

The spatial distribution of shallow-water (<150 m) black corals (Cnidaria: Antipatharia) in the Hawaiian Archipelago

DANIEL WAGNER

NOAA, Papahānaumokuākea Marine National Monument, 1845 Wasp Boulevard, Building 176, Honolulu, HI 96818, USA

The Hawaiian Archipelago contains some of the best surveyed black coral populations on the globe; however, most previous surveys have grouped all black coral species into a single category. As a result, the unique ecological features of individual species have not been identified. This study mapped the spatial distribution of eight antipatharian species (Antipathes griggi, Antipathes grandis, Cirrhipathes cf. anguina, Stichopathes echinulata, Stichopathes? sp., Aphanipathes verticillata, Acanthopathes undulata and Myriopathes cf. ulex) found in shallow-waters (<150 m) along the Hawaiian Archipelago, and compared data on substrate type, depth and temperature among species. All black coral species were exclusively recorded on hard substrates and were generally widely distributed along the Hawaiian Islands. Additionally, antipatharian species were found at overlapping depths and temperatures, although there were significant differences in the mean depths and temperatures between most species. In cases where species did not have significant differences in mean depths, the overlapping species had different colony and polyp morphologies, which may serve to minimize competition by allowing species to grow most efficiently under particular current regimes. This study represents one of the first to map the spatial distribution of sympatric antipatharian species, and indicates that individual species exploit unique environments in terms of depth and temperature or have unique morphologies to avoid overlap.

Keywords: Antipathidae, mapping, Myriopathidae, precious corals, records

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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 north-west. 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 (DeMartini & Friedlander, 2004; Kane *et al.*, 2014). 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, 2003, 2005; Baco, 2007; Parrish & Baco, 2007).

The Antipatharia is an anthozoan order within the subclass Hexacorallia, encompassing seven families, 43 genera and over 235 species (Wagner *et al.*, 2012). 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 (Wagner *et al.*, 2012). 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, down to abyssal depths of over 8600 m for species in the Western Pacific (reviewed by Wagner *et al.*, 2012). Despite this wide bathymetric range, black corals are primarily found in deep waters below the photic zone, with over 75% of described species occurring below 50 m (Cairns, 2007). At these depths, black corals are often abundant and dominant components of the sessile invertebrate fauna, and create a habitat for a myriad of species and associates (reviewed by Wagner *et al.*, 2012). 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) (Baco, 2007; Parrish & Baco, 2007). Second, black corals are culturally important 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; Chun, 1994). Third, Hawai'i is the only place in the United States, and only one of

Corresponding author:

D. Wagner

Email: daniel.wagner@noaa.gov

few places in the world, where black coral is harvested commercially for the precious coral jewellery industry, which is supplied by SCUBA divers that collect the species *Antipathes griggi* Opreško, 2009, *Antipathes grandis* Verrill, 1928 and *Myriopathes* cf. *ulex* (Ellis and Solander, 1786) at depths between 40 and 70 m (reviewed by Grigg, 2001). As a result of collaborations between scientists and the Hawaiian black coral fishery, antipatharian populations have been well documented in Hawai'i, especially in comparison to most other geographic locations (Wagner *et al.*, 2012). Consequently, a large collection of specimens and records exists for this group in Hawai'i. However, because of taxonomic uncertainties, most previous surveys have not examined ecological features to the level of individual species. The purpose of this study was to map populations of Hawaiian shallow-water (<150 m) antipatharian species, which is a first order approach to revealing ecological differences between species. Specifically, data on geographic position, depth, substrate type and temperature were analysed in relation to species, in order to determine whether there are differences in these habitat parameters between different antipatharian species. The depth zone examined as part of this study included mesophotic coral ecosystems (MCEs), which are light-dependent coral reefs and associated organisms found below the depth limits of conventional SCUBA diving (30 m), and extending to depths of 150 m in regions with high water clarity like Hawai'i (Kahng *et al.*, 2010). MCEs are notoriously undersurveyed worldwide due to the logistical challenges of accessing areas below the depth limits of conventional SCUBA diving.

MATERIALS AND METHODS

Antipatharian records from Hawaiian waters were retrieved from: (1) the literature; (2) museum specimens; (3) recently collected specimens; and (4) archived video/photo records. Only records <150 m were retrieved, because this depth is considered the depth limit of MCEs in the Hawaiian Islands (Kahng *et al.*, 2010) and because records below this depth were far scarcer and more uncertain. Literature records were obtained from over 400 articles that were collected as part of a literature review on the biology and ecology of black corals (Wagner *et al.*, 2012). Examined museum specimens included all Hawaiian black corals deposited at the Bernice P. Bishop Museum (BPBM) in Honolulu, Hawai'i, and the National Museum of Natural History, Smithsonian Institution in Washington, DC (USNM). Recently collected specimens were obtained on a series of expeditions throughout the Hawaiian Archipelago between 2006 and 2014 using SCUBA, mixed-gas technical diving and the Hawai'i Undersea Research Laboratory (HURL) manned submersibles *Pisces IV* and *V*. Video/photo records were acquired from Hawaiian deep-sea explorations conducted by HURL and the Monterey Bay Aquarium Research Institute (MBARI), and included dives conducted by the manned submersibles *Makali'i*, *Pisces IV* and *Pisces V*, as well as the remotely operated vehicles *RCV-150* and *Tiburon*. Each black coral record was mapped, and the following information was recorded where available: (1) species; (2) latitude/longitude; (3) depth; (4) *in situ* temperature; and (5) substrate type. In cases where species assignments could not be made from video/photo records alone, identifications were made using specimens collected in surrounding areas.

Temperature data was only available for HURL and MBARI records, and was retrieved from the CTD data recorder of the respective underwater vehicle at the time black coral colonies were collected or photographed.

RESULTS

The Hawaiian Archipelago has been extensively surveyed for antipatharians, with individual surveys targeting areas from Hawai'i Island to Kure Atoll; however, the vast majority of historical surveys are restricted to the inhabited Main Hawaiian Islands (Figure 1). A total of 862 individual black coral records were available from waters surrounding the Hawaiian Islands at depths ranging between 9 and 150 m (Figure 1). Archived video/photo records from HURL provided the largest proportion of records ($N = 332$), followed by recent specimen collections ($N = 258$), literature records ($N = 143$), USNM museum specimens ($N = 113$), BPBM museum specimens ($N = 12$) and MBARI records ($N = 4$) (Figure 1). All black corals were exclusively recorded on hard substrates. Some colonies were located within close proximity to patches of sand; however, black corals were always firmly anchored to hard substrates. Eight different species were identified among the reviewed records, and included: (1) *Antipathes griggi*; (2) *Antipathes grandis*; (3) *Cirrhopathes* cf. *anguina* (Dana, 1846); (4) *Stichopathes echinulata* Brook, 1889; (5) *Stichopathes?* sp.; (6) *Aphanipathes verticillata* Brook, 1889; (7) *Acanthopathes undulata* (Van Pesch, 1914); and (8) *Myriopathes* cf. *ulex* (Figure 2; see Wagner, 2011 for detailed descriptions). All antipatharian species were recorded from overlapping locations within the Hawaiian Islands, although there were differences in the geographic spread of individual species along the archipelago (Figure 3). Most species were widely distributed along the Hawaiian Islands, including *Antipathes griggi* from Hawai'i to Pearl and Hermes Atoll, *Antipathes grandis* from Hawai'i to Ni'ihau, *C. cf. anguina* from Hawai'i to north-west of Brooks Banks, *Stichopathes echinulata* from Hawai'i to Lisianski, *Stichopathes?* sp. from Hawai'i to French Frigate Shoals, *Acanthopathes undulata* from Hawai'i to Laysan and *M. cf. ulex* from Hawai'i to Pearl and Hermes Atoll (Figure 3). In contrast, *Aphanipathes verticillata* was recorded only from recent collections (2008–2009) performed in the Keyhole Pinnacle area of the Au'au Channel (Figure 3). In terms of bathymetric distributions, all antipatharian species were found at overlapping depths (Figure 4), although there were significant differences in the mean depth between species one-way ANOVA $P < 0.0001$. Within the examined depth range (0–150 m), *Stichopathes?* sp. had the shallowest depth distribution (mean = 30.0 m, range = 9–58 m), followed by *Antipathes griggi* (mean = 48.9 m, range = 9–110 m), *C. cf. anguina* (mean = 51.0 m, range = 9–150 m), *Antipathes grandis* (mean = 83.3 m, range = 24–146 m), *M. cf. ulex* (mean = 85.7 m, range = 30–150 m), *Acanthopathes undulata* (mean = 90.0 m, range = 32–150 m), *Aphanipathes verticillata* (mean = 105.5 m, range = 88–130 m) and *Stichopathes echinulata* (mean = 124.8 m, range = 90–150 m) (Figure 4). In most cases, 95% confidence intervals of mean depths did not overlap between species, with the exception of *Antipathes griggi* overlapping with *C. cf. anguina*, and *Antipathes grandis* overlapping with *M. cf. ulex*. In terms of temperature, records were only available for six of the eight species identified

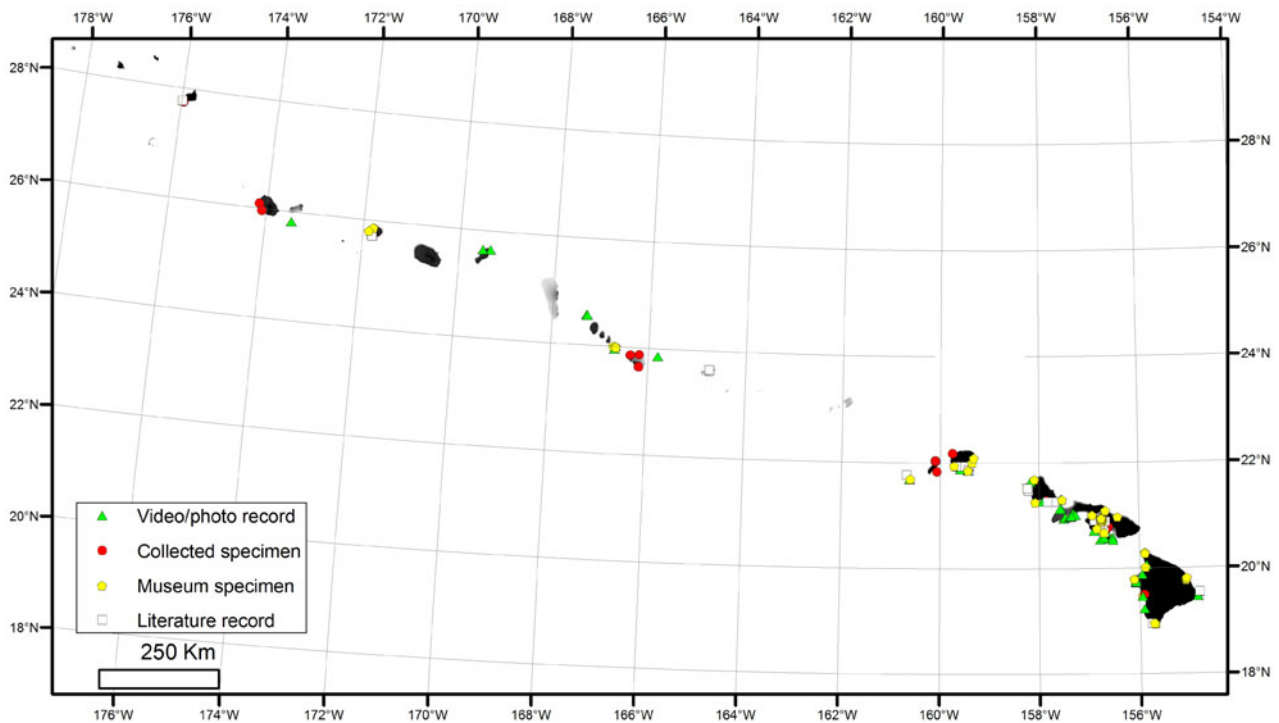


Fig. 1. Map showing the locations of shallow-water (<150 m) antipatharian records examined as part of this study. Black coral records include video/photo records from HURL and MBARI, museum specimens deposited at the USNM and BPBM, and recently collected specimens ($N = 862$).

within the examined depth range (0–150 m) (Table 1). As with depth, mean temperatures were significantly different between species (one-way ANOVA $P < 0.0001$), a pattern that is expected given the general correlation between temperature and depth. *Antipathes griggsi* was recorded at the warmest temperatures, followed by *C. cf. anguina*, *Antipathes grandis*, *M. cf. ulex*, *Aphanipathes verticillata*, *Stichopathes echinulata* and *Acanthopathes undulata* (Table 1). In most cases, 95% confidence intervals of mean temperatures did not overlap between species, with the exception of *Antipathes griggsi* overlapping with *C. cf. anguina*, and *Aphanipathes verticillata* overlapping with *M. cf. ulex* and *Stichopathes echinulata*.

DISCUSSION

Studies on biogeographical distributions are very rare within the order Antipatharia, because the vast majority of species are known only from their type locality and consequently have limited geographic ranges (Wagner *et al.*, 2012). This is due to taxonomic uncertainties within the Antipatharia, as well as the lack of historical surveys focusing on this taxonomic order. That said, some geographic locations have been relatively well surveyed for antipatharians, including the Gulf of Mexico, the Mediterranean and the Hawaiian Archipelago (reviewed by Wagner *et al.*, 2012). In fact, antipatharian populations from the Hawaiian Islands are some of the best documented on the globe (Wagner *et al.*, 2012). This is due, in large part, to a commercial black coral fishery that has operated in Hawai'i since the late 1950s (reviewed by Grigg, 2001) and has led to many surveys across the archipelago. However, the vast majority of these surveys are restricted to the inhabited Main Hawaiian Islands (Figure 1), and in particular to the shores of Maui, Kaua'i and Hawai'i, which are home to the largest

populations of commercially valuable Hawaiian black corals in the state (Grigg, 2001). Records of black corals from the North-western Hawaiian Islands are far scarcer, because fewer surveys have targeted those areas (Wagner *et al.*, 2011). The only survey that has quantified population densities of antipatharians in the North-western Hawaiian Islands notes densities of up to 0.047 colonies m^{-2} for *Antipathes griggsi* and 0.690 colonies m^{-2} for *Myriopathes cf. ulex* (Wagner *et al.*, 2011). In contrast, densities exceeding 1 colony m^{-2} exist at several locations throughout the Main Hawaiian Islands for these two species (Grigg, 2001). Future surveys targeting reefs in the North-western Hawaiian Islands will be needed to determine whether black corals are less abundant there.

The results of this study indicate that Hawaiian shallow-water antipatharian species are widely distributed across the archipelago, with the possible exception of *Aphanipathes verticillata*, which to date has only been recorded in Hawaii from the Au'au Channel (Figure 3). However, *Aphanipathes verticillata* superficially resembles *Antipathes griggsi* in terms of colony morphology and, therefore, distinguishing these two species on videos, photographs or *in situ* is very difficult (Figure 2; Opresko *et al.*, 2012). Consequently, the narrow range of *Aphanipathes verticillata* may be because this species has been misidentified as *Antipathes griggsi* in the past. Besides the Au'au Channel, *Aphanipathes verticillata* is also known from Mauritius and Okinawa, although the Hawaiian form is considered a distinct subspecies (*Aphanipathes verticillata mauiensis*) due to the unique morphological features of its skeletal spines (Opresko *et al.*, 2012). Mauritius, Okinawa and Hawai'i are all separated by large geographic distances, which suggests that *Aphanipathes verticillata* is also likely to be present in other locations, including within the Hawaiian Islands. Future surveys will be needed to verify whether

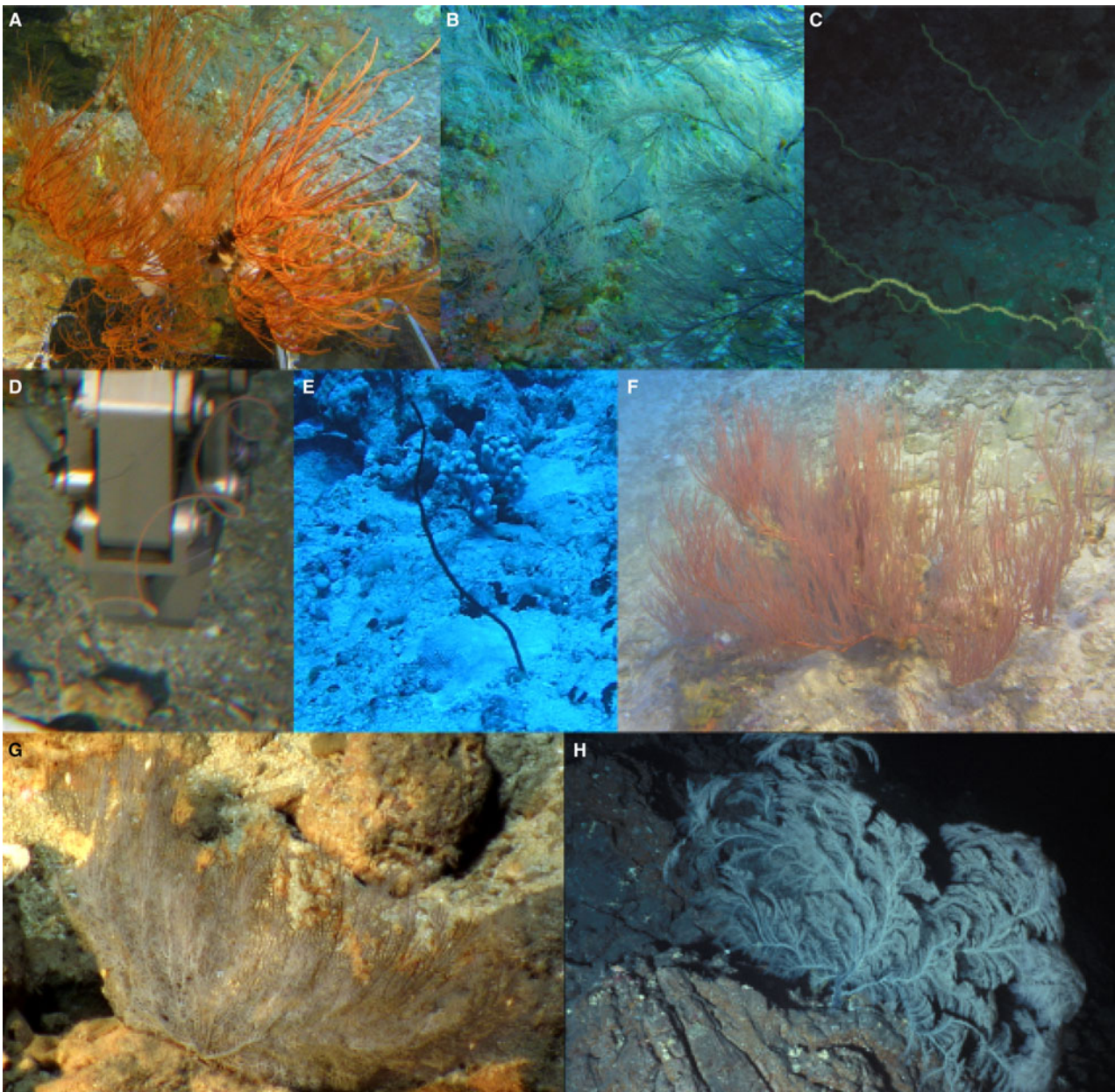


Fig. 2. *In situ* photographs of Hawaiian shallow-water (<150 m) antipatharian species. (A) *Antipathes griggi*, (B) *Antipathes grandis*, (C) *Cirrhipathes cf. anguina*, (D) *Stichopathes echinulata*, (E) *Stichopathes? sp.*, (F) *Aphanipathes verticillata*, (G) *Acanthopathes undulata* and (H) *Myriopathes cf. ulex* (photographs courtesy of HURL).

Aphanipathes verticillata has a limited distribution within the Hawaiian Archipelago.

Based on all available records, Hawaiian shallow-water antipatharian species coexist on hard substrates within similar geographic, depth and temperature ranges (Figure 3). These results are consistent with previous antipatharian surveys in other parts of the globe, which note that multiple black coral species typically coexist sympatrically (Goenaga, 1977; Warner, 1981; Grange & Singleton, 1988; Oakley, 1988; Sanchez *et al.*, 1998; Sanchez, 1999; Tazioli *et al.*, 2007). Collectively, these observations indicate that there are generalities in the physical habitat requirements of shallow-water (<150 m) antipatharians. Specifically, previous studies note that almost all black corals require hard substrates for attachment, and are often found in areas with strong currents and

low-light levels (reviewed by Wagner *et al.*, 2012). The principle of competitive exclusion predicts that for multiple species to coexist, they must be unique in terms of their microhabitat or use of resources (Gause, 1932; Hardin, 1960). The results of this study indicate that there are several similarities in the habitats of all Hawaiian shallow-water (<150 m) antipatharian species, including the need for hard substrates and overlapping geographic, bathymetric and temperature distributions. In most cases, however, individual species appear to be specialized in exploiting a particular microhabitat in terms of depth and temperature (Figure 4; Table 1), parameters which are themselves interrelated. In contrast, individual species are not differentiated by substrate type, as all species were exclusively recorded on hard substrates. The requirement for hard substrate appears to be generally true across the order Antipatharia, with the

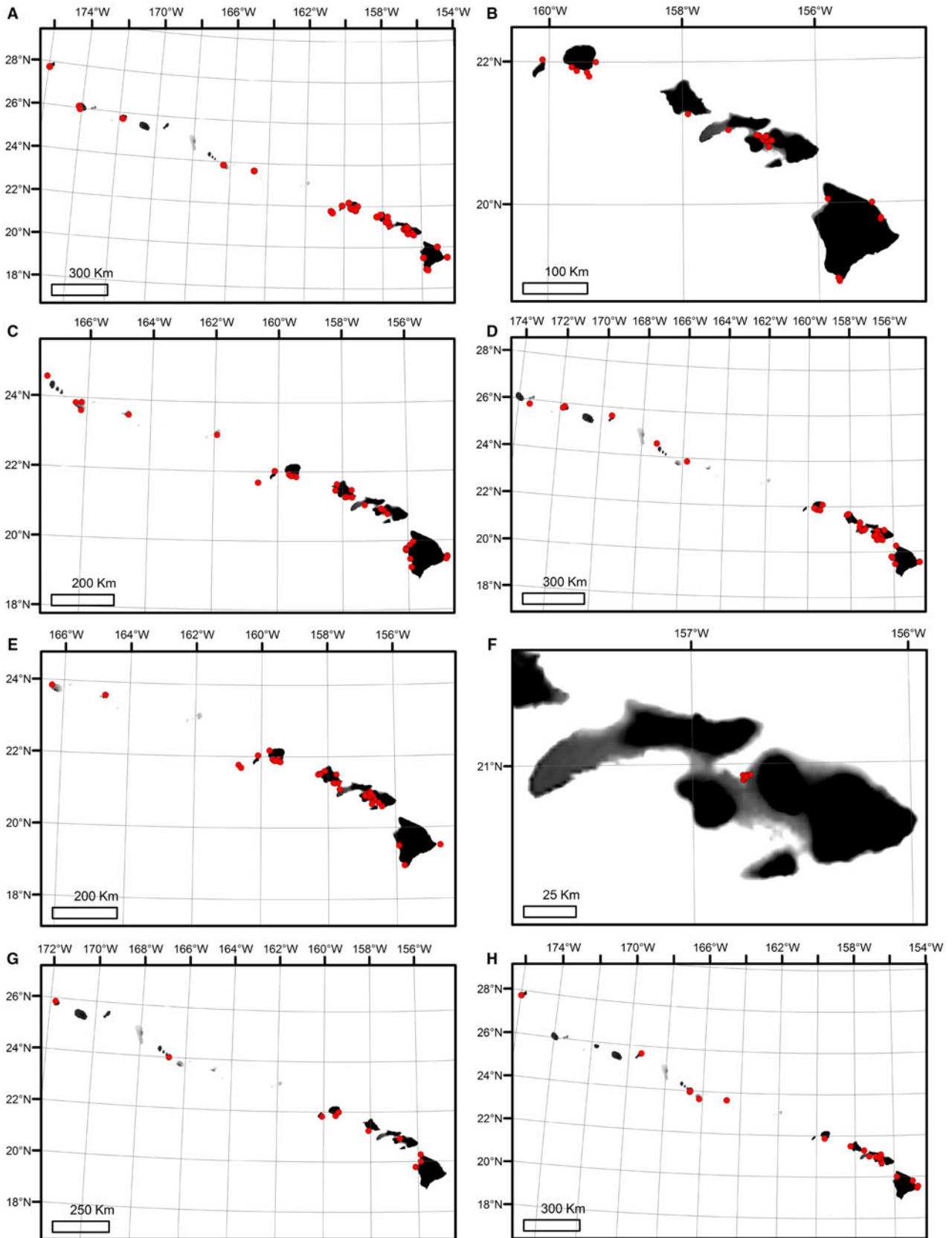


Fig. 3. Map showing the spatial distribution of Hawaiian shallow-water (<150 m) black coral species. (A) *Antipathes griggi*, (B) *Antipathes grandis*, (C) *Cirrhipathes cf. anguina*, (D) *Stichopathes echinulata*, (E) *Stichopathes?* sp., (F) *Aphanipathes verticillata*, (G) *Acanthopathes undulata* and (H) *Myriopathes cf. ulex*.

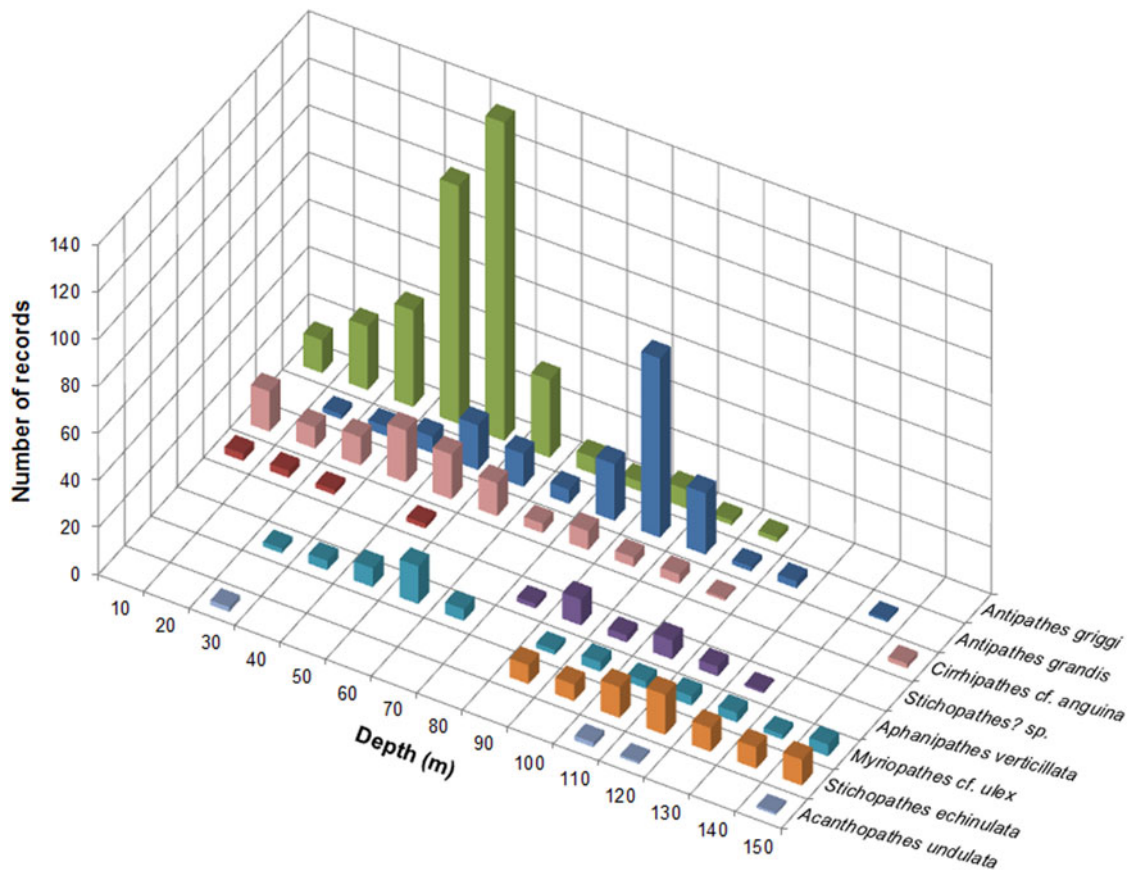


Fig. 4. Hawaiian shallow-water (<150 m) black coral records by depth and species. Depths represent upper bin limits. Records include published reports from the literature, museum specimens deposited at the USNM and BPBM, specimens collected on a series of expeditions throughout the archipelago in 2006–2014 and archived video/photo records from HURL and MBARI (N = 862).

exception of species within the genus *Schizopathes*, which have a modified, hook-like holdfast for support on soft bottoms (Opresko, 1997, 2002). Apart from this deep-water genus (>750 m), all other antipatharians possess a basal plate that is firmly anchored to hard substrates.

There are large overlaps in the bathymetric distribution between Hawaiian antipatharian species (Figure 4). For example, the species *Antipathes griggi*, *Antipathes grandis*, *Cirrhipathes cf. anguina*, *Stichopathes sp.?*, *Acanthopathes*

undulata and *M. cf. ulex* are all present within depths accessible through conventional SCUBA diving (40 m), whereas *Aphanipathes verticillata* and *Stichopathes echinulata* do not start appearing until depths below 80 m (Figure 4). Despite these large overlaps in the depth distribution of individual species, each species appears to have a preferred depth range which they exploit (Figure 4). The mean depth was significantly different for each species, with the exception of no statistically significant differences between *Antipathes griggi* and *C. cf. anguina*, and *Antipathes grandis* and *M. cf. ulex*. Similar to depth distributions, mean temperatures were significantly different between species, with the exception of no significant differences between *Antipathes griggi* and *C. cf. anguina*, and *M. cf. ulex* and *Stichopathes echinulata*. Interestingly, in cases in which species have overlapping mean depths and temperatures, the involved species have very different morphologies (Figure 2). *Antipathes griggi* has a bushy, irregularly branched corallum, whereas *C. cf. anguina* is an unbranched wire-coral (Figure 2). Similarly, *Antipathes grandis* has a bushy corallum, *M. cf. ulex* has fan-shaped colonies and *Stichopathes echinulata* is an unbranched wire coral (Figure 2). Furthermore, polyp sizes are significantly different between each pair of species with overlapping depth ranges (see Wagner, 2011). Thus, although *Antipathes griggi* and *C. cf. anguina*, *Antipathes grandis* and *M. cf. ulex*, and *M. cf. ulex* and *Stichopathes echinulata* inhabit very similar habitats in the Hawaiian Islands, they may avoid competition by exploiting different resources through their distinct morphologies and polyp sizes.

Table 1. Temperature data by species for Hawaiian shallow-water (<150 m) black corals. Data was retrieved from the CTD recorder of the underwater vehicle at the time colonies were photographed or collected. Temperature records were only available for six of the eight antipatharian species identified within the examined depth range.

| Species | N | Mean (°C) | Minimum (°C) | Maximum (°C) |
|----------------------------------|-----|-----------|--------------|--------------|
| <i>Antipathes griggi</i> | 114 | 26.25 | 22.30 | 27.41 |
| <i>Cirrhipathes cf. anguina</i> | 42 | 26.27 | 21.92 | 27.69 |
| <i>Antipathes grandis</i> | 58 | 24.25 | 20.01 | 26.91 |
| <i>Myriopathes cf. ulex</i> | 8 | 22.56 | 20.52 | 26.99 |
| <i>Aphanipathes verticillata</i> | 10 | 21.19 | 19.88 | 22.96 |
| <i>Stichopathes echinulata</i> | 28 | 21.08 | 19.59 | 22.91 |

Specifically, different colony morphologies and polyp sizes may allow species to specialize on feeding most efficiently under a particular current flow regime. While current regime was not analysed as part of this study, both current direction and speed have been shown to be important in shaping the spatial distribution of sessile suspension feeders (Chamberlain & Graus, 1975; Baynes & Szmant, 1989). Unfortunately, data sets for these two variables are not available across the survey areas examined as part of this study, and consequently future studies will have to examine whether there are differences in these variables between the environmental ranges of black coral species. In relation to current flow regime, previous studies note that in areas where current direction is primarily uni-directional, fan-shaped antipatharians are common and oriented perpendicular to currents; an orientation that maximizes contact between feeding surfaces and suspended food (reviewed by Wagner *et al.*, 2012). Future studies will need to examine whether black coral species specialize on exploiting particular microenvironments in terms of current direction and speed, but the observed morphological differences between the species examined as part of this study indicate that currents may be important in shaping their spatial distributions.

Another interesting feature in the depth distributions of Hawaiian antipatharians is that at least some species appear to be mostly limited to depths shallower than 120 m (Figure 4), an observation that is consistent with previous surveys of Hawaiian antipatharians (Grigg, 2001; Kahng & Grigg, 2005; Wagner *et al.*, 2010). The depth of 120 m corresponds to the top of the thermocline in the Main Hawaiian Islands (Grigg *et al.*, 2008), suggesting that temperature may be an important factor in limiting the bathymetric distributions of some black coral species. While this correlation does not necessarily signify a causal relationship, temperature is thought to be one of the main factors limiting distributions of ectothermic organisms at high latitudes, as well as in deep water (Pörtner, 2002; Grigg, 2006). Exposures to low temperatures have been shown to adversely affect feeding, reproduction and growth of corals (Palardy *et al.*, 2005; Putnam *et al.*, 2008; De Putron & Ryland, 2009), and in more severe cases cause large-scale mortalities (Roberts *et al.*, 1982; Coles & Fadlallah, 1991; Laboy-Nieves *et al.*, 2001; Hoegh-Guldberg *et al.*, 2005). The absence of some black coral species below the top of the thermocline in the Main Hawaiian Islands (120 m; Figure 4) suggests that they may be negatively affected by temperature. The top of the thermocline is found at shallower depths in the North-western Hawaiian Islands, shoaling to depths of 60 m at Pearl and Hermes Atoll (Grigg *et al.*, 2008). Interestingly, the only black coral survey that has targeted reefs at depths between 50 and 80 m at Pearl and Hermes Atoll did not record any black corals below 60 m (Wagner *et al.*, 2011). Even though these observations are very limited, they suggest that low temperatures may set a lower depth limit for some black coral species. In this regard, *in situ* temperatures recorded for the various species as part of this study (Table 1) may aid in designing future controlled experiments to test for the effects of temperature on black coral survival.

Although the Hawaiian Archipelago is one of the best surveyed areas for antipatharians on the planet, some areas, such as the uninhabited North-western Hawaiian Islands, still remain only marginally explored. The initial surveys across the Hawaiian Archipelago reported here suggest that many

of the black coral species found in the Hawaiian Islands have broad distributions across the archipelago. Furthermore, this study is one of the first to examine the microenvironments of sympatric antipatharian species in terms of geographic position, depth and temperature. The results indicate that while there are several similarities in the habitats amongst shallow-water (<150 m) antipatharian species, individual species exploit unique environments in terms of depth or temperature, or possess unique morphologies to minimize overlap.

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Correspondence should be addressed to:

D. Wagner
NOAA, Papahānaumokuākea Marine National Monument
1845 Wasp Boulevard, Building 176, Honolulu, HI 96818 USA
email: daniel.wagner@noaa.gov