antipathidae	USNM 99817	10/27/1967	R/V Cromwell	183	Lāna'i	20.751	-156.843
<i>Stichopathes echinulata</i>	Antipathidae	P4-221-0010	11/20/2009	HURL P4-221	120	Maui	–	–
<i>Stichopathes echinulata</i>	Antipathidae	P4-223-0040	11/23/2009	HURL P4-223	160	Maui	–	–
<i>Stichopathes echinulata</i>	Antipathidae	F-073a	12/11/2007	HURL P4-202	172	Kaua'i	21.853	-159.434
<i>Stichopathes</i> sp. (white morphotype)	Antipathidae	P4-226-9	12/1/2009	HURL P4-226	332	Ni'ihau	21.817	-160.071
<i>Stichopathes</i> sp.	Antipathidae	F-211	10/29/2008	D. Wagner	10	O'ahu	21.260	-157.709
<i>Stichopathes</i> sp.	Antipathidae	F-251	10/31/2008	D. Wagner	27	Kaua'i	21.928	-158.339
<i>Stichopathes</i> sp.	Antipathidae	F-399	3/4/2009	D. Wagner	23	Kaua'i	21.887	-159.602
<i>Stichopathes</i> sp.	Antipathidae	F-400	3/4/2009	D. Wagner	23	Kaua'i	21.887	-159.602
<i>Stichopathes</i> sp.	Antipathidae	F-408	3/4/2009	D. Wagner	30	Kaua'i	21.889	-159.583
<i>Stichopathes</i> sp.	Antipathidae	F-409	3/4/2009	D. Wagner	30	Kaua'i	21.889	-159.583
<i>Stichopathes</i> sp.	Antipathidae	F-488	5/4/2009	D. Wagner	15	Kaua'i	21.881	-159.492
<i>Stichopathes</i> sp.	Antipathidae	F-489	5/4/2009	D. Wagner	15	Kaua'i	21.881	-159.492
<i>Stichopathes</i> sp.	Antipathidae	F-570	8/1/2009	D. Wagner	35	Maui	20.885	-156.730
<i>Stichopathes</i> sp.	Antipathidae	F-608	8/30/2009	D. Wagner	58	Necker	23.634	-164.742
<i>Stichopathes</i> sp.	Antipathidae	F-618	8/30/2009	D. Wagner	58	Necker	23.634	-164.741
<i>Stichopathes</i> sp.	Antipathidae	F-637	7/2/2010	D. Wagner	10	O'ahu	21.260	-157.709

Species	Family	Sample number	Date	Collector	Depth (m)	Locality	Latitude	Longitude
<i>Stichopathes</i> sp.	Antipathidae	F-213b	9/4/2009	D. Wagner	27	Ni'ihau	22.022	-160.097
<i>Acanthopathes undulata</i>	Aphanipathidae	USNM 100409	–	R/V Siboga	113	Indonesia	–	–
<i>Acanthopathes undulata</i>	Aphanipathidae	P4-223-0041	11/23/2009	HURL P4-223	160	Maui	–	–
<i>Acanthopathes undulata</i>	Aphanipathidae	USNM 99801	7/11/1902	R/V Albatross	130-269	Hawai'i	20.008	-155.879
<i>Acanthopathes undulata</i>	Aphanipathidae	USNM 77103	5/16/1902	R/V Albatross	144-238	Laysan	25.865	-171.786
<i>Acanthopathes undulata</i>	Aphanipathidae	USNM 99581	12/6/1968	T.A. Clarke	30-37	O'ahu	–	–
<i>Acanthopathes undulata</i>	Aphanipathidae	USNM 99584	10/23/1970	R/V Cromwell	108-198	Hawai'i	19.784	-156.108
<i>Acanthopathes undulata</i>	Aphanipathidae	USNM 99807	10/30/1976	R/V Cromwell	165	–	–	–
<i>Acanthopathes undulata</i>	Aphanipathidae	P4-226-2	12/1/2009	HURL P4-226	263	Ni'ihau	21.824	-160.069
<i>Acanthopathes undulata</i>	Aphanipathidae	BPBM 966	3/7/1983	HURL M83-151	259	O'ahu	–	–
<i>Aphanipathes verticillata</i>	Aphanipathidae	MCZ 68	–	R/V Siboga	–	Mauritius	–	–
<i>Aphanipathes verticillata</i>	Aphanipathidae	F-048	4/3/2008	HURL P4-204	96	Maui	20.937	-156.765
<i>Aphanipathes verticillata</i>	Aphanipathidae	F-050	4/3/2008	HURL P4-204	113	Maui	20.953	-156.736
<i>Aphanipathes verticillata</i>	Aphanipathidae	F-054	4/4/2008	HURL P4-205	101	Maui	20.951	-156.769
<i>Aphanipathes verticillata</i>	Aphanipathidae	F-056	4/4/2008	HURL P4-205	111	Maui	20.950	-156.753
<i>Aphanipathes verticillata</i>	Aphanipathidae	F-057	4/4/2008	HURL P4-205	99	Maui	20.951	-156.752
<i>Aphanipathes verticillata</i>	Aphanipathidae	F-064	4/5/2008	HURL P4-206	93	Maui	20.942	-156.759
<i>Aphanipathes verticillata</i>	Aphanipathidae	F-065	4/5/2008	HURL P4-206	103	Maui	20.941	-156.760
<i>Aphanipathes verticillata</i>	Aphanipathidae	F-069	4/5/2008	HURL P4-206	114	Maui	20.943	-156.758
<i>Aphanipathes verticillata</i>	Aphanipathidae	F-363	2/22/2009	HURL P5-716	88	Maui	20.941	-156.761
<i>Aphanipathes verticillata</i>	Aphanipathidae	F-364	2/22/2009	HURL P5-716	114	Maui	20.940	-156.761
<i>Aphanipathes verticillata</i>	Aphanipathidae	F-366	2/22/2009	HURL P5-716	113	Maui	20.941	-156.761
<i>Aphanipathes verticillata</i>	Aphanipathidae	F-367	2/22/2009	HURL P5-716	126	Maui	20.940	-156.761
<i>Aphanipathes verticillata</i>	Aphanipathidae	F-368	2/22/2009	HURL P5-716	130	Maui	20.941	-156.761
<i>Aphanipathes verticillata</i>	Aphanipathidae	F-443	4/7/2009	HURL P5-739	127	Maui	20.941	-156.761
<i>Aphanipathes verticillata</i>	Aphanipathidae	F-444	4/7/2009	HURL P5-739	91	Maui	20.942	-156.759
<i>Aphanipathes verticillata</i>	Aphanipathidae	F-447	4/7/2009	HURL P5-739	88	Maui	20.941	-156.761
<i>Aphanipathes verticillata</i>	Aphanipathidae	F-449	4/7/2009	HURL P5-739	92	Maui	20.941	-156.761
<i>Aphanipathes verticillata</i>	Aphanipathidae	F-450	4/7/2009	HURL P5-739	121	Maui	20.942	-156.759
<i>Aphanipathes verticillata</i>	Aphanipathidae	USNM 99727	11/14/1981	R.F. Bolland	79	Okinawa	26.500	127.848
<i>Myriopathes cf. ulex</i>	Myriopathidae	F-066	4/5/2008	HURL P4-206	96	Maui	20.943	-156.758
<i>Myriopathes cf. ulex</i>	Myriopathidae	F-596	8/17/2009	D. Wagner	61	Pearl & Hermes	27.762	-175.983
<i>Myriopathes cf. ulex</i>	Myriopathidae	F-597	8/17/2009	D. Wagner	61	Pearl & Hermes	27.762	-175.983
<i>Myriopathes cf. ulex</i>	Myriopathidae	F-598	8/17/2009	D. Wagner	61	Pearl & Hermes	27.762	-175.983
<i>Myriopathes cf. ulex</i>	Myriopathidae	F-599	8/17/2009	D. Wagner	61	Pearl & Hermes	27.762	-175.983
<i>Myriopathes cf. ulex</i>	Myriopathidae	F-600	8/17/2009	D. Wagner	61	Pearl & Hermes	27.762	-175.983
<i>Myriopathes cf. ulex</i>	Myriopathidae	F-601	8/17/2009	D. Wagner	61	Pearl & Hermes	27.762	-175.983
<i>Myriopathes cf. ulex</i>	Myriopathidae	F-602	8/17/2009	D. Wagner	61	Pearl & Hermes	27.762	-175.983
<i>Myriopathes cf. ulex</i>	Myriopathidae	F-603	8/17/2009	D. Wagner	61	Pearl & Hermes	27.762	-175.983
<i>Myriopathes cf. ulex</i>	Myriopathidae	F-604	8/25/2009	D. Wagner	70	Pearl & Hermes	27.764	-175.986
<i>Myriopathes cf. ulex</i>	Myriopathidae	F-605	8/25/2009	D. Wagner	70	Pearl & Hermes	27.764	-175.986
<i>Myriopathes cf. ulex</i>	Myriopathidae	F-617	8/30/2009	D. Wagner	58	Necker	23.634	-164.741
<i>Myriopathes cf. ulex</i>	Myriopathidae	F-002a	9/11/2004	HURL P5-570	58	Maui	20.879	-156.759
<i>Myriopathes cf. ulex</i>	Myriopathidae	USNM 99827	9/29/1970	R/V Cromwell	326	O'ahu	21.298	-157.538
<i>Myriopathes cf. ulex</i>	Myriopathidae	USNM 99928	–	–	41	–	–	–
<i>Myriopathes cf. ulex</i>	Myriopathidae	USNM 1010727	9/12/2002	HURL P4-049	170	Brooks Bank	24.005	-166.676
<i>Myriopathes cf. ulex</i>	Myriopathidae	USNM 1010729	9/12/2002	HURL P4-049	255	Brooks Bank	24.004	-166.674
<i>Myriopathes cf. ulex</i>	Myriopathidae	USNM 1092637	7/11/1902	R/V Albatross	130-269	Hawai'i	20.008	-155.879

undulata (**Table 3.1**). For recently collected specimens, entire colonies were photographed *in situ*, and 5-10 tissue samples were clipped from each colony and preserved in 10% formaldehyde in seawater. Morphometric measurements of polyps and spines were made from photographs of preserved specimens as described by Wagner et al. (2010). Additionally, samples were prepared for SEM of skeletal spines, and viewed under a S-4800 Hitachi Field Emission SEM (Hitachi High-Technologies Corporation, Tokyo, Japan) at the University of Hawai‘i at Mānoa (Wagner et al. 2010). Literature records of Hawaiian black corals were reviewed with the purpose of synonymizing different names that have previously been used for the same morphospecies. In cases where species assignments could not be verified from literature records alone, authors were contacted and species identifications were made using previously collected specimens, *in situ* photographs and/or collection information provided by authors.

Results

Based on the overall morphology of colonies, polyps and skeletal spines, the 161 examined samples belong to three families (Antipathidae, Aphanipathidae and Myriopathidae), six genera (*Antipathes*, *Cirrhopathes*, *Stichopathes*, *Aphanipathes*, *Acanthopathes* and *Myriopathes*), and eight different species (**Tables 3.1-3.2**). Five species were identified by directly comparing Hawaiian specimens to type material and included (1) *Antipathes griggi* Opresko, 2009, (2) *Antipathes grandis*, Verrill, 1928, (3) *Stichopathes echinulata* Brook, 1889, (4) *Aphanipathes verticillata* Brook, 1889, and (5) *Acanthopathes undulata* (Van Pesch 1914) (**Tables 3.1-3.2**). Additionally, specimens that

Table 3.2. Morphometric comparison of Hawaiian antipatharian species examined as part of this study. Unless otherwise noted, listed values represent means and ranges (in parentheses). (* = polyp density measured on one side of corallum only; ** = there is no distinction between polypar and abpolypar spines in *C. cf. anguina*; *** = polypar spine measurements of *A. undulata* include both hypostomal and circumpolypar spines; **** = forked spines are only present on the main stem and thicker branches of *M. ulex*).

	<i>Antipathes griggi</i> Opresko, 2009	<i>Antipathes grandis</i> Verrill, 1928	<i>Cirripathes cf. anguina</i> (Dana, 1846)	<i>Stichopathes echinulata</i> Brook, 1889	<i>Stichopathes?</i> <i>sp.</i>	<i>Aphanipathes verticillata</i> Brook, 1889	<i>Acanthopathes undulata</i> (Van Pesch, 1914)	<i>Myriopathes cf. ulex</i> (Ellis & Solander, 1786)
COLONY:								
Branching pattern	Bushy	Bushy	Unbranched	Unbranched	Unbranched	Bushy	Fan-shaped	Fan-shaped
Max. height (m)	3	3	2	1	5	1	0.5	3
Terminal branch diameter with tissue at midpoint (mm)	0.87 (0.46-1.66)	0.52 (0.31-0.79)	2.78 (1.39-6.12)	1.00 (0.74-1.22)	3.21 (1.74-5.55)	0.90 (0.60-1.23)	0.67 (0.55-0.91)	0.36 (0.24-0.64)
POLYPS:								
Transverse diameter (mm)	1.12 (0.58-1.75)	0.84 (0.35-1.42)	2.03 (0.67-4.45)	0.98 (0.51-1.35)	1.82 (0.82-3.98)	1.35 (0.72-1.81)	0.87 (0.50-1.15)	0.56 (0.32-0.92)
Polyp spacing (mm)	1.43 (0.57-2.83)	1.12 (0.47-1.78)	2.39 (0.92-4.76)	1.33 (0.81-1.93)	1.82 (1.02-3.44)	1.71 (0.89-2.76)	1.26 (1.01-1.58)	0.84 (0.31-1.71)
Density (polyps/cm)	7 (5-10)	9 (6-14)	4 (3-7)*	8 (6-10)	6 (4-8)	6 (5-8)	8 (7-8)	12 (8-15)
SPINES:								
Forks or apical knobs present	Yes	No	Yes	No	Yes	No	No	Yes (on main stem)****
Secondary spines present	Yes	No	No	No	Yes	No	No	No
Polypar spine height (µm)	181 (105-382)	87 (49-168)	213 (110-380)**	139 (81-190)	352 (199-785)	163 (90-266)	249 (85-460)***	122 (76-196)
Abpolypar spine height (µm)	127 (68-243)	62 (31-110)	213 (110-380)**	89 (54-147)	212 (95-442)	115 (54-201)	204 (113-329)	92 (51-172)
Spine spacing (µm)	379 (209-654)	280 (131-469)	524 (167-1806)	367 (187-670)	666 (276-1246)	324 (200-507)	234 (155-361)	177 (70-366)
HABITAT:								
Depth range (m)	10-99	27-127	9-82	129-183	10-58	88-130	30-263	41-326

are consistent with the descriptions of *Cirrhopathes anguina* (Dana, 1846) and *Myriopathes ulex* (Ellis & Solander, 1786) were identified among the examined samples. However, because the type material of both *C. anguina* and *M. ulex* is lost and the original descriptions are very brief, Hawaiian specimens cannot be conclusively assigned to these species until neotypes are designated and a thorough taxonomic study is undertaken. Finally, the examined material included an undescribed wire coral species, which is tentatively assigned to the genus *Stichopathes*. The diagnostic characters of the Hawaiian morphospecies identified as part of this study are highlighted in **Figures 3.1-3.8** and **Table 3.2**, and discussed in the systematic section and taxonomic key below.

Systematic section

Family ANTIPATHIDAE Ehrenberg, 1834

The Antipathidae is characterized by polyps that (1) are usually larger than 1 cm in transverse diameter (range = 1-3 mm), (2) are not elongated in the transverse plane, (3) possess ten mesenteries (six primary and four secondary), and (4) have sagittal tentacles (the two tentacles that are perpendicular to the branch bearing the polyp) that are substantially longer than its lateral tentacles (the four tentacles that are nearly parallel to the branch bearing the polyp) when fully expanded (Opresko 2005b; Opresko & Sanchez 2005; Bo 2008; Moon & Song 2008a). However, this latter feature is frequently lost as part of the preservation process. The Antipathidae has historically been considered a taxonomic dumping ground, and is the oldest and most speciose antipatharian family (Daly et al. 2007; Bo 2008). Consequently, colony and skeletal spine morphology are very heterogeneous within in this family. Several taxa that formally belonged to the

Antipathidae have been transferred to new families (Opresko 2001; Opresko 2002; Opresko 2003b; Opresko 2004; Opresko 2005a; Opresko 2006); however, the family is still not monophyletic and future taxonomic revisions are needed (Daly et al. 2007).

Genus *Antipathes* Pallas, 1766

Antipathes is the oldest antipatharian genus and is distinguished by colonies that are all branched, with branching patterns varying from fan-shaped to bushy (Opresko 1972; Opresko & Sanchez 2005). Like the Antipathidae, *Antipathes* is also considered a taxonomic dumping ground that is morphologically heterogenous (Opresko & Baron-Szabo 2001; Daly et al. 2007; Bo 2008; Moon & Song 2008a). Even though many species have been removed from *Antipathes* and added to new genera (Opresko & Cairns 1994; Opresko 2001; Opresko 2002; Opresko 2003b; Opresko 2004; Opresko 2006), the genus still groups together many uncertain species and is in need of revision (Bo 2008).

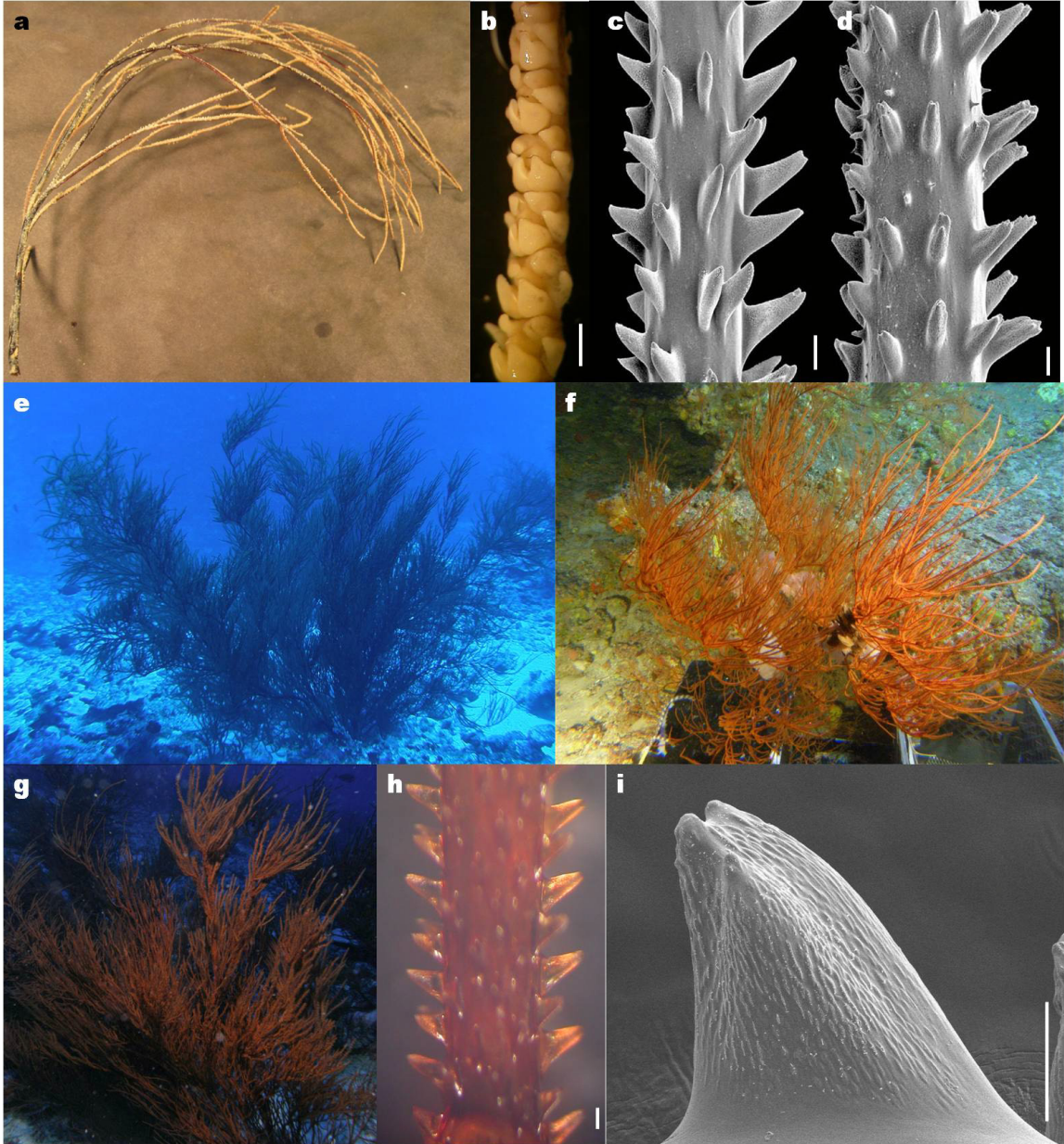
Antipathes griggsi Opresko, 2009

- Antipathes dichotoma* – (Bayer 1961: pg. 8).
- Antipathes grandis* – (Grigg 1964: pg. 1-74, fig. 2-4, 7, 9, 11-13, 17, 22, 24).
- Antipathes grandis* – (Grigg 1965: pg. 244-260, fig. 1, 3, 5-10).
- Antipathes dichotoma* – (Grigg 1974: pg. 235-240).
- Antipathes dichotoma* – (Grigg 1976: pg. 1-48, fig. 1, 4, 15).
- Antipathes dichotoma* – (Grigg & Opresko 1977: pg. 242-261, fig. 9-10).
- Antipathes dichotoma* – (Grigg 1984: pg. 57-74).
- Antipathes dichotoma* – (Grigg 1993: pg. 50-60, fig. 5).
- Antipathes dichotoma* – (Pyle & Chave 1994: pg. 92).
- Antipathes dichotoma* – (Montgomery & Crow 1998: pg. 103-108).
- Antipathes dichotoma* – (Montgomery 2002: pg. 157-164).
- Antipathes dichotoma* – (Grigg 2001: pg. 291-299, fig. 2-3).
- Antipathes dichotoma* – (Grigg 2002: pg. 13).
- Antipathes dichotoma* – (Grigg et al. 2002: pg. 79, fig. 6-7).
- Antipathes* sp. – (Opresko 2003a: pg. 491).
- Antipathes dichotoma* – (Grigg 2003: pg. 121-122).
- Antipathes dichotoma* – (Grigg 2004: pg. 1-6).
- Antipathes dichotoma* – (Greenfield & Randall 2004: pg. 513).
- Antipathes dichotoma* – (Boland & Parrish 2005: pg. 411-420).
- Antipathes dichotoma* – (Kahng & Grigg 2005: pg. 556-562).
- Antipathes* sp. – (Fenner 2005: pg. 96, 99, 3 unnumbered fig. on pg. 96 & 99).
- Antipathes* sp. – (Hoover 2006: pg. 69, unnumbered fig. on pg. 69).

Antipathes dichotoma – (Roark et al. 2006: pg. 1-14).
Antipathes dichotoma – (Parrish & Baco 2007: pg. 159, 170).
Antipathes cf. dichotoma – (Parrish & Baco 2007: pg. 185).
Antipathes cf. curvata – (Parrish & Baco 2007: pg. 159, 162, 164, 170, 173, 185, fig. 4.5(right)).
Antipathes dichotoma – (Kahng & Kelley 2007: pg. 684, 686).
Antipathes cf. curvata – (Baco 2007: pg. 112).
Antipathes griggi – (Opresko 2009b: pg. 277-291, fig. 1a-b, 2a-f, 3a-d, 4a-f).
Antipathes griggi – (Wagner et al. 2010: pg. 271-290, fig. 9e-h).
Antipathes griggi – (Grigg 2010: pg. 1-9).
Antipathes griggi – (Wagner et al. 2011a: pg. 249-255, fig. 2).
Antipathes griggi – (Wagner et al. 2011b: pg. 1323-1328, fig. 2a-b).
Antipathes griggi – (Wagner et al. 2011c: pg. 211-225, fig. 1c-d, 4a).

The Hawaiian species *Antipathes griggi* (**Figure 3.1**) was previously identified as *A. dichotoma* (Bayer 1961), a species originally described from off Marseilles in the Mediterranean Sea (Pallas 1766; Opresko 2003a). Subsequent comparisons between specimens from Hawai‘i and the Mediterranean Sea revealed substantial morphological differences (Opresko 2003a). As a result, the Hawaiian “*A. dichotoma*” has been assigned the new name of *Antipathes griggi* (Opresko 2009b). Surveys for *A. griggi* have been particularly frequent in Hawai‘i, because it is the main species targeted by the Hawaiian black coral fishery (Grigg 1993; Grigg 2001; Grigg 2004; Parrish & Baco 2007). Opresko (2009b) presented a detailed taxonomic description of *A. griggi*, and the main diagnostic features are briefly summarized here. *A. griggi* colonies can reach heights of up to 3 m, and are extensively branched with eight or more orders of branching (**Figure 3.1e-f**). Branches are arranged irregularly on all sides of the corallum on the lower part of the colony, and become more planar on the highest order branches (**Figure 3.1e-f**). Terminal branches reach up to 10 cm in length without becoming branched. Spines are conical, some have bifurcations towards their apex, and are covered with elongated tubercles over the biggest portion of their surface (**Figure 3.1i**). At midpoint, the terminal branches usually measure 0.46-1.66 mm in diameter with tissue, and contain polypar spines that are on average 181 μm tall (range= 105-382 μm), and abpolypar spines that are on average 127 μm tall (range= 68-243 μm). Smaller secondary spines, up to 40 μm tall, are

Figure 3.1a-d. *Antipathes griggi* holotype (USNM 52436) showing **a.** entire specimen, **b.** polyps on terminal branch under light microscopy (scale bar = 1mm), and **c-d.** skeletal spines on terminal branch under SEM (scale bars = 100 μ m). **e-g.** *A. griggi* colonies *in situ*; **h.** skeletal spines under light microscopy (scale bar = 100 μ m); **i.** close-up of polypar spine under SEM (scale bar = 50 μ m). (Photos courtesy of **e.** and **g.** Tony Montgomery, and **f.** HURL)



present on some portions of the corallum, especially on thicker branches (**Figure 3.1d**). On branchlets and smaller branches, spines are arranged in axial rows, with adjacent rows offset in a spiral pattern around the corallum (**Figure 3.1c-d**). Polyps average 1.12 mm in transverse diameter (range= 0.58-1.75 mm), and are typically spaced 1.43 mm apart (range= 0.57-2.83 mm), resulting in 7 polyps per cm (range= 5-10). The tissues of living colonies are colored brown to bright red (**Figure 3.1e-f**).

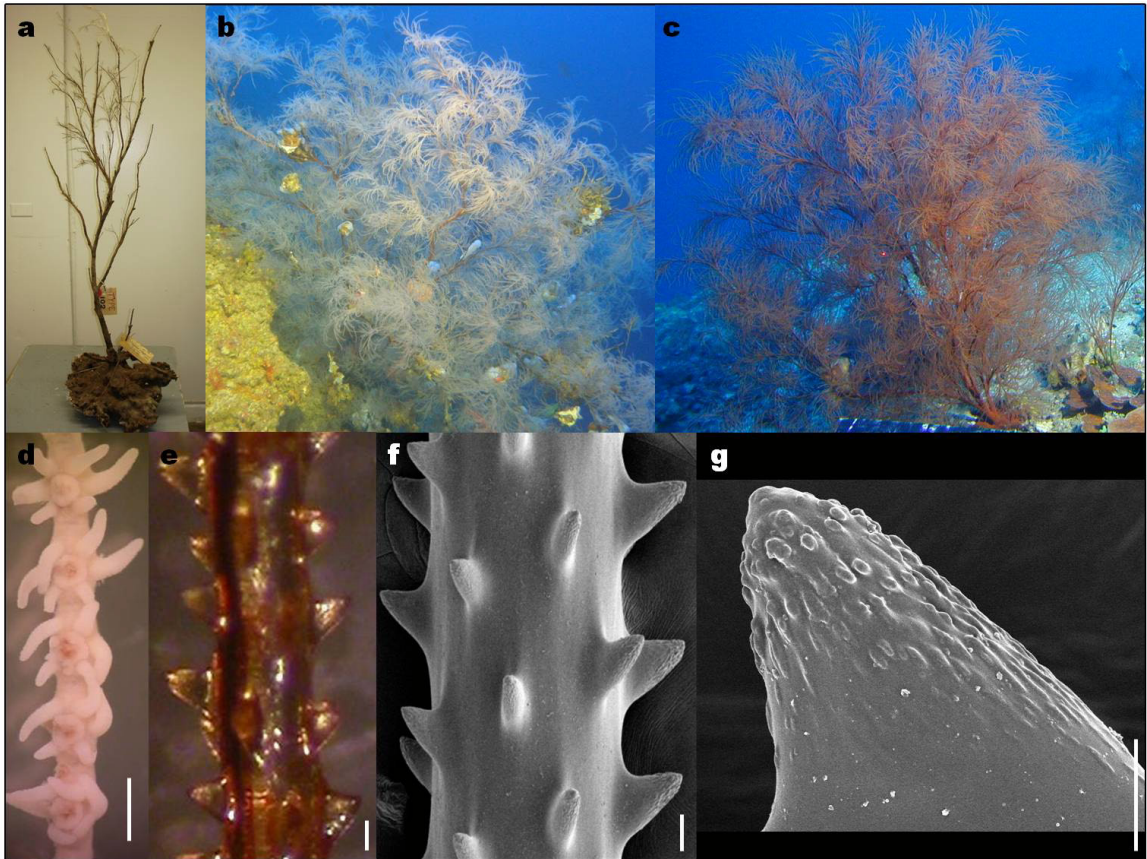
To date, specimens identified as *A. griggsi* have only been reported from the Hawaiian Archipelago from the islands of Hawai‘i to Laysan at depths ranging between 10-110 m (**Table 3.1**; Opresko 2009; Wagner et al. 2011a). However, colonies with similar morphologies, identified as *A. dichotoma*, have also been reported from other Indo-West Pacific locations including the Philippines, Indonesia, Palau, China, Guam and Johnston Atoll (Van Pesch 1914; Grigg 1975; Zhou & Zou 1984; Zou & Zhou 1984; Zhou & Zou 1992; Chave & Malahoff 1998; Paulay et al. 2003; Rogers et al. 2007; Qi et al. 2009). These locations are all outside the range of *A. dichotoma*, which is only known from the Mediterranean Sea and East Atlantic (Opresko 2003a; Bo 2008). Like the previous misidentification of *A. dichotoma* from Hawai‘i (see above), these misidentified *A. dichotoma* records may also be *A. griggsi*. However, detailed taxonomic investigations of specimens from the Indo-West Pacific will have to be undertaken to confirm this. Currently, there are no museum specimens of *A. griggsi* that were collected in waters outside of Hawai‘i.

Antipathes grandis Verrill, 1928

- Antipathes grandis* – (Verrill 1928: pg. 7, 9, fig. 1i-m, pl. IIc).
Antipathes grandis – (Grigg 1974: pg. 235-240).
Antipathes grandis – (Grigg 1976: pg. 1-48).
Antipathes grandis – (Grigg & Opresko 1977: pg. 242-261, fig 1, 11).
Antipathes grandis – (Grigg 1984: pg. 57-74).
Antipathes grandis – (Grigg 1993: pg. 50-60).
Antipathes grandis – (Grigg 2001: pg. 291-299).
Antipathes grandis – (Grigg 2002: pg. 13).
Antipathes grandis – (Grigg 2003: pg. 121-122).
Antipathes grandis – (Grigg 2004: pg. 1-6).
Antipathes grandis – (Fenner 2005: pg. 100, 2 unnumbered fig. on pg. 100).
Antipathes grandis – (Boland & Parrish 2005: pg. 411-420).
Antipathes grandis – (Kahng & Grigg 2005: pg. 556-562).
Antipathes grandis – (Parrish & Baco 2007: pg. 159, 162, 164, 170, 185, fig.4.5(left)).
Antipathes grandis – (Baco 2007: pg. 112).
Antipathes grandis – (Kahng & Kelley 2007: pg. 684, 686).
Antipathes grandis – (Wagner et al. 2010: pg. 271-290, fig. 2-7, 8a-b, 9a-d, 10).
Antipathes grandis – (Grigg 2010: pg. 1-9).
Antipathes grandis – (Wagner et al. 2011b: pg. 1323-1328, fig. 2c).
Antipathes grandis – (Wagner et al. 2011c: pg. 211-225, fig. 1a-b, 2a).

Like its sympatric congener *Antipathes griggi*, *A. grandis* (**Figure 3.2**) is also commercially harvested in Hawai‘i to supply the precious coral jewelry industry (Grigg 1984; Grigg 1993; Grigg 2001; Grigg 2004; Parrish & Baco 2007; Grigg 2010; Wagner et al. 2010). *A. grandis* was the first antipatharian species described from Hawaiian waters (Verrill 1928). A detailed taxonomic redescription of *A. grandis* is presented by Wagner et al. (2010), and briefly summarized here. Colonies can reach massive heights of over 3 m, and are extensively branched. Branches are long, distally-directed, and disposed irregularly on all sides of the corallum (**Figure 3.2a-c**). Terminal branchlets reach lengths of up to 10 cm without becoming subbranched and typically measure 0.52 mm in diameter with tissue at their midpoint (range = 0.31-0.79 mm). The spines on terminal branches are conical and never bifurcated towards their apex, and covered with circular to elongated oval-shaped tubercles over the distal half of their surface (**Figure 3.2f-g**). Polypar spines are slightly larger (range = 49-168 μm) than abpolypar spines (range = 31-110 μm) and both tend to be inclined distally (**Figure 3.2e-f**). There are no

Figure 3.2a. *Antipathes grandis* holotype (BPBM 102); **b-c.** colonies of *A. grandis* *in situ*; **d.** preserved polyps on terminal branch under light microscopy (scale bar = 1 mm); **e.** skeletal spines on terminal branch under light microscopy (scale bar = 100 μ m); **f.** skeletal spines on terminal branch under SEM (scale bar = 100 μ m); **g.** close-up of polypar spine under SEM (scale bar = 25 μ m). (**b-c.** Photos courtesy of HURL).



secondary spines present on any parts of the corallum. On branchlets and smaller branches spines are arranged in axial rows, with adjacent rows offset in a spiral pattern around the corallum (**Figure 3.2e-f**). On average, polyps are 0.84 mm in transverse diameter (range = 0.35-1.42 mm) and spaced 1.12 mm apart (range = 0.47-1.78 mm), resulting in 9 polyps per centimeter (range = 6-14). The color of living colonies ranges between red, pale-red and white (**Figure 3.2b-c**).

A. grandis was originally described from a specimen collected off Maui (Verrill 1928), and subsequently reported throughout the Main Hawaiian Islands from Hawai'i to Ni'ihau at depths between 27-127 m (Grigg 1974; Grigg 1976; Grigg & Opresko 1977; Grigg 2001; Grigg 2004; Boland & Parrish 2005; Kahng & Grigg 2005; Wagner et al. 2010). Additionally, there are two reports of this species from the waters off China (Zhou & Zou 1984; Zou & Zhou 1984), however, these records cannot be confirmed until specimens from that locality are examined.

Genus *Cirrhopathes* (Blainville, 1834)

The genus *Cirrhopathes* was originally established to differentiate antipatharian taxa with unbranched colonies from those with branched colonies (Blainville 1834). Later, Brook (1889) created *Stichopathes*, another genus with unbranched colonies, and used polyp arrangement as the diagnostic feature to differentiate between *Cirrhopathes* and *Stichopathes*. Polyps are arranged irregularly on all sides of the corallum in *Cirrhopathes*, whereas polyps are positioned in a single row on one side of the corallum in *Stichopathes* (Brook 1889). More recently, a third genus, *Pseudocirrhopathes*, has been

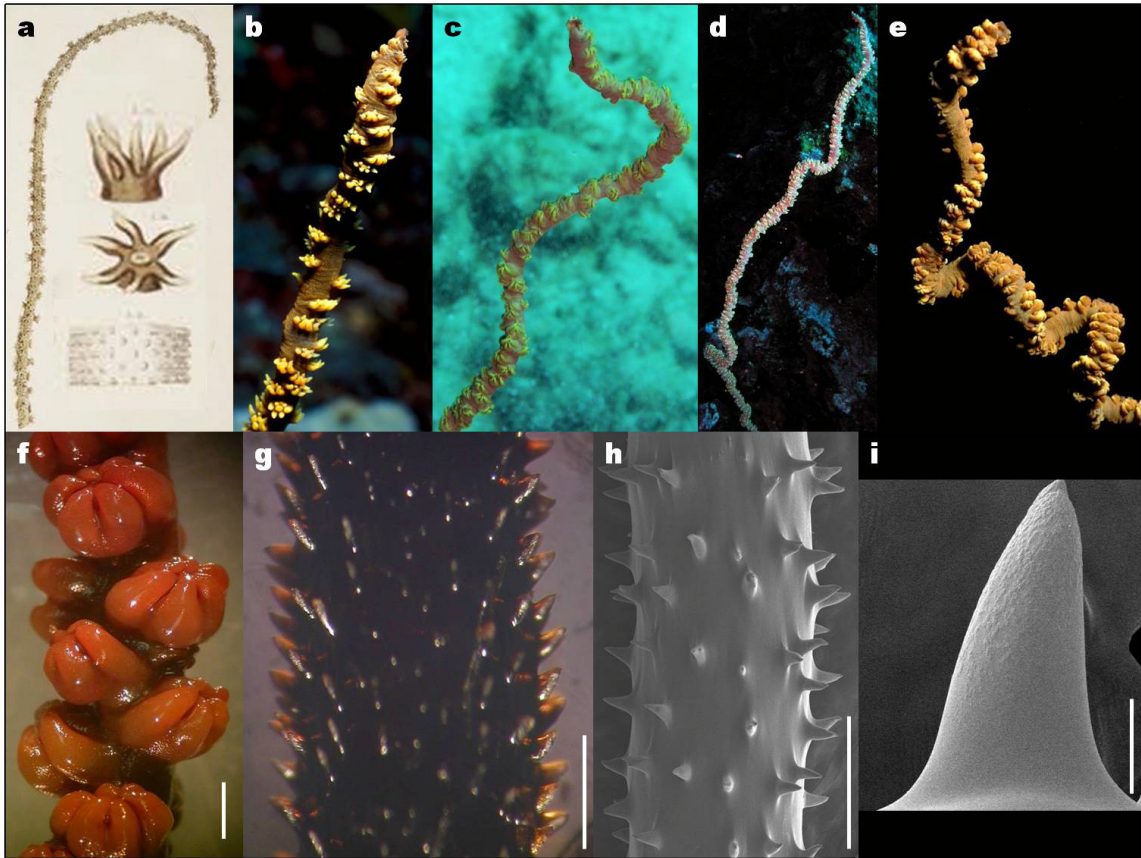
established for yet another group of antipathids with unbranched colonies (Bo et al. 2009a). Like *Cirrhopathes*, *Pseudocirrhopathes* also has polyps arranged irregularly on all sides of the corallum, but differs by having spines with distinct tubercles that are arranged in verticils, and tentacles that cannot completely contract (Bo et al. 2009a). As a result, *Cirrhopathes* is now characterized by (1) unbranched colonies, (2) polyps that are arranged irregularly on all sides of the corallum, and (3) spines that are not arranged in verticils (Brook 1889; Silberfeld 1909; Summers 1910; Van Pesch 1914; Zou & Zhou 1982; Zou & Zhou 1984; Echeverria 2002; Moon & Song 2008a; Bo et al. 2009a).

Cirrhopathes cf. anguina (Dana, 1846)

- Cirrhopathes* sp. – (Davis & Cohen 1968: pg. 749-761, fig. 1(top)-2).
Cirrhopathes anguina – (Grigg & Opresko 1977: pg. 242-261, fig. 4).
Cirrhopathes anguina – (Grigg 1993: pg. 50).
Antipathes anguina – (Grigg 1993: pg. 56).
Cirrhopathes anguina – (Montgomery & Crow 1998: pg. 103-108).
Cirrhopathes sp. – (Coles et al. 1998: pg. 24).
Cirrhopathes anguina – (Greenfield & Randall 2004: pg. 513-514, fig. 55).
Cirrhopathes sp. – (Maragos et al. 2004: pg. 230).
Cirrhopathes anguina – (Fenner 2005: pg. 97, unnumbered fig. on pg. 97).
Cirrhopathes anguina – (Hoover 2006: pg. 71, fig. a-b).
Cirrhopathes anguina – (Parrish & Baco 2007: pp. 159, 185).
Cirrhopathes sp. – (Wagner et al. 2010: pg. 270-291, fig. 10).
Cirrhopathes cf. anguina – (Wagner et al. 2011b: pg. 1323-1328, fig. 2d).
Cirrhopathes cf. anguina – (Wagner et al. 2011c: pg. 211-225, fig. 1f-g).

Davis and Cohen (1968) published the first account of *Cirrhopathes cf. anguina* from Hawai'i (**Figure 3.3**) as part of a description of the associated fauna of this wire coral: a gobiid fish and a palaemonid shrimp. Later descriptions of this species also highlighted these characteristic faunal associates of the wire coral (Greenfield & Randall 2004; Fenner 2005; Hoover 2006). Based on previous literature accounts and specimens examined as part of this study (**Table 3.1**), the following features characterize *C. cf. anguina*. Colonies are unbranched and can reach vertical heights of 2 m or more. The corallum is usually straight in small colonies, and becomes irregularly sinusoidal in large

Figure 3.3a. Plate accompanying Dana's (1846) original description of *Cirrhopathes anguina*, a species for which the type material is now lost. **b-e.** *In situ* photographs of *Cirrhopathes* cf. *anguina* colonies from Hawaiian waters; **f.** preserved polyps of Hawaiian species under light microscopy (scale bar = 1 mm); **g.** spines of Hawaiian species under light microscopy (scale bar = 1 mm); **h-i.** spines of Hawaiian species under scanning electron microscopy (scale bars: h = 1 mm; i = 50 μ m). (**b-e.** Photos courtesy of Jim Maragos).



colonies (**Figure 3.3b-e**). The corallum diameter is generally 1.39-6.12 mm at midheight. Polyps are of variable size, ranging from 0.67-4.45 mm in transverse diameter, and are arranged irregularly on all sides of the corallum (**Figure 3.3b-f**). The spacing between adjoining polyps varies between 0.92-4.76 mm. The color of coenenchyme is typically brown with yellow or green tentacles, but the coloration of tentacles varies between yellow, green, red, white and pink (**Figure 3.3b-e**). Skeletal spines are conical in shape, some of which have bifurcations towards the apex, and are covered with circular to elongated oval-shaped tubercles over the distal half of their surface (**Figure 3.3h**). Spines are generally 110-380 μm tall, and arranged in regular rows, with adjoining rows offset in a spiral pattern around the corallum (**Figure 3.3g-h**). Within a row, spines spacing is highly variable and ranges between 167-1806 μm .

This Hawaiian wire coral species has previously been identified as *Cirrhopathes anguina* Dana, 1846 (Grigg & Opresko 1977), a species originally described from the reefs off Vanua Lebu Island, Fiji (Dana 1846). The description of *C. anguina* is rather brief and highlights yellowish tentacles that are brownish-gray at their base, and spines that are laterally compressed and sub-acute, features that are also evident in the Hawaiian specimens examined here (**Figure 3.3**). Unfortunately, the type material of *C. anguina* is lost (D. Opresko pers. comm.), and therefore no further comparisons can be made until a neotype is designated. Pending such a taxonomic revision, the name *Cirrhopathes cf. anguina* is used to refer to the Hawaiian wire coral described here (**Figure 3.3**).

Specimens examined as part of this study were collected throughout the Hawaiian Islands including the islands of Maui, O‘ahu, Kaua‘i, Ni‘ihau, French Frigate Shoals,

Necker and Laysan at depths between 9-82 m, as well as in the Line Islands off Palmyra Atoll at 43 m (**Table 3.1**). *C. anguina* has previously been reported throughout the Indo-West Pacific at depths ranging between 2-158 m (Dana 1846; Gray 1857; Brook 1889; Cooper 1903; Cooper 1909; Van Pesch 1914; Pax 1932; Tsuda et al. 1977; Humes 1979; Bruce 1982; Zou & Zhou 1982; Zou & Zhou 1984; Heard 1986; Okiyama & Tsukamoto 1989; Montgomery & Crow 1998; Okuno 1998; Jones et al. 2000; Paulay et al. 2003; Greenfield & Randall 2004; Parrish & Baco 2007; Rogers et al. 2007; Bo 2008; Moon & Song 2008a). However, a thorough taxonomic survey will be needed to determine whether these Indo-West Pacific records correspond to the same Hawaiian species described here.

Genus *Stichopathes* Brook, 1889

Like *Cirrhopathes*, the genus *Stichopathes* is characterized by unbranched colonies (see above). Brook (1889) established polyp arrangement as the main diagnostic feature to distinguish between these two unbranched genera. Polyps are arranged irregularly on all sides of the corallum in *Cirrhopathes* (see above), whereas *Stichopathes* colonies have polyps that are arranged in a single row on one side of the corallum. However, the validity of these two genera has been questioned by several authors (Van Pesch 1914; Pax 1918; Pasternak 1977; Bo 2008). *Pseudocirrhopathes*, a third genus with unbranched colonies, was recently established for colonies with polyps that are arranged irregularly on all sides of the corallum, and spines that are positioned in verticills (Bo et al. 2009a; see above). Further taxonomic revisions among unbranched antipathids are, however, needed (Van Pesch 1914; Pax 1918; Pasternak 1977; Bo 2008). Pending such

revisions, polyp arrangement is the only character that distinguishes *Stichopathes* from other unbranched antipatharian genera (Blainville 1834; Brook 1889; Bo et al. 2009a).

***Stichopathes echinulata* Brook, 1889**

Stichopathes cf. *echinulata* – (Brook 1889: pg. 92, Pl. XII fig. 9).

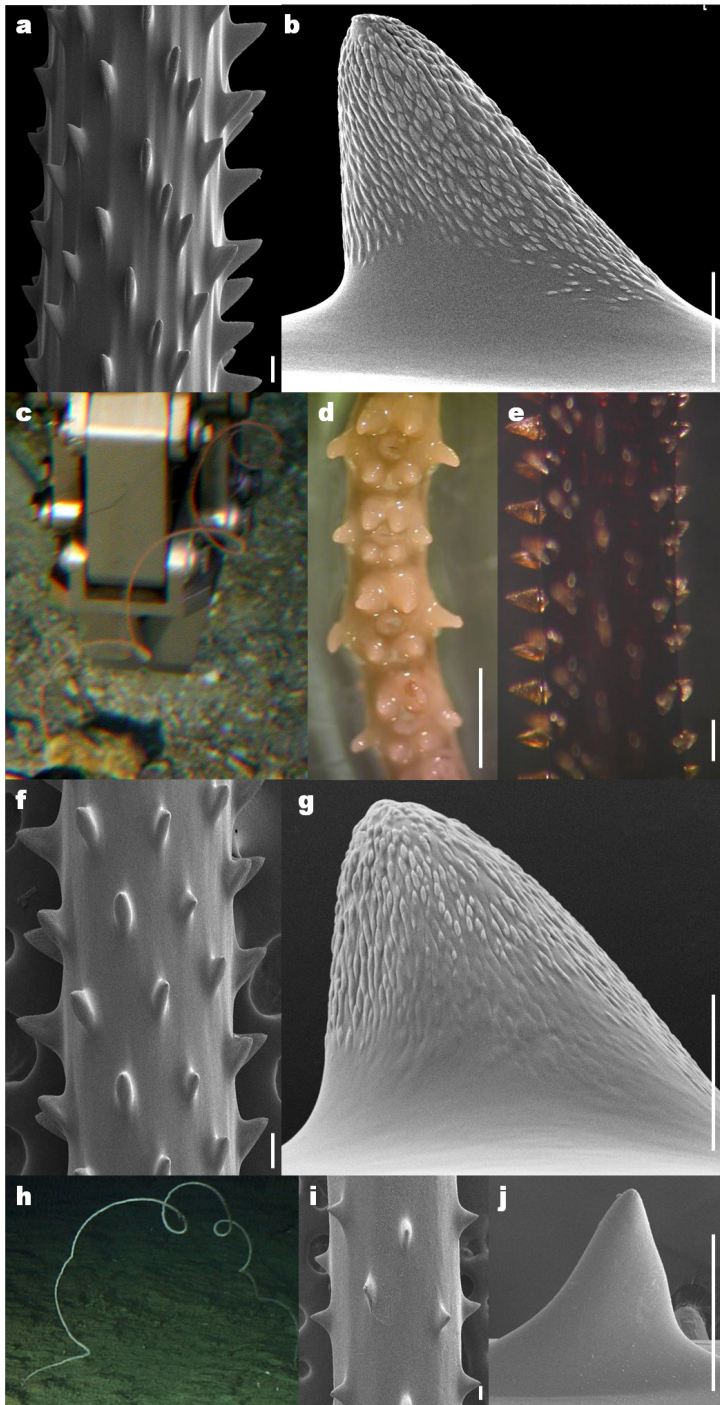
Stichopathes cf. *echinulata* – (Grigg & Opresko 1977: pg. 242-261).

Stichopathes cf. *echinulata* – (Wagner et al. 2011b: pg. 1325).

Stichopathes echinulata – (Wagner et al. 2011c: pg. 211-225, fig. 1h, 2b).

Stichopathes echinulata was originally described from specimens collected off Mauritius (Brook 1889). The original species description is rather brief, but highlights spines that are short, triangular and distally inclined, and arranged in regular rows, with nine or ten rows visible in one aspect (Brook 1889). Based on comparisons with the original description of *S. echinulata* (Brook 1889), Grigg and Opresko (1977) reported a morphologically similar species from Hawaiian waters (**Figure 3.4**). At the time, Grigg and Opresko (1977) did not have *S. echinulata* type material available for comparisons, and because the original species description is rather brief (Brook 1889), they did not conclusively assign the Hawaiian species to *S. echinulata*. As part of this study, a small fragment of the *S. echinulata* holotype was examined under SEM (**Table 3.1, Figure 3.4a-b**). The shape, size and arrangement of the spines of the holotype is very similar to the Hawaiian species examined here (**Figure 3.4e-g**). Consequently, the Hawaiian specimens are assigned to *S. echinulata*, and used to emend the description of the species as follows. Colonies are up to 1 m in height or more and coiled distally forming multiple spirals. At midheight, colonies typically measure 0.74-1.22 mm in diameter with tissue. Polyps are arranged in a single row on one side of the corallum, and spaced 0.81-1.93 mm apart, resulting in 6-10 polyps per cm (**Figure 3.4d**). Skeletal spines are arranged in regular rows, with adjoining rows offset in a spiral pattern around the corallum. Within a

Figure 3.4a-b. Skeletal spines of *Stichopathes echinulata* holotype (USNM 100371) under SEM (scale bars = 100 μ m). **c-g.** Hawaiian *S. echinulata* colonies **c.** *in situ*; **d.** preserved polyps under light microscopy (scale bar = 1 mm); **e.** skeletal spines under light microscopy (scale bar = 200 μ m); **f.** skeletal spines under SEM (scale bars = 100 μ m); and **g.** close-up of polypar spine under SEM (scale bar = 50 μ m). **h-j.** Hawaiian *Stichopathes* sp. with white tissues **h.** *in situ*; **i-j.** Skeletal spines under SEM (scale bars = 100 μ m). (**c,h.** Photos courtesy of HURL).



row, spines are typically spaced 187-670 μm apart. Spines are conical, inclined distally, never bifurcated towards their apex, and covered with oval-shaped tubercles over the biggest portion of their surface (**Figure 3.4b,g**). Polypar spines are generally 81-190 μm tall and abpolypar spines are typically 54-147 μm tall. The coloration of living colonies was only noted for a few samples that were recently collected for this study (**Table 3.1**), but all were light brown. Colonies with similar overall morphologies but with white tissues have also been reported from Hawaiian waters (**Figure 3.4h**; Chave & Malahoff 1998). Only a single colony with white tissues was examined as part of this study (**Table 3.1**; **Figure 3.4h**). However, its skeletal spines are substantially different from *S. echinulata*, in that its spines are more triangular, and only covered by faint tubercles towards the very tip of spines (**Figure 3.4i-j**), whereas *S. echinulata* has distinct tubercles on the biggest portion of its spines (**Figure 3.4b,g**). Furthermore, the skeletal spines of the white morphotype are smaller than *S. echinulata*, with polypar spines ranging between 99-142 μm and abpolypar spines varying between 42-137 μm . Unfortunately only a single specimen of the white morphotype was available for comparisons, however, the substantial morphological differences in spine shape, most certainly indicate that it is a different species (**Figure 3.4i-j**).

S. echinulata was originally described from Mauritius (Brook 1889), but subsequently reported from Portuguese East Africa (Summers 1910), the Seychelles (Cooper 1909), and Madagascar (Humes 1967). All Hawaiian specimens examined as part of this study were collected from the Main Hawaiian Islands of Hawai‘i, Lāna‘i, Maui and Kaua‘i in 108-198 m (**Table 3.1**).

Stichopathes? sp.

Unbranched species – (Grigg 1964: pg. 10)

Stichopathes sp. – (Montgomery & Crow 1998: pg. 103-108).

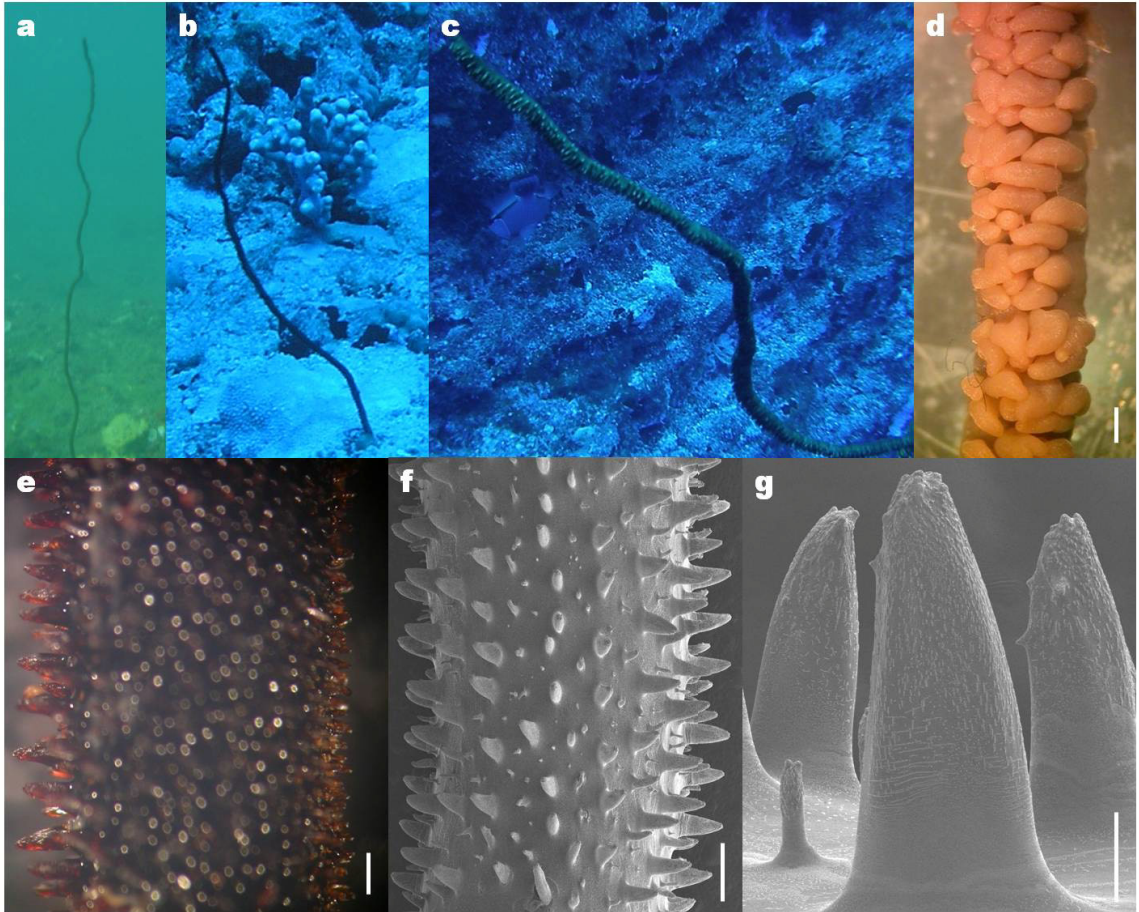
Stichopathes cf. *echinulata* – (Fenner 2005: pg. 98, unnumbered fig. on pg. 98).

Stichopathes cf. *echinulata* – (Hoover 2006: pp. 71, unnumbered fig. on bottom of pg. 71).

Stichopathes sp. – (Wagner et al. 2011c: pg. 211-225, fig. 1i).

Within depths accessible through regular SCUBA diving (< 40 m), two unbranched black corals can be found in Hawaiian waters in areas with high flow regimes and reduced light intensities: one with green or yellow polyps that are arranged irregularly on all sides of the corallum (*Cirrhopathes* cf. *anguina*; see above), and another with brown polyps that are arranged in a single row on one side of the corallum (**Figure 3.5**) (Grigg 1964; Montgomery & Crow 1998; Fenner 2005; Hoover 2006). The latter represents an undescribed species that has been assigned to the genus *Stichopathes* based on the arrangement of its polyps, which are always positioned in a single row on one side of the corallum (Montgomery & Crow 1998; Fenner 2005; Hoover 2006). However, the skeletal spines of this Hawaiian wire coral are very different from other *Stichopathes* spp., which never have bifurcations or apical knobs towards their apex (Brook 1889; Schultze 1903; Roule 1905; Thomson 1905; Cooper 1909; Summers 1910; Van Pesch 1914; Goenaga 1977; Opresko & Genin 1990; Opresko & Sanchez 2005; Moon & Song 2008a). In contrast, apical bifurcations are common on most of the spines of this Hawaiian wire coral species (**Figure 3.5e-g**). Therefore, the assignment to the genus *Stichopathes* is very questionable, and this Hawaiian wire coral may therefore represent both an undescribed genus and species. Colonies of this species are unbranched and can attain extreme lengths of up to 5 m (Grigg 1964). The corallum of small colonies is relatively straight, and becomes more irregular sinusoidal or spiraled in large colonies (**Figure 3.5a-c**). At midheight, colonies generally measure 1.74-5.55 mm in diameter

Figure 3.5. *Stichopathes?* sp. **a-c.** *in situ*; **d.** preserved polyps under light microscopy (scale bar = 1 mm); **e.** skeletal spines under light microscopy (scale bar = 500 μ m); **f.** skeletal spines under SEM (scale bar = 500 μ m); and **g.** close-up of polypar spines under SEM (scale bar = 100 μ m).



with tissue. Polyps are arranged in a single row on one side of the corallum and are crowded together tightly (**Figure 3.5d**). On average, polyps measure 1.82 mm in transverse diameter (range=0.82-3.98 mm) and are spaced 1.82 mm apart (range=1.02-3.44 mm), resulting in 6 polyps per cm (range= 4-8). Skeletal spines are covered by elongated tubercles over the largest portion of their surface and are usually bifurcated towards their apex (**Figure 3.5f-g**). Polypar spines are distinctly larger on the polypar side, where they range between 199-785 μm in height, whereas abpolypar spines vary between 95-442 μm in height. Smaller, secondary spines ($<100 \mu\text{m}$) are present throughout the corallum (**Figure 3.5g**). The color of living colonies is greenish brown (**Figure 3.5a-c**).

Specimens examined as part of this study were collected throughout the Hawaiian Archipelago from the islands of Maui to Necker at depths ranging between 10-58 m (**Table 3.1**). A morphologically similar species has also been reported from Indonesia (M. Bo pers. comm.), but specimens from that locality will have to be examined to confirm those records.

Family **APHANIPATHIDAE** Opresko, 2004

The Aphanipathidae is characterized by polyps with 10 mesenteries (6 primary and four secondary), that are 0.5-1.3 mm in transverse diameter, and have short sagittal and lateral tentacles (shorter than the polyp diameter) that are nearly of the same length when fully expanded (Opresko 2004; Opresko & Sanchez 2005; Daly et al. 2007; Bo 2008). Furthermore, the skeletal spines of the Aphanipathidae often penetrate through the

soft tissues, are typically adorned with conical tubercles, and do not possess bifurcations towards their apex like many members of the Antipathidae (Opresko 2004; Opresko & Sanchez 2005; Daly et al. 2007; Bo 2008). The family Aphanipathidae is divided into the two subfamilies Aphanipathinae and Acanthopathinae based on the relative sizes of skeletal spines in the area underneath a polyp (Opresko 2004). The name of the family Aphanipathidae is derived from the Greek root *aphano* meaning invisible, in reference to its inconspicuous polyps which are often obscured through elongated spines that penetrate through the coenenchyme (Brook 1889).

Subfamily **Aphanipathinae** Opresko, 2004

The subfamily Aphanipathinae is distinguished by having skeletal spines of consistently similar heights on the side of the corallum bearing the polyps (Opresko 2004). In contrast, the subfamily Acanthopathinae (see below) has members whose skeletal spines are reduced in size in the areas directly below the oral opening (the hypostomal spines), and then give way to elongated spines in the areas underneath the outer edges of polyps (the circumpolypar spines). Spines of intermediate length are present between polyps in the Acanthopathinae (Opresko 2004).

Genus *Aphanipathes* Brook, 1889

The genus *Aphanipathes* is characterized by colonies that are irregularly branched like a bush or broom, and skeletal spines that penetrate through the coenenchyme (Brook 1889; Pax 1932; Opresko & Baron-Szabo 2001; Opresko 2004).

Aphanipathes verticillata Brook, 1889

Aphanipathes verticillata – (Brook 1889: pg. 125-126, Pl. XII fig. 25-25a).

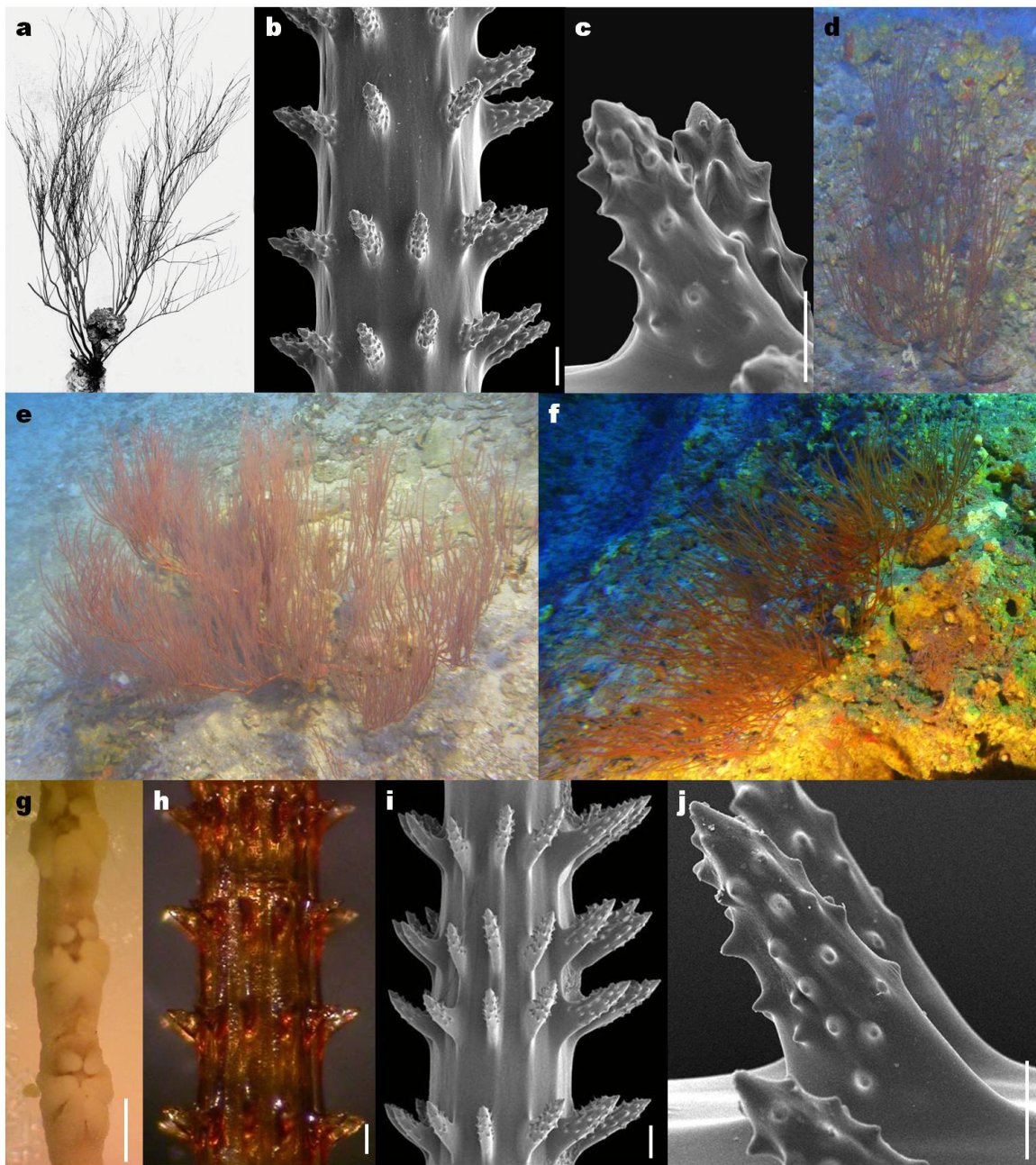
Undescribed Aphanipathidae – (Wagner et al. 2010: pg. 274, fig. 10).

Aphanipathes sp. – (Wagner et al. 2011b: pg. 1325).

Aphanipathes verticillata – (Wagner et al. 2011c: pg. 211-225, fig. 1j, 2c).

During black coral surveys conducted off West Maui in 2008-2009, numerous specimens superficially resembling *Antipathes griggi* were collected (Opresko et al. in prep.). Upon closer examination of the skeletal spines, these specimens proved to be morphologically very different from *A. griggi*, and similar to *Aphanipathes verticillata* Brook, 1889, a species never before reported from the Hawaiian Archipelago. Subsequent comparisons of the *A. verticillata* holotype to Hawaiian specimens revealed morphological similarities of the corallums and skeletal spines (**Figure 3.6**), and lead to the new report of *A. verticillata* from Hawaiian waters (Opresko et al. in prep.). A detailed taxonomic description of both the *A. verticillata* holotype and the Hawaiian specimens is currently in preparation (Opresko et al in prep.), and briefly summarized here. Colonies are up to 1 m in height or more, with up to 10 orders of branching. The branches are generally pointed straight upwards or slightly curved (**Figure 3.6d-f**). On terminal branchlets, polypar spines are typically 90-266 μm tall and abpolypar spines generally 54-201 μm in height. Skeletal spines are arranged in verticils with spines in the same row typically spaced 200-507 μm apart (**Figure 3.6h-j**). Spines are covered with distinct conical tubercles over the largest portion of their surface of both polypar and abpolypar spines. Polyps are on average 1.35 mm in transverse diameter (range=0.72-1.81 mm), arranged on a single side of the corallum on terminal branches, and spaced 0.89-2.76 mm apart, resulting in 6 polyps per cm (range=5-8) (**Figure 3.6g**).

Figure 3.6a-c. *Aphanipathes verticillata* holotype (MCZ 68) showing **a.** entire specimen, **b-c.** skeletal spines under SEM (scale bars: b = 100 μ m; c = 50 μ m). **d-j.** Hawaiian *A. verticillata* specimens showing **d-f.** colonies *in situ*, **g.** preserved polyps on terminal branch under light microscopy (scale bar = 1 mm), **h.** skeletal spines on terminal branch under light microscopy (scale bar = 100 μ m), **i.** skeletal spines on terminal branch under SEM (scale bar = 100 μ m), and **j.** close-up of polypar spine under SEM (scale bar = 50 μ m). (**d-f.** Photos courtesy of HURL).



A. verticillata was originally described from specimens collected off Mauritius (Brook 1889). Later, two other *A. verticillata* specimens were collected off Okinawa at a depth of 79 m (**Table 3.1**). All Hawaiian specimens examined as part of this study were collected at depths between 88-130 m in the Keyhole Pinnacle region of the Au‘Au Channel, located between the islands of Maui and Lāna‘i (**Table 3.1**).

Subfamily **Acanthopathinae** Opresko, 2004

The subfamily Acanthopathinae is characterized by skeletal spines of different heights in the areas underneath polyps. Hypostomal spines are reduced in size, whereas circumpolypar spines are substantially elongated. Spines of intermediate length are present between polyps in the Acanthopathinae (Opresko 2004). The name of this subfamily is derived from the Greek root *acantho* meaning spiny, in reference to the enlarged size of its circumpolypar spines (Opresko 2004).

Genus **Acanthopathes** Opresko, 2004

The genus *Acanthopathes* is characterized by colonies that are branched in a single plane like a fan, and spines that are either greatly reduced or absent in the areas directly below the oral cone (Opresko 2004).

Acanthopathes undulata (Van Pesch, 1914)

Aphanipathes undulata – (Van Pesch 1914: pg. 87-89, fig. 74-76, Pl. VIII fig. 8).

Antipathes undulata – (Grigg & Opresko 1977: pg. 242-261, fig. 5).

Acanthopathes undulata – (Opresko 2004: pg. 232).

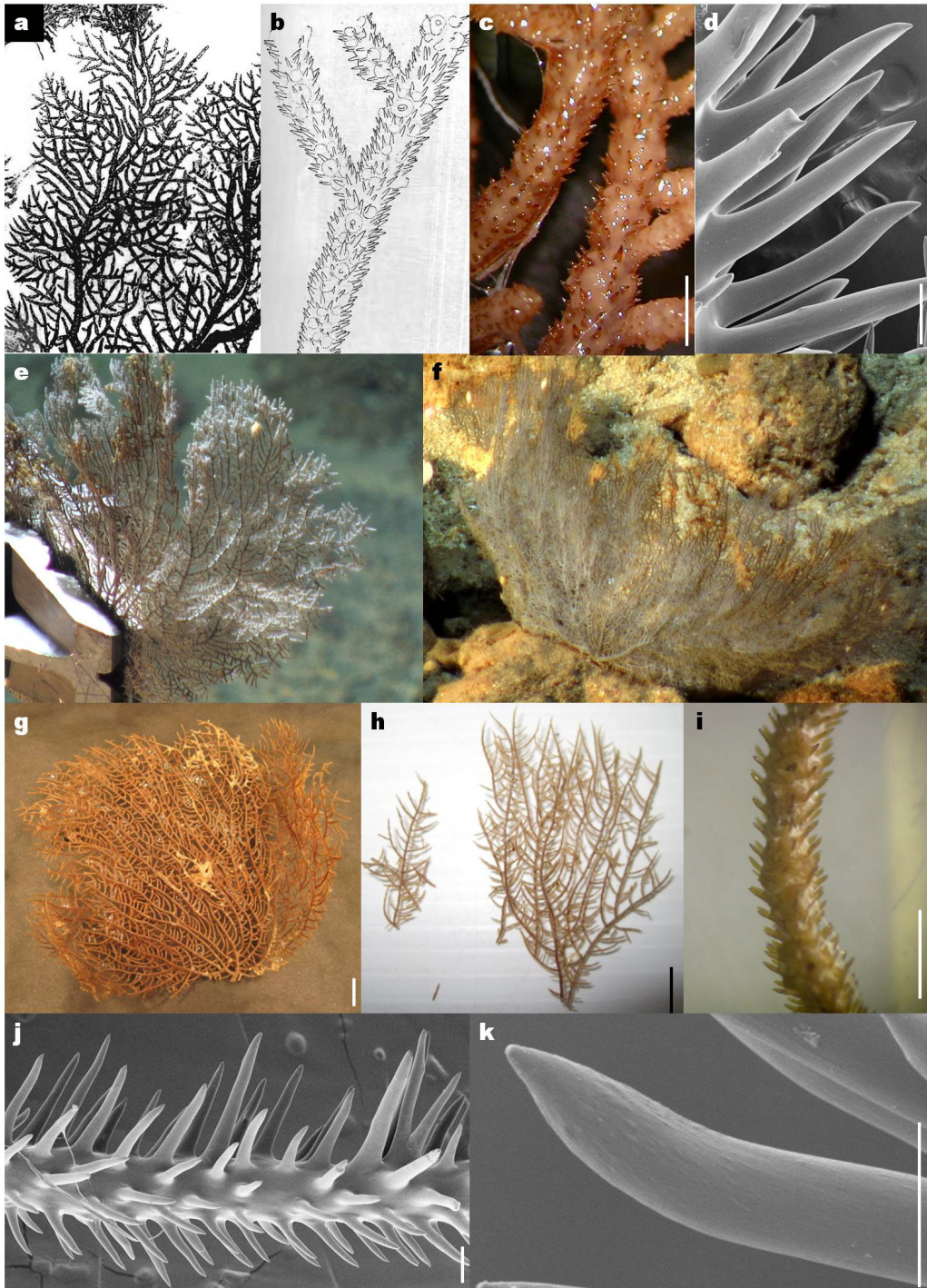
Acanthopathes undulata – (Eldredge 2006: pg. 65).

Acanthopathes undulata – (Parrish & Baco 2007: pg. 186).

Acanthopathes undulata – (Wagner et al. 2011b: pg. 1325).

Grigg and Opresko (1977) were the first to identify *Antipathes undulata* (Van Pesch, 1914) from the Hawaiian Islands (**Figure 3.7**). In 2004, Opresko reassigned *A. undulata* to the newly established antipatharian family Aphanipathidae and the new genus *Acanthopathes*, resulting in the name *Acanthopathes ulex* (Opresko 2004; Eldredge 2006). Van Pesch's (1914) original description of this species emphasized (1) colonies that are fan-shaped and planar, (2) spines that are distally inclined, needle-like, covered with minute tubercles towards the distal half, generally 375-450 μm tall, spaced 150-225 μm apart, and penetrated through the tissues of the polyps, and (3) polyps that are arranged on one side of the colony and spaced 1.1 mm apart. These features are all consistent with the Hawaiian specimens examined here (**Figure 3.7**). Additionally, a fragment of the holotype was examined under SEM, and its spines are also very similar to the Hawaiian specimens in terms of shape, arrangement and size (**Figure 3.7d, j-k**). Furthermore, this comparison also highlights the differences in relative sizes of the skeletal spines on the side of the branch bearing the polyp, being greatly reduced underneath the oral cone, and enlarged towards the outer edges of polyps (**Figure 3.7i-j**). Collectively, the comparison of *A. undulata* type material to Hawaiian specimens corroborates previous identifications of this species from Hawaiian waters (Grigg & Opresko 1977; Chave & Malahoff 1998; Eldredge 2006; Parrish & Baco 2007). Additionally, this comparison revealed several characteristic features of the species, which have previously not been described. Colonies are fan-shaped, typically smaller than 50 cm in height, and are extensively branched giving the appearance of a net (**Figure 3.7e-h**). Polyps are arranged on a single side of fan-shaped colonies, are typically 0.87 mm in transverse diameter (range=0.50-1.15 mm) and spaced 1.26 mm apart

Figure 3.7a-b. Plates accompanying the original description of *Acanthopathes undulata* (Van Pesch 1914); **c.** spines of schizoholotype (USNM 100409) under light microscopy (scale bar = 1 mm); **d.** spines of schizoholotype under SEM (scale bar = 100 μ m); **e-f.** *in situ* photographs of colonies from Hawaiian waters; **g-h.** specimens from Hawai'i (scale bars = 1 cm); **i.** spines and polyps on terminal branch under light microscopy (scale bar = 1 mm); **g.** spines on terminal branch under SEM (scale bar = 100 μ m); close-up of spine under SEM (scale bar = 30 μ m). (**e-f.** Photos courtesy of HURL).



(range=1.01-1.58 mm), resulting in 8 polyps per cm (range=7-8) (**Figure 3.7c, i**). The spines are needle-like in shape and penetrate through the soft tissues, except for the area underlying the oral cone (**Figure 3.7c, i**). On the side of the fan not bearing the polyps, spines are uniform in height and average 204 μm (range=113-329 μm). In contrast, the side of the colony bearing polyps contains skeletal spines of varying lengths (**Figure 3.7j**). The tallest spines are located in the area underneath the outer edges of polyps and reach heights of 270-459 μm , whereas the shortest spines are situated in the area underneath the oral cone and reach heights of 85-257 μm . Skeletal spines are smooth or gently adorned with fine papillae towards the distal portion of the spine (**Figure 3.7d, k**). Spines are arranged in regular rows with adjoining rows being offset in a spiral pattern around the corallum (**Figure 3.7j**). Within a row, spine spacing is typically variable and ranges between 155-361 μm . The color of living colonies is grayish-white, and is influenced by the skeletal spines that penetrate through tissues and give colonies a brownish hint (**Figure 3.7e-f**).

Acanthopathes undulata was originally described from specimens collected at a depth of 113 m in the Solor Strait off Indonesia (Van Pesch 1914), and later reported from Hawai'i (Grigg & Opresko 1977; Chave & Malahoff 1998; Eldredge 2006; Parrish & Baco 2007) and the Mariana Islands (Paulay et al. 2003). All Hawaiian specimens examined as part of this study were collected throughout the Hawaiian Islands from Hawai'i to Laysan at depths ranging between 30-269 m (**Table 3.1**).

Family **MYRIOPATHIDAE** Opresko, 2001

The Myriopathidae are characterized by polyps with 10 mesenteries (six primary and four secondary), that are 0.5-1.0 mm in transverse diameter and possess short tentacles with rounded tips. The skeletal spines of the Myriopathidae are usually blade-like or needle-like on smaller branches, and frequently forked or antler-like on the main stem and larger branches (Opresko 2001; Opresko & Sanchez 2005; Daly et al. 2007; Bo 2008; Moon & Song 2008b). The name of the Myriopathidae is derived from the Greek word *myriophylla* meaning many branches, in reference to the extensive branching of colonies within this family.

Genus **Myriopathes** Opresko, 2001

The genus *Myriopathes* contains colonies whose highest order branches are pinnulated, i.e., they contain ramifications that are arranged symmetrically in one plane like a fern. Furthermore, *Myriopathes* pinnules are themselves always branched giving rise to secondary and tertiary subpinnules (Opresko 2001; Moon & Song 2008b).

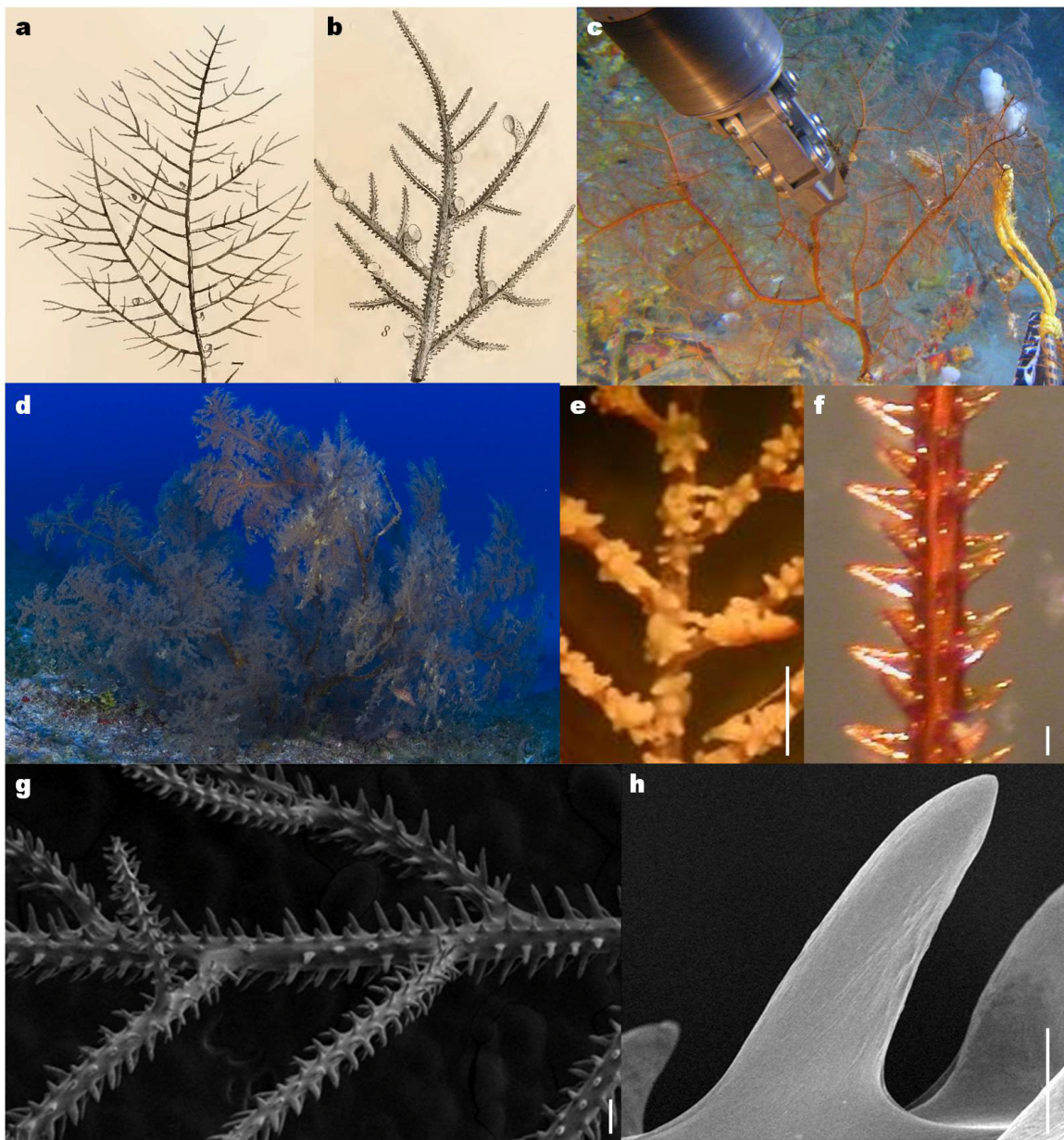
Myriopathes cf. ulex (Ellis & Solander, 1786)

- Antipathella* sp. – (Grigg 1964: pg. 11, 14, fig. 5)
- Antipathes ulex* – (Grigg & Opresko 1977: pg. 244)
- Antipathes ulex* – (Grigg 1993: pg. 50, 56).
- Antipathes ulex* – (Montgomery & Crow 1998: pg. 103-108).
- Antipathes ulex* – (Chave & Malahoff 1998: pg. 40, fig. 93).
- Myriopathes ulex* – (Opresko 2001: pg. 349, 351-352).
- Antipathes ulex* – (Montgomery 2002: pg. 157-164).
- Myriopathes ulex* – (Fenner 2005: pg. 101, 2 unnumbered fig. on pg. 101).
- Antipathes ulex* – (Boland & Parrish 2005: pg. 411-420).
- Myriopathes ulex* – (Eldredge 2006: pg. 65).
- Myriopathes ulex* – (Hoover 2006: pg. 70, unnumbered fig. on pg. 70).
- Myriopathes ulex* – (Parrish & Baco 2007: pg. 162-163, 170, 186).
- Myriopathes ulex* – (Kahng & Kelley 2007: pg. 684).
- Myriopathes ulex* – (Bo 2008: unnumbered fig. in app. 1).
- Antipathes ulex* – (Grigg 2010: pg. 3).
- Myriopathes ulex* – (Wagner et al. 2011a: pg. 249-255, fig. 3).
- Myriopathes ulex* – (Wagner et al. 2011b: pg. 1325).
- Myriopathes ulex* – (Wagner et al. 2011c: pg. 212, 214).

Along with *Antipathes griggsi* and *A. grandis*, *Myriopathes* cf. *ulex* (**Figure 3.8**) represents the third antipatharian species that has been targeted by the Hawaiian black coral fishery (Grigg 1993; Grigg 2010; Wagner et al. 2011a). However, in comparison to *A. griggsi* and *A. grandis*, harvesting of *M. cf. ulex* is much less frequent, because the species is quite rare in the 40-75 m depth zone where black coral harvesting takes place in Hawai'i (Grigg 2001; Grigg 2002; Boland & Parrish 2005). Grigg (1964) presented the first published account of *M. cf. ulex* from Hawai'i (as *Antipathella* sp.). Since then, brief descriptions of this Hawaiian species were presented by Chave and Malahoff (1998), Fenner (2005) and Hoover (2006). The main distinguishing features of this species, are its large (up to 3 m), fan-shaped colonies that consist of small feather-like branchlets or pinnules (**Figure 3.8a-c**). This characteristic branching pattern gives rise to the common name of this species: feathery black coral. Polyps are on average 0.56 mm in transverse diameter (range= 0.32-0.92 mm), and generally spaced 0.84 mm apart (range=0.31-1.71), resulting in 12 polyps per cm (range 8-15). On the highest order branches, spines are blade- to needle-like in shape and inclined distally (**Figure 3.8f-h**), with polypar spines generally 122 μ m in height (range= 76-196 μ m), and abpolypar spines typically 92 μ m in height (range= 51-172 μ m). Spines are smooth or covered with faint papillae, and are arranged in regular rows on the highest order branches, with spines in the same row typically spaced 177 μ m apart (range= 70-366 μ m). On the main stem and thicker branches, many spines are forked at their apex.

Grigg and Opresko (1977) were the first to identify *Antipathes ulex* Ellis and Solander, 1786 from Hawaiian waters. In 2001, Opresko reassigned *A. ulex* to the newly established antipatharian family Myriopathidae and the new genus *Myriopathes*, resulting

Figure 3.8a-b. Plates accompanying the original description of *Myriopathes ulex* (Ellis & Solander 1786), a species for which the type material is now lost. **c-d.** *In situ* photographs of colonies from Hawaiian waters; **e.** preserved polyps of Hawaiian species under light microscopy (scale bar = 1 mm); **f.** spines on terminal branch under light microscopy (scale bar = 100 μ m); **g.** spines on terminal branch under SEM (scale bar = 200 μ m); close-up of polypar spine under SEM (scale bar = 50 μ m). (Photos courtesy of **c.** HURL, and **d.** Greg McFall).



in the name *Myriopathes ulex* (Opresko 2001; Eldredge 2006). The original species description is rather brief and highlighted short skeletal spines and numerous epibionts including barnacles, which Ellis and Solander (1786) incorrectly identified as the ovaries of the black coral. The two plates accompanying the species description show a planar and pinnulated branching pattern (**Figure 3.8a-b**), features that are also characteristic of the Hawaiian specimens examine here (**Figure 3.8c-e**). Unfortunately, type material of *M. ulex* has been lost (Opresko 2001), and therefore no further comparisons can be made until a neotype is designated. Pending such taxonomic revisions, the name *Myriopathes* cf. *ulex* is used to refer to the Hawaiian specimens examined here, which were collected throughout the Hawaiian Archipelago from Hawai'i Island to Pearl and Hermes Atoll at depths ranging between 41-326 m (**Table 3.1**). *Myriopathes ulex* was originally described from Indonesia (Ellis & Solander 1786), but subsequently reported throughout the Indo-West Pacific at depths ranging between 25-364 m (Blainville 1834; Gray 1857; Brook 1889; Van Pesch 1914; Grigg & Opresko 1977; Colin & Arneson 1995; Chave & Malahoff 1998; Parrish & Baco 2007; Rogers et al. 2007; Bo 2008; Moon & Song 2008b). However, a thorough taxonomic investigation is needed to verify whether these records correspond to the same species that is present in Hawaiian waters.

Species key of Hawaiian shallow-water antipatharians

- 1a. Colonies unbranched (wire like) 2
- 1b. Colonies branched..... 4

- 2a. Polyps in multiple rows.....*Cirrhopathes* cf. *anguina*
- 2b. Polyps in a single row 3

- 3a. Polyps ~1 mm in diameter with adjacent polyps separated by a well defined interpolypar space*Stichopathes echinulata*

3b. Polyps ~1.85 mm in diameter with adjacent polyps crowded together tightly	<i>Stichopathes?</i> sp.
4a. Colonies bushy	5
4b. Colonies fan-shaped.....	7
5a. Spines arranged in verticils around thinner branches	<i>Aphanipathes verticillata</i>
5b. Spines not arranged in verticils around thinner branches	6
6a. Some spines with bifurcation on apex and secondary spines (≤ 40 μm tall) present on thicker branches	<i>Antipathes griggi</i>
6b. Spines without bifurcations on apex, and no secondary spines present on any parts of the corallum	<i>Antipathes grandis</i>
7a. Colonies small (<0.5 m) and densely reticulated giving the appearance of a net	<i>Acanthopathes undulata</i>
7b. Colonies large (< 3m) with highest order branches forming symmetric pinnules like a fern	<i>Myriopathes cf. ulex</i>

Conclusion

The use of traditional taxonomic characters, including branching pattern, polyp and skeletal spine morphology, provides a comprehensive basis for the classification of the shallow-water Hawaiian black coral fauna, an assemblage that has been previously grouped due to taxonomic constraints in ecological surveys. As a result, potential ecological differences amongst various antipatharian species have not been identified, which is information for the management of the Hawaiian black coral fishery. At least three different species with different habitat preferences have been targeted by the Hawaiian black coral fishery (*Antipathes griggi*, *A. grandis* and *Myriopathes cf. ulex*); however, the fishery has historically been managed as a single stock, in large part due to difficulties in identifying the targeted species. In addition to fishery management applications, the combined use of various morphological characters may help in future

systematic studies among the Antipatharia, a taxonomic order that has been notoriously problematic (Opresko 1972; Molodtsova 2005; Daly et al. 2007; Bo 2008).

CHAPTER 4. SEXUAL REPRODUCTION STUDY

Introduction

Black corals are used to manufacture precious coral jewelry, and as a result are targeted by commercial fisheries in several regions around the globe including throughout Asia, Latin America, the Caribbean and Hawai'i (Grigg 1975; Grigg 1976; Noome & Kristensen 1976; Castorena & Metaca 1979; Humann 1983; Grigg 1984; Kenyon 1984; Kerstitch 1989; Grigg 1993; Romero 1997; Grigg 2001; Maldonado 2003; Padilla & Lara 2003; Huang & Ou 2010; Tsounis et al. 2010). Like fisheries targeting other precious corals, antipatharian fisheries have traditionally exhibited a cyclic pattern of discovery of a population, exploitation, depletion, followed by exploration for new harvesting grounds, a boom and bust cycle that resembles mining more than a fishery (Grigg 1976; Castorena & Metaca 1979; Grigg 1984; Grigg 1993; Romero 1997; Tsounis et al. 2010). In contrast to that typical pattern, the Hawaiian black coral fishery has maintained consistent landings for more than 50 years through a management program of catch quotas and minimum size limits of harvested colonies (Grigg 1976; Grigg 1984; Grigg 1993; Grigg 2001; Parrish & Baco 2007; Grigg 2010). However, recent declines in population densities of Hawaiian black corals have raised questions about whether regulations need to be redefined in order to regain a sustainable harvest (Grigg 2003; Grigg 2004; Kahng & Grigg 2005). Unfortunately very little is known about the basic life history of black corals, which complicates effective management of the fishery (Grigg 2001; Grigg 2004). In 2006, the Western Pacific Regional Fishery Management Council (WPRFMC) held a workshop to review the state of the Hawaiian black coral fishery and

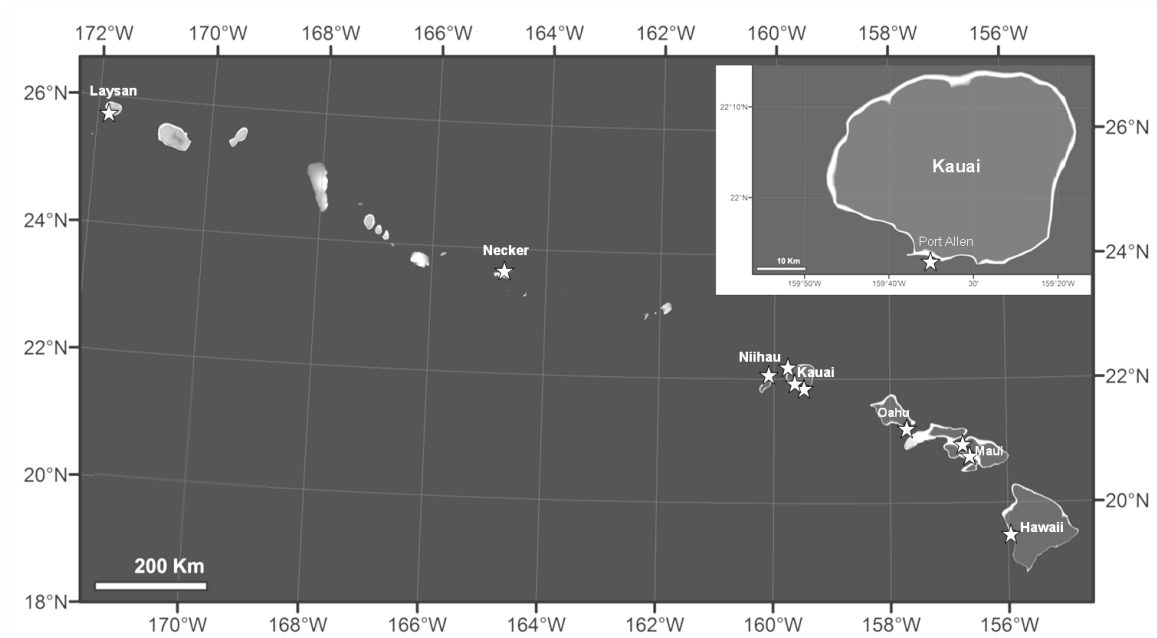
to identify future research priorities (WPRFMC 2006). Among the established research objectives, studies on the reproduction of commercially valuable Hawaiian black corals were recognized as a top priority (WPRFMC 2006). The purpose of this chapter is to present the results of a study on the sexual reproduction of commercially valuable Hawaiian black corals, which addressed this research priority. The species *Antipathes griggsi*, *Antipathes grandis* and *Myriopathes* cf. *ulex* have all been targeted by the Hawaiian precious coral fishery (Grigg 1976; Grigg 2001; Boland & Parrish 2005; WPRFMC 2006; Parrish & Baco 2007; Grigg 2010; Wagner et al. 2010; Wagner et al. 2011a). However, over 90% of the coral harvested in Hawaiian waters consists of *A. griggsi* (Oishi 1990; Parrish & Baco 2007), and therefore this species was chosen as the focus of the study. Specific objectives were to obtain information on the following reproductive parameters of *A. griggsi*: (1) reproductive strategy (gonochorism vs. hermaphroditism), (2) mode of reproduction (spawner vs. brooder), (3) reproductive cycle, (4) minimum size of sexual maturity, and (5) maximum depth of reproduction.

Materials and methods

Sample collections

Samples used for this study were collected on a series of cruises conducted from 2006-2010 (N = 220), and were obtained throughout the known range of *A. griggsi*, from the islands of Hawai‘i to Laysan at depths ranging between 10-100 m (**Figure 4.1**). The taxonomic identity of specimens was confirmed by examining skeletal spine morphology under scanning electron microscopy (SEM) as described by Wagner et al. (2010). Heights of all sampled colonies were measured to the nearest 10 cm by using a tape measure

Figure 4.1. Map showing the locations where *Antipathes griggi* colonies were sampled as part of this study. A total of 220 specimens were collected throughout the known range of *A. griggi*, from the islands of Hawai'i to Laysan at depths between 10-100 m. INSET: Study site off Port Allen Harbor, Kaua'i where monthly collections were performed for one year. (Base map and bathymetry data courtesy of HURL).



underwater, or by photographing colonies with parallel lasers projected onto them (Olsen & Wood 1980; Grigg 2004; Reed et al. 2005; Wagner et al. 2010). Samples consisting of 3-5 cm branches were clipped from each colony, preserved in 10% seawater buffered formalin, and transferred to 70% ethanol after 3-5 days. Additionally, monthly collections were performed for one year at a site located off Port Allen Harbor, Kaua'i (21°53.353'N 159°34.980'W) at depths ranging between 30-40 m (**Figure 4.1**). At the site, ten colonies were tagged with a label attached to the base, and sampled between July 2008 and July 2009 as described above. Temperature and photoperiod time-series data were obtained at the Port Allen site, and examined in relation to gametogenesis. Temperature measurements were taken once every 15 min for the duration of the study with the aid of a HOBO Pro v2 temperature logger ($\pm 0.2^{\circ}\text{C}$; Onset Computer Corporation, Bourne, MA) anchored at the site. Photoperiods were calculated using sunrise and sunset data from the U.S. Naval Observatory Astronomical Applications Department (<http://www.usno.navy.mil/USNO/astronomical-applications/data-services/rs-one-day-us>).

Histology

A total of 10 polyps (selected to have a similar size) were dissected from the skeleton of each specimen, and subsequently dehydrated by sequential submersions in 70% ethanol for 30 min, 95% ethanol for 1.5 h and 100% ethanol for 6 h, followed by clearing in xylene for 4 h. Samples were then infiltrated with molten paraffin wax at 70°C for 16 h and poured into standard moulds. Serial histological cross-sections, spaced 50 μm apart, were cut at 5-10 μm using a Leica RM 2155 rotary microtome (Leica

Microsystems GmbH, Wetzlar, Germany). Slides were stained with Masson's Trichrome using the following staining steps: xylene for 5 min, 100% ethanol for 5 min, haematoxylin Z for 25 min, wash in running tap water for 15 min, phosphomolybic acid for 5 min, light green for 5 min, 100% ethanol for 5 min, 100% for 2 min and xylene for 5 min (Wagner et al. 2011b; Wagner et al. 2011c). Stained slides were viewed and photographed under an Olympus BX51 compound microscope with camera attachment (Olympus Corporation, Tokyo, Japan). Individual polyps were scored as either containing or lacking gametes, and reproductive output was measured as the percentage of polyps containing gametes (Ward 1995; Parker et al. 1997; Sakai 1998; Ward et al. 2000; Zakai et al. 2000; Bo 2008; Torres et al. 2008). For those individuals containing gametes, sex and reproductive stage was determined for a total of 100 gametes per specimen. Spermatogenesis was staged as described by Parker et al. (1997) (see **Figure 4.2**). Oocyte diameters were estimated for 100 oocytes per specimen using feret diameter measurements (Walton 1948) obtained using the image analysis software Image J (Wayne Rasband, National Institute of Health, Bethesda, MD). Only oocytes sectioned through the germinal vesicle were measured in order to standardize measurements to the widest axis of oocytes (Davis 1982; Parker et al. 1997; Waller et al. 2005; Waller & Baco 2007). Previtellogenic oocytes were differentiated from vitellogenic oocytes by being smaller in size ($< 70 \mu\text{m}$) and by staining dark purple as opposed to bright red due to the absence of yolk (which is eosinophilic; **Figure 4.2**). Oocyte size-frequency distributions were graphed for female colonies by binning oocyte diameters in $10 \mu\text{m}$ increments.

Results

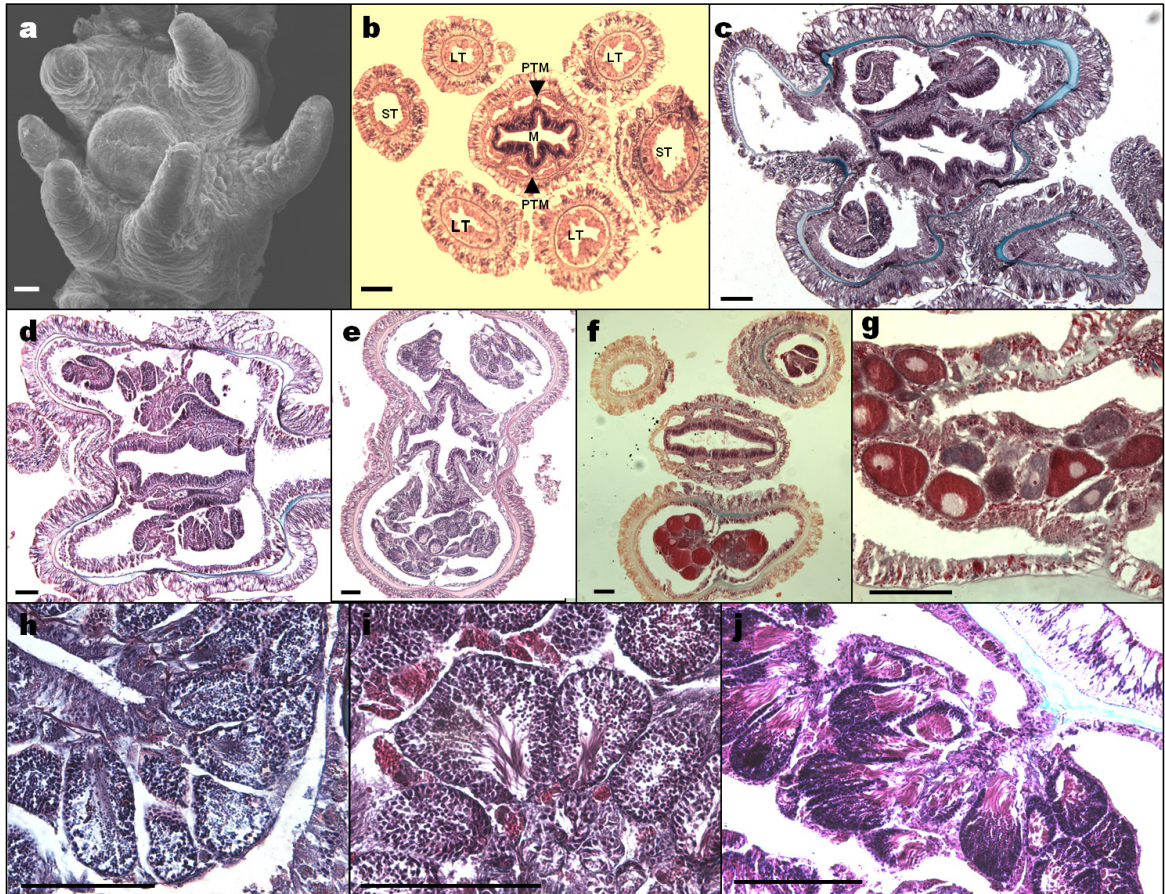
Reproductive strategy

All colonies were strictly gonochoric, as none of the examined specimens contained both oocytes and spermatocysts in different polyps either simultaneously or sequentially. Of the total of 220 *A. griggsi* colonies that were sampled on a single date (**Figure 4.1**), 95 (43.2%) did not contain any gametes, whereas 64 (29.1%) contained oocytes and 61 (27.7%) contained spermatocysts. The ratio of male to female colonies was not significantly different from 1:1 at any of the total of 20 collection sites (one sample t-test, $p > 0.796$). Of the ten tagged colonies that were sampled on a monthly basis off South Kaua‘i (**Figure 4.1**), five were males and five were females. The sex of each tagged colony stayed the same throughout the duration of the study (July 2008-July 2009). Externally, there were no apparent morphological differences between males and females in any of the samples, and the presence of oocytes or spermatocysts was the only character that allowed for the distinction between sexes. When gametes were present, these were always found in association with the primary transverse mesenteries, which extended into the cavity of lateral tentacles in many cases (**Figure 4.2**).

Mode of reproduction

No developing embryos or larvae were observed in any of the examined polyps, and none of the oocytes exhibited any signs of fertilization (**Figure 4.2**). Spawning was not observed *in situ* or in histological sections (e.g., rupture of mesenterial tissues and accumulation of gametes in the gastric cavity), and could therefore only be inferred by

Figure 4.2a. Scanning electron micrograph of *Antipathes griggi* polyp, and **b-j.** histological cross-sections through polyps of *A. griggi* showing, **b.** locations of primary transverse mesenteries which bear the filaments and gametes (M = mouth; PTM = primary transverse mesentery; LT = lateral tentacles; ST = sagittal tentacles); **c.** male polyp during non-reproductive season without gametes; **d.** female polyp during non-reproductive season without gametes; **e.** stage 3 spermatocysts along primary transverse mesenteries inside body cavity; **f.** oocytes along primary transverse mesentery extending into the cavities of lateral tentacles; **g.** vitellogenic and previtellogenic oocytes in close proximity to each other; **h.** stage1 spermatocysts; **i.** stage 2 spermatocysts; and **j.** stage 3 spermatocysts (scale bars =100 μ m).



the disappearance of gametes during time-series collections (see below). Externally, none of the examined polyps contained brooded larvae or eggs on their surfaces.

Reproductive cycle

Oocyte size-frequency distributions were not significantly different among the five female colonies for any of the collection dates (one-way ANOVA, $p > 0.05$; Wallace 1985). Similarly, spermatocyst stage-frequency distributions were not significantly different among the five male colonies across sampling dates (one-way ANOVA, $p > 0.05$). Therefore frequency distribution data were pooled for both female and male colonies in each month. Reproductive output, measured as the proportion of polyps containing gametes, closely tracked seasonal temperature fluctuations (**Figure 4.3**). None of the samples collected in March-May contained any gametes, coinciding with the period of lowest mean temperatures (~ 23 °C; **Figure 4.3**). Reproductive output and mean temperatures increased between June-August, and then decreased between August-March (**Figure 4.3**). Both male and female colonies had a similar seasonal pattern of reproductive output, although there were slight temporal differences between sexes (**Figures 4.3-4.4**). All male polyps were completely void of spermatocysts by January, whereas a few female polyps ($< 3\%$) still contained oocytes through February (**Figures 4.3-4.4**). Gamete maturity stages generally increased from June through December (**Figure 4.4**). For male colonies, spermatocysts were mostly in early stages of development (stages 1 and 2) in June-August, and then progressively became dominated by spermatocysts in late developmental stages through December (stage 3; **Figure 4.4**). Similarly, female colonies had polyps containing a high proportion of previtellogenic

Figure 4.3a. Percentage of polyps containing gametes across time at the Port Allen site, expressed as a proportion of the contribution of both male and female colonies to the total amount. Error bars represent standard deviations. **b.** Photoperiod (grey lines) and mean daily temperature (red dots) measured at the Port Allen site.

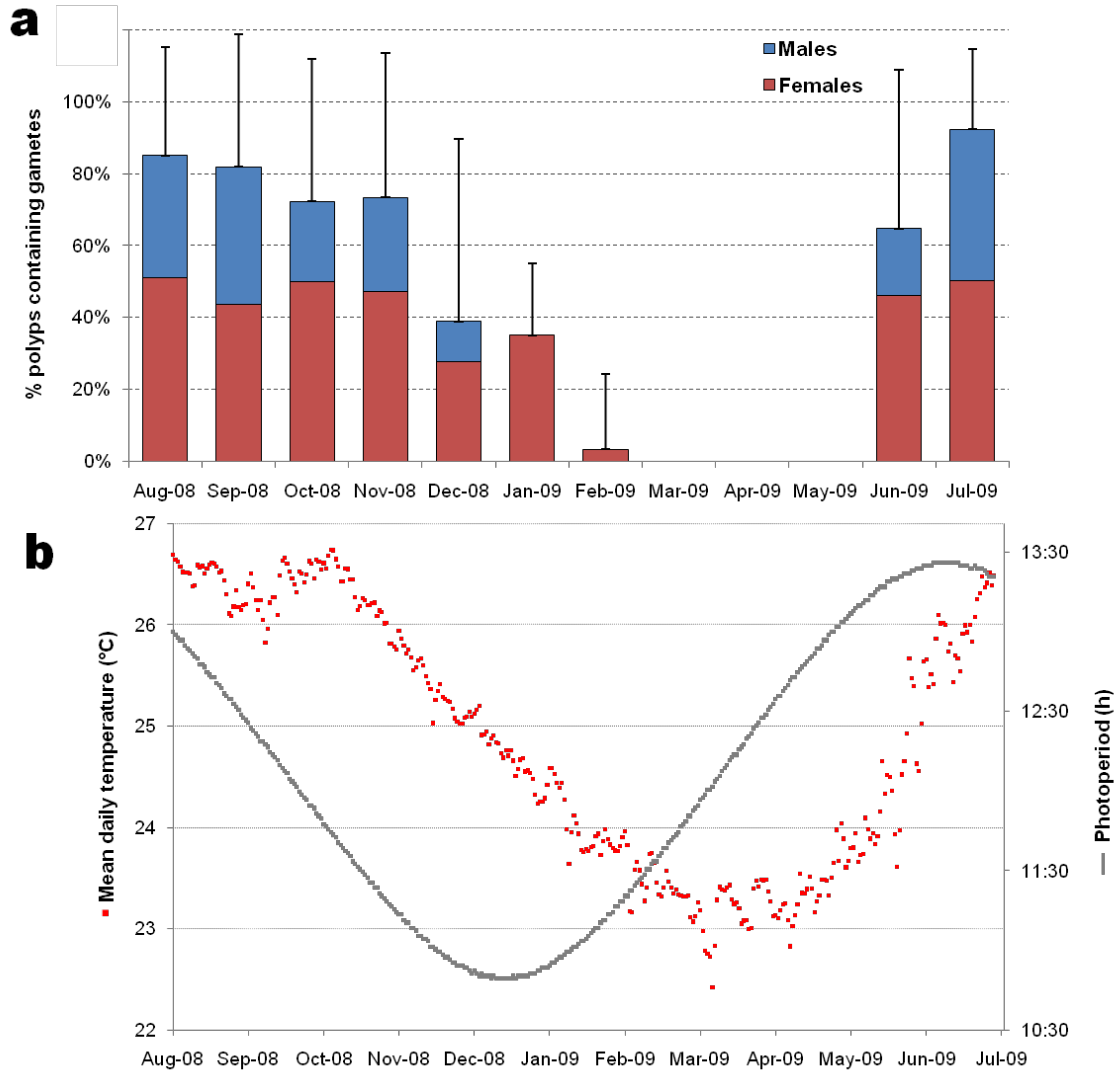
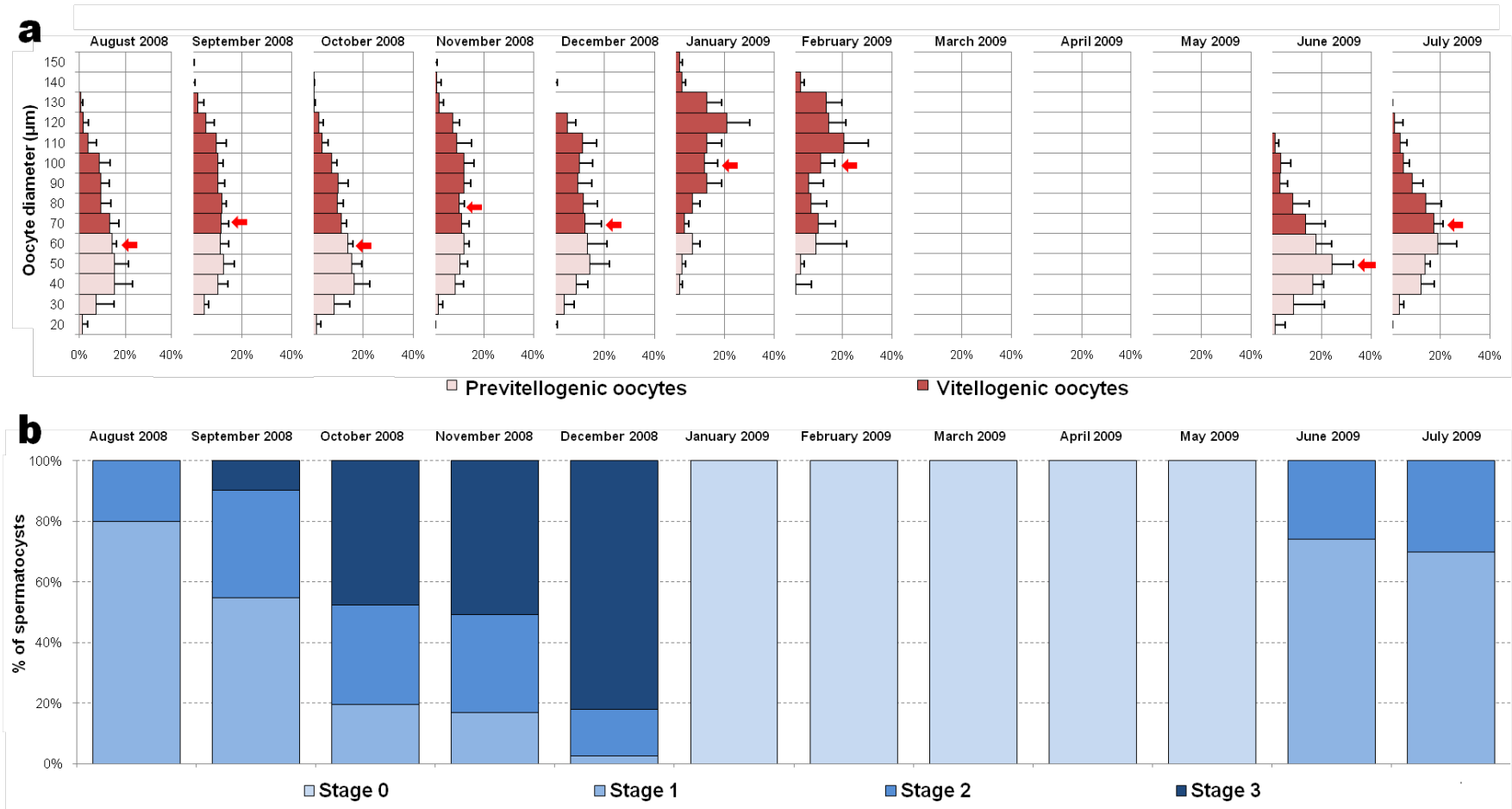


Figure 4.4. Percentage of oocytes per size class for five female colonies that were tagged at the Port Allen site. Arrows point toward mean oocyte diameter. Error bars represent standard deviations. **b.** Percentage of spermatocysts per reproductive stage for five male colonies tagged at the Port Allen site.



oocytes in June-August, which gradually progressed to a higher proportion of vitellogenic oocytes of larger size classes in January-February (**Figure 4.4**). However, female colonies contained oocytes of a large range of size and maturity stage throughout the reproductive season (**Figure 4.4**), with immature oocytes often occurring within close proximity to mature oocytes even within the same mesentery (**Figure 4.2**).

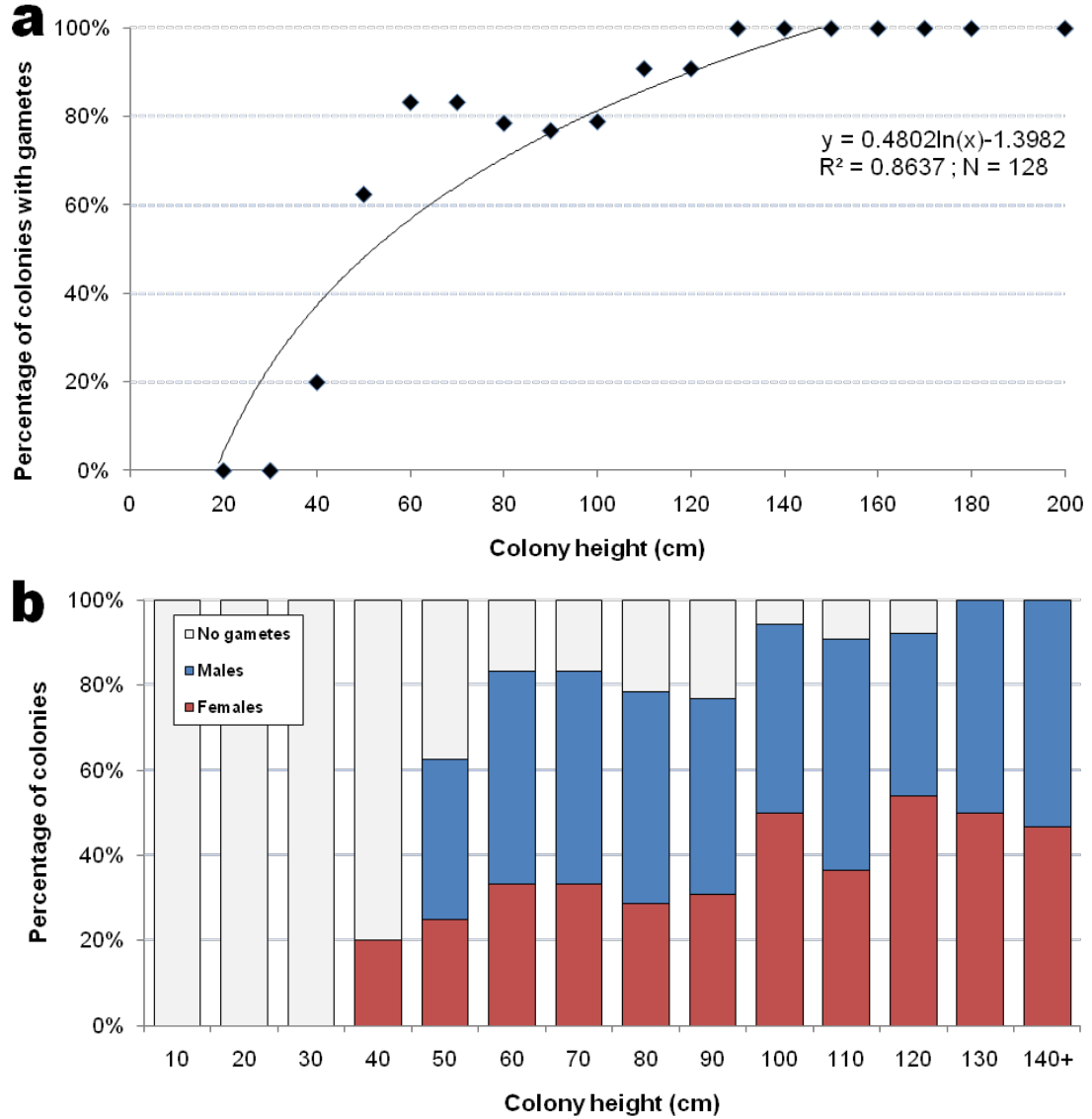
Minimum size of sexual maturity

Of the total 128 colonies that were sampled during the reproductive season (June-December; see above), 39 (38.3%) did not contain any gametes. All colonies smaller than 40 cm (N=19) did not contain any gametes and were thus considered sexually immature (**Figure 4.5**). The proportion of mature colonies increased with increasing colony height, from 20% for colonies measuring 40-49 cm, to ~60% for colonies with a height of 50-59 cm, to ~80% for colonies measuring 60-69 cm (**Figure 4.5**). All colonies that were taller than 130 cm were sexually mature (**Figure 4.5**).

Maximum depth of sexual reproduction

Despite intense sampling of black coral colonies at depths ranging between 75-130 m (N=76), only five *A. griggsi* colonies were sampled below 75 m, with the deepest colony occurring at 100 m. Below 75 m, most of the sampled colonies belonged to the species *Antipathes grandis* (68.4%) and *Aphanipathes verticillata* (25.0%). Despite being rare, all five *A. griggsi* colonies that were sampled below a depth of 75 m contained mature gametes.

Figure 4.5. Proportion of colonies containing gametes during the reproductive season of *A. griggi* (June-December) as a function of **a.** colony height, and **b.** colony height and sex. Colony sizes represent lower bin limits of a particular size category.



Discussion

Reproductive strategy

Among samples containing gametes, all contained either oocytes or spermatocysts, but never both within the same individual (**Figure 4.2**). Additionally, all tagged colonies (N=10) were of the same sex throughout the duration of this study (July 2008 and July 2009), indicating that colony sex is relatively stable in *A. griggi*. Collectively, these observations suggest that *A. griggi* is a gonochoric species with a 1:1 sex ratio. However, because the sex of individual colonies was only monitored over one year, sex changes (i.e., sequential hermaphroditism) occurring over longer time periods cannot be excluded as a possible reproductive strategy for *A. griggi*. Nevertheless, if sex changes do occur in *A. griggi*, they are not related to size, because both males and females were identified among similarly sized colonies (**Figure 4.5**). Consistent with this, Parker et al. (1997) reported that there is no relationship between sex and colony size in *Antipathella fiordensis* populations from New Zealand. Unfortunately, both this study and that of *A. fiordensis* in New Zealand (Parker et al. 1997), only monitored sex of individual colonies over a single reproductive season, and therefore it is not possible to distinguish between gonochorism and sequential hermaphroditism unambiguously. To date only two studies have monitored the sex of antipatharian colonies over multiple reproductive seasons (Goenaga 1977; Bo 2008). Goenaga (1977) examined the sexual reproduction of two *Stichopathes* spp. in Puerto Rico over three years, and reported that both species were gonochoric. In contrast, Bo (2008) studied the sexuality of *Cirrhopathes* sp. in Indonesia over two years, and noted that some colonies changed sex over the course of the study and were thus sequential hermaphrodites. In addition to these

two studies that have monitored the sexuality of individual colonies over multiple years (Goenaga 1977; Bo 2008), numerous studies have examined the sexuality of antipatharian species using specimens that were collected over a shorter time span (< 1 month; Von Koch 1878; Brook 1889; Schultze 1903; Roule 1905; Cooper 1909; Van Pesch 1914; Pax 1932; Opresso & Genin 1990; Opresko 2003b; Molodtsova & Pasternak 2005; Opresko 2005a; Molodtsova 2006; Gaino et al. 2008; Gaino & Scoccia 2008; Moon & Song 2008b; Bo et al. 2009a; Gaino & Scoccia 2009; Gaino & Scoccia 2010; Wagner et al. 2011c). All of these studies report finding oocytes or spermatocysts but never both within the same individual. However, like the current study, sequential hermaphroditism cannot be ruled out in any of these cases, and it is therefore unknown whether gonochorism or sequential hermaphroditism is more widespread within the order Antipatharia.

While the results of this study do not allow us to determine conclusively whether *A. griggsi* is gonochoric or sequentially hermaphroditic, they do indicate that *A. griggsi* is not a simultaneous hermaphroditic species, because none of the examined specimens contained both oocytes and spermatocysts (**Figure 4.2**). Likewise, most previous examinations of antipatharians have failed to detect simultaneous hermaphroditic colonies (reviewed by Wagner et al. 2011c). The only exception to this trend is *Stichopathes saccula*, for which Pax et al. (1987) report finding mixed colonies with both male and female polyps. Collectively, these results indicate that simultaneous hermaphroditism is rare among antipatharian corals.

When gametes were present in *A. griggi*, they were always found in association with the primary transverse mesenteries, which reached into the cavity of lateral tentacles in many cases (**Figure 4.2**). While there has been some dispute over whether the transverse and sagittal planes have been correctly defined within the Antipatharia (Schultze 1896b), this chapter continues to use the terminology used by most previous authors (Brook 1889; Van Pesch 1914; Pax 1918; Hyman 1940; Opresko 1972; Schmidt 1972; Pax et al. 1987), in which the transverse plane lies parallel to the branch bearing the polyp, whereas the sagittal plane lies perpendicular to the branch bearing the polyp (**Figure 4.2**). All previous examinations of antipatharians have found gametes within the primary transverse mesenteries, which in some cases extend into the cavity of lateral tentacles (reviewed by Wagner et al. 2011c). These previous reports are consistent with the observations of this study, and collectively suggest that gamete location is evolutionary conserved among the order Antipatharia.

Mode of reproduction

No developing embryos or larvae were observed within any of the examined polyps and none of the oocytes exhibited any signs of fertilization. These results are consistent with all previous histological examinations of antipatharians, which have failed to detect any signs of internal fertilization (reviewed by Wagner et al. 2011c). Additionally, none of the samples examined as part of this study contained brooded larvae or eggs on their surfaces, thus indicating that *A. griggi* is not a brooding species. Consequently, *A. griggi* is a spawner and either (1) spawns both oocytes and spermatocysts into the water column with fertilization occurring externally (i.e.,

broadcast spawning), or (2) retains oocytes until they are fertilized internally and then rapidly spawns fertilized eggs (i.e., pseudo-brooding). However, distinguishing between these two fertilization strategies is difficult, because it requires sampling either right before or during a spawning event (Harrison & Wallace 1990; Vermeij et al. 2004; Kahng et al. 2008). Unfortunately, spawning of *A. griggi* was not observed in this study, and could therefore only be inferred by the disappearance of gametes during time-series collections (**Figures 4.3-4.4**). Unfortunately there are only few direct observations on the spawning behavior of antipatharians (Goenaga 1977; Miller 1996; Gaino & Scoccia 2009), and these do not allow us to determine whether female colonies spawn fertilized or unfertilized eggs. Goenaga (1977) observed the spawning of a single *Stichopathes* sp. male colony in an aquarium. On the following day all female colonies kept in the same aquarium spawned, and Goenaga (1977) concluded that females released oocytes in response to male pheromones and that fertilization is thus likely external. Several authors have studied the sexual reproduction of *Antipathella fiordensis* in New Zealand (Grange 1988; Miller & Grange 1995; Miller 1996; Parker et al. 1997), however, spawning has never been observed *in situ*, and has only been inferred by the disappearance of gametes. Spawning has, however, been artificially induced in *A. fiordensis* colonies raised in aquaria, with externally fertilized eggs developing into ciliated planulae (200 μm in length) within 36 hours of fertilization (Miller 1996). Also in aquarium cultures, Gaino and Scoccia (2009) observed male polyps of *Cupressopathes pumila* releasing buoyant spheres (consisting of sperm in various stages of sperm differentiation) from their mouths. Unfortunately, Gaino and Scoccia (2009) did not have any female *C. pumila* specimens for comparisons, and it is therefore unknown whether fertilization occurs

internally or externally in this species. In addition to these few direct observations on the spawning behavior of antipatharians, there is also indirect evidence of spawning from histological examinations (Cooper 1909; Opresko 2005a; Gaino et al. 2008; Gaino & Scoccia 2010). In histological sections of male *Cirrhipathes* cf. *anguina* polyps from Indonesia, Gaino et al. (2008) observed lysing of cells bordering the mesenteries and sperm accumulating in the gastric cavity. Gaino et al. (2008) hypothesized that *C.* cf. *anguina* polyps would subsequently release sperm through the mouth, as has been observed in preserved polyps of *Antipathella subpinnata* from the Mediterranean (Gaino & Scoccia 2010). Such signs of spawning were not apparent in any of the *A. griggi* polyps examined as part of this study, perhaps reflecting that none of the samples were collected close to spawning times. All *A. griggi* samples were collected during daytime surveys, and spawning may occur during the night, as is predominant among shallow-water (< 40 m) corals (Stimson 1978; Fadlallah 1983; Wallace 1985; Babcock et al. 1986; Szmant 1986; Harrison & Wallace 1990; Richmond & Hunter 1990; Glynn et al. 1991; Dahan & Benayahu 1997; Fautin 2002; Carroll et al. 2006; Harrison 2011). Future nighttime surveys, particularly around the months of November and December when the greatest decline in gamete-containing polyps is seen will be needed to confirm whether *A. griggi* spawns at night.

Few studies on antipatharians report external signs of polyp deterioration as a result of sexual maturation (Cooper 1909; Opresko 2005). Among *Bathypathes patula* specimens from the Indian Ocean, Cooper (1909) noted that colonies could be classified into three different stages of progressive sexual maturity. In the first stage, the gonad-

bearing parts of the polyp contained small oocytes and were well separated from the central mouth-bearing part by a longitudinal septum. In the second stage, the oocytes were enlarged around the longitudinal septum, causing the mouth-bearing part to appear degenerate. In the third stage, the mouth-bearing part and tentacles were missing altogether, and oocytes were clearly visible through the polyp's body wall. Cooper (1909) speculated that oocytes would be liberated in a subsequent stage through the rupture and death of the tissues of polyps. Such polyp deterioration as a result of sexual maturity has also been described more recently for specimens of *Heliopathes pacifica* from the North Pacific, where polyps filled with oocytes had either no tentacles or a single pair of tentacles (Opresko 2005a). No signs of polyp deterioration were observed in any of the *A. griggsi* samples examined as part of this study, indicating that individual polyps do not deteriorate as a result of sexual maturity and therefore likely survive multiple spawning events.

Reproductive cycle

While time-series samples were only collected during a single reproductive season, the seasonal pattern in reproductive output and gametogenic stages strongly suggests that *Antipathes griggsi* has an annual reproductive cycle (**Figures 4.3-4.4**). Additionally, spawning appears to occur repeatedly throughout the reproductive season of *A. griggsi*, because the reproductive output dropped continuously between July and March (**Figures 4.3**). Consistent with this interpretation, immature oocytes were often observed in close proximity to mature oocytes even within the same mesentery (**Figure 4.2**), indicating that spawning occurs in successive events.

To date, few studies have examined the reproductive seasonality of black corals (Grigg 1976; Goenaga 1977; Schmidt & Zissler 1979; Parker et al. 1997; Bo 2008; Gaino & Scoccia 2008; Gaino & Scoccia 2010). All of these studies were conducted in shallow water (<70 m), and report a seasonality in the appearance and disappearance of gametes, which at least in some cases have been correlated to seasonal temperature fluctuations (Schmidt & Zissler 1979; Parker et al. 1997; Gaino & Scoccia 2010). Parker et al. (1997) report that *Antipathella fiordensis* has an annual gametogenic cycle that is highly synchronous both within and between colonies, and spawns in the month of March coinciding with the warmest temperatures in New Zealand. Gaino & Scoccia (2010) examined *Antipathella subpinnata* specimens collected from the Mediterranean, and found no fertile colonies in September-November when water temperatures were low (14°C), and fertile colonies in August when temperatures were higher (16°C). Schmidt and Zissler (1979) noted that several tropical Indo-Pacific antipatharians in the genera *Antipathes* and *Cirrhipathes* reproduced in the two mid-summer months. Like in all these previous antipatharian studies (Grigg 1976; Goenaga 1977; Schmidt & Zissler 1979; Parker et al. 1997; Bo 2008; Gaino & Scoccia 2008; Gaino & Scoccia 2010), the reproductive cycle of *A. griggsi* coincided with seasonal temperature fluctuations, because periods of decreasing reproductive output coincided temporally with decreasing water temperatures, whereas periods of increasing reproductive output, coincided with increasing water temperatures (**Figures 4.3**). Seasonal changes in temperature have also been correlated to the reproductive seasonality of numerous species of shallow-water (<40 m) scleractinian corals (reviewed by Harrison & Wallace 1990; Wallace 2011). That said, none of these temporal correlations necessarily imply a causal relationship between

temperature and reproductive seasonality, and identifying whether such a causal relationship exists, would require manipulative experiments in laboratory cultures. Some controlled laboratory experiments have shown that the initiation of gametogenesis is not controlled by temperature, but rather by photoperiod in the sea star *Pisaster ochraceus* (Pearse & Eernisse 1982) and the sea urchin *Eucidaris tribuloides* (McClintock & Watts 1990). Similarly, a meta-analysis of twelve species of shallow-water (<40 m) scleractinian corals from the Caribbean, demonstrated that photoperiod is a better predictor than temperature in synchronizing reproductive seasonality, presumably by acting as a cue to initiate gametogenesis (Van Woesik et al. 2006). In this study, both *A. griggsi* oocytes and spermatocysts first appeared in June, coinciding with the time of the year with longest photoperiods (**Figures 4.3**). However, determining whether these long photoperiods trigger the initiation of gametogenesis in *A. griggsi* will require manipulating this variable in laboratory cultures. Regardless of what environmental variable actually causes the reproductive seasonality in *A. griggsi*, the results of this study indicate that reproductive output is correlated to seasonal temperature fluctuations.

Minimum size of sexual maturity

The smallest *A. griggsi* colony containing gametes was 40 cm in height, however, only a few colonies in this size class were mature (20%; **Figure 4.5**). The proportion of sexually mature colonies increased with increasing colony size from ~60% for colonies measuring 50-59 cm, to over 80% for colonies taller than 60 cm. These results are consistent with those of Grigg (1976), who found gametes in few *A. griggsi* colonies as small as 40 cm, and sexually mature colonies in the majority of colonies measuring 64-80

cm. Current regulations prohibit commercial harvesting of *A. griggi* colonies that are smaller than 122 cm (Grigg 2010; Tsounis et al. 2010). The results of this study indicate that most (~90%), but not all, colonies that reach this legal harvesting limit are sexually mature (**Figure 5**). Therefore, a slight increase in the legal harvesting limit (130 cm) would ensure that all colonies have a chance to reproduce before being exposed to fishing mortality. Given the recent declines in population densities of *A. griggi* (Grigg 2003; Grigg 2004; Kahng & Grigg 2005), increasing the legal limit of harvested colonies may be a prudent strategy to ensure continued sustainability of the fishery.

Maximum depth of reproduction

Due to logistical constraints of conducting SCUBA diving at depths below 75 m, commercial divers have traditionally harvested Hawaiian black corals at depths between 40-75 m, primarily in the Au‘Au channel between the islands of Maui and Lāna‘i, and to a lesser extent in the waters off South Kaua‘i (Gage 1962; Grigg 1964; Grigg 2001; Parrish & Baco 2007; Grigg 2010). However, dense black coral populations exist off the islands of Hawai‘i, Maui and Kaua‘i at depths down to 110 m (Grigg 1976; Grigg 2001; Grigg et al. 2002; Grigg 2004; Kahng & Grigg 2005; Kahng & Kelley 2007; Parrish & Baco 2007; Wagner et al. 2010), and it had previously been thought that that reseeding of fished populations may depend on large colonies below the harvesting depth zone (> 75 m) (Grigg 1976; Grigg 2001). The results of this study indicate that the depth refuge of *A. griggi* colonies below the harvesting zone has been greatly overestimated in the past. Despite intense sampling efforts at depths below 75 m, which included a total of 76 black coral colonies sampled during twelve separate submersible dives, only five *A. griggi*

colonies were collected (6.6%). Below 75 m, the majority of sampled colonies consisted of *A. grandis* (68.4%) and *Aphanipathes verticillata* (25.0%). While all *A. griggi* colonies collected below 75 m were sexually mature, the low population densities suggest that fertilization success is likely low at these depths. Numerous studies of diverse marine organisms, ranging from fish to snails to urchins and corals, have documented that fertilization success of isolated free-spawning individuals is negligible (Pennington 1985; Levitan 1991; Levitan et al. 1991; Levitan et al. 1992; Oliver & Babcock 1992; Babcock et al. 1994; Harrison & Jamieson 1999). Thus, the low occurrence of *A. griggi* colonies below 75 m suggests that while reproduction is possible at depths up to 100 m, it does not occur frequently, and these isolated colonies likely contribute little to the overall population. Alternatively, the low population densities of *A. griggi* at increasing depths may be due larvae preferentially settling in shallower water. Unfortunately there are no direct observations of larvae within the order Antipatharia (Wagner et al. 2011c), and therefore it is unknown whether *A. griggi* is absent from deeper reefs (> 100 m) due to the settlement behavior of its larvae.

Conclusion

In contrast to precious coral fisheries in other parts of the world, the Hawaiian black coral fishery has maintained steady catch levels for more than 50 years. However, recent declines in population densities have renewed scrutiny on the black coral fishery and raised questions about whether regulations need to be redefined to maintain a sustainable harvest. Complicating efforts to effectively manage the fishery is the limited knowledge on the basic life history of black corals, and in particular the lack of available

information on their reproductive processes. To address this knowledge gap, this study investigated the sexual reproduction of *Antipathes griggi*, which is the dominant species targeted by the Hawaiian black coral fishery. The results indicate that *A. griggi* is likely gonochoric with a 1:1 sex-ratio, although sequential hermaphroditism over successive reproductive seasons cannot be ruled out. Furthermore, both males and females were present among similarly sized colonies, indicating that if sex changes occur in *A. griggi*, they are not related to size. No larvae or fertilized eggs were observed in any of the samples, indicating that *A. griggi* is likely a broadcast spawner. As reported for other shallow-water (< 70 m) black corals, *A. griggi* has an annual reproductive cycle that is related to seasonal temperature fluctuations, with reproduction occurring between June-December when temperatures are highest. Furthermore, spawning occurs continuously throughout the reproductive season. The proportion of sexually mature colonies increased with increasing colony size, from 20% for 40 cm tall colonies, to 100% for colonies measuring 130 cm or more. Currently, fishing regulations prohibit commercial harvesting of colonies < 122 cm. This study indicates that most (~90%), but not all, colonies that can be legally harvested in Hawai'i are sexually mature. A slight increase in the legal harvesting limit (130 cm) would therefore ensure that all colonies have a chance to reproduce before being exposed to fishing mortality. Additionally, the results of this study indicate that the supposed depth refuge from harvest does not really exist. While *A. griggi* exists to depths of 100 m, it is rare deeper than the 75 m limit at which commercial harvest occurs in Hawai'i. There is reason to believe that reproductive success of isolated colonies at depths of 75-100 m is likely to be low. Given that the population size and depth refuge of *A. griggi* colonies below the harvesting zone appears to have been greatly

overestimated in the past, this study calls into question the population models used for the management of the fishery. Future studies will need to reevaluate the sizes of *A. griggsi* populations that are exposed and protected from fishing mortality.

LIST OF ORIGINAL ARTICLES

Kahng SE, Garcia R, Spalding H, Brokovich E, **Wagner D**, Weil E, Hinderstein L & Toonen RJ (2010). Community ecology of mesophotic coral reef ecosystems. *Coral Reefs* 29: 255-275.

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