

Sexual reproduction of the Hawaiian black coral *Antipathes griggi* (Cnidaria: Antipatharia)

D. Wagner · R. G. Waller · A. D. Montgomery ·
C. D. Kelley · R. J. Toonen

Received: 17 October 2011 / Accepted: 23 January 2012
© Springer-Verlag 2012

Abstract The Hawaiian black coral fishery has maintained steady catch levels for over 50 years. However, recent declines in the biomass of commercially valuable Hawaiian black corals question whether regulations need to be redefined for sustainable harvesting. Fishery management efforts are complicated by the limited information on the basic life history and reproduction of black corals. To address this knowledge gap, we used histological techniques to

investigate sexual reproductive processes within *Antipathes griggi*, the dominant species targeted by the fishery. Our results indicate that *A. griggi* is likely gonochoric with a 1:1 sex ratio and has an annual reproductive cycle. Furthermore, the percentage of polyps containing gametes dropped continuously throughout the reproductive season, indicating that spawning occurs in successive events with greatest intensity between November and December. Current fishing regulations prohibit harvesting of colonies <90 cm in height in state waters, and colonies <120 cm in height in federal waters. This study indicates that ~80% meeting the state harvesting limit, and ~90% of colonies meeting the federal limit, are sexually mature. Therefore, increasing these minimum size harvesting limits would ensure that more colonies can reproduce before being exposed to fishing mortality. 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.

Communicated by Biology Editor Dr. Mark Vermeij

D. Wagner
Department of Oceanography, University of Hawai'i at Mānoa,
1000 Pope Road, Honolulu, HI 96822, USA

Present Address:

D. Wagner (✉)
Papahānaumokuākea Marine National Monument,
6600 Kalaniana'ole Highway, Suite 300, Honolulu,
HI 96825, USA
e-mail: Daniel.Wagner@noaa.gov

R. G. Waller
Darling Marine Center, University of Maine,
193 Clarks Cove Road, Walpole, ME 04573, USA

A. D. Montgomery
U.S. Fish and Wildlife Service, 300 Ala Moana Boulevard,
Room 3-122, Honolulu, HI 96850, USA

C. D. Kelley
Hawai'i Undersea Research Laboratory, University of Hawai'i at
Mānoa, 1000 Pope Road, Honolulu, HI 96822, USA

R. J. Toonen
Hawai'i Institute of Marine Biology, 46-007 Lilipuna Road,
Kaneohe, HI 96744, USA

Keywords Anthozoa · Antipathidae · Coral spawning · Gametogenesis · Precious coral

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 Asia, Latin America, the Caribbean, and Hawai'i (Grigg 1975, 1976, 1984, 1993, 2001; Noome and Kristensen 1976; Castorena and Metaca 1979; Kenyon 1984; Romero 1997; Maldonado 2003; Padilla and Lara 2003; Huang and 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, 1984, 1993, 2010; Castorena and Metaca 1979; Romero 1997; Tsounis et al. 2010). In contrast, the Hawaiian black coral fishery has maintained consistent landings for more than 50 years through a successful management program that uses catch quotas and minimum size limits of harvested colonies (Grigg 1976, 1984, 1993, 2001, 2010; Parrish and Baco 2007). Deep-water surveys (40–110 m) performed in the Au‘au Channel between the islands of Maui and Lāna‘i in 1975 and 1998, indicated stability in both recruitment and growth of commercially valuable black coral populations, and led to the conclusion that the fishery had been sustainable over this time period (Grigg 2001). However, subsequent surveys performed in the channel in 2001 indicated a 25% decline in the biomass of black coral colonies since 1975, with likely causes including increases in harvesting pressure and competition with the invasive octocoral *Carijoa* sp. (Grigg 2004). Together, these developments have 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 2003, 2004; Kahng and Grigg 2005). Unfortunately, very little is known about the basic life history of black corals, which complicates effective management of the fishery (Grigg 2001, 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). Here, we seek to address this research priority by examining sexual reproductive processes among commercially valuable Hawaiian black corals. The species *Antipathes griggi* Opreško 2009, *Antipathes grandis* Verrill, 1928, and *Myriopathes* cf. *ulex* (Ellis and Solander, 1786) have all been targeted by the Hawaiian precious coral fishery (Grigg 1976, 2001, 2010; Oishi 1990; Boland and Parrish 2005; WPRFMC 2006; Parrish and Baco 2007; Wagner et al. 2010, 2011a). However, over 90% of the coral harvested in Hawaiian waters consists of *A. griggi* (Oishi 1990; Parrish and Baco 2007), and therefore this species was chosen as the focus of this study. Our specific objectives were to obtain information on the following reproductive parameters of *A. griggi*: (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

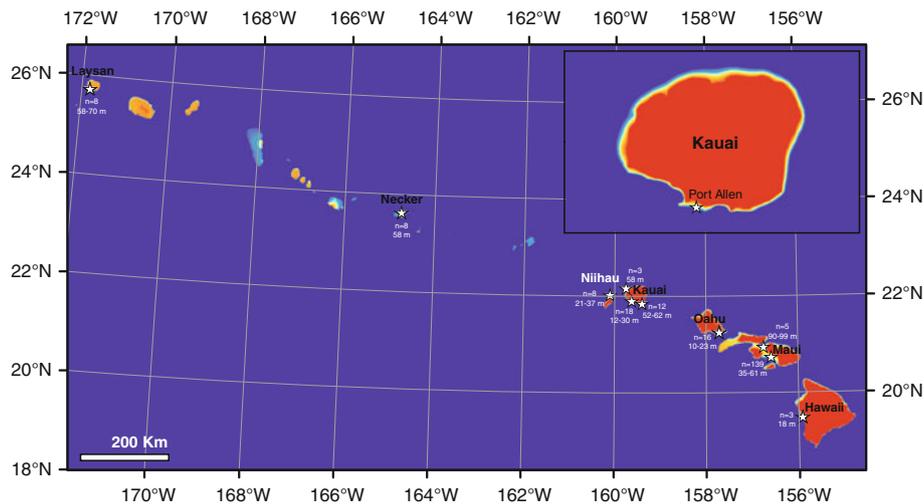
Sample collections

A total of 220 colonies were sampled on a series of cruises conducted between 2006 and 2010 and were obtained throughout the known range of *A. griggi* (Wagner et al. 2011a), from Hawai‘i Island to Laysan at depths ranging between 10 and 99 m (Fig. 1). Samples were collected using (1) the Hawai‘i Undersea Research Laboratory’s manned submersibles *Pisces IV* and *V*, (2) mixed gas technical diving, and (3) traditional open-circuit SCUBA. 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 underwater or by photographing colonies with parallel lasers projected onto them (Olsen and Wood 1980; Grigg 2004; Reed et al. 2005; Wagner et al. 2010). Samples consisting of 3–5 cm branchlets were clipped from the mid-section of each colony, preserved in 10% seawater buffered formalin, and transferred to 70% ethanol after 3–5 days. Additionally, monthly collections were performed for 1 year at a site located off Port Allen Harbor, Kaua‘i (21°53.353′N 159°34.980′W) at depths ranging between 30 and 40 m (Fig. 1). At this site, ten colonies (80–160 cm in height) were tagged with a label attached to the base, and branchlets were sampled as described above between July 2008 and July 2009 for histological work. Additionally, temperature and photoperiod time-series data were obtained at the Port Allen site and examined in relation to the gametogenesis results from the histological work described below. 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

Like other antipatharians, smaller immature polyps are sometimes found interspersed within branches containing larger polyps in *A. griggi* (see Wagner et al. 2011b). These considerably smaller polyps are always immature, and therefore they were not used in histological preparations. A total of 10 polyps were dissected from the skeleton of each sampled colony 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

Fig. 1 Map of sampling locations where 220 colonies were sampled throughout the known range of *Antipathes griggi*, from the islands of Hawai'i to Laysan at depths between 10 and 99 m. *Inset*: Study site off Port Allen, Kaua'i where monthly collections were performed for 1 year



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 as described by Wagner et al. (2011b). 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 colonies containing gametes, sex and reproductive stage were determined for a total of 100 spermatozoa or oocytes per specimen (10 polyps). Spermatozoa was staged as described by Parker et al. (1997) (see Fig. 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 and Baco 2007). Previtellogenic oocytes were differentiated from vitellogenic oocytes by being smaller in size (<70 μm) and by staining dark purple as opposed to bright red (Fig. 2). Oocyte size-frequency distributions were graphed for female colonies by binning oocyte diameters in 10 μm increments.

Results

Reproductive strategy

All examined specimens were strictly gonochoric, because none of the examined polyps or colonies contained both

oocytes and spermatozoa. Of the total of 220 *A. griggi* colonies that were sampled as part of this study (Fig. 1), 95 (43.2%) did not contain any gametes, whereas 64 (29.1%) contained oocytes and 61 (27.7%) contained spermatozoa. The ratio of male to female colonies was not significantly different from 1:1 at any of the 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 (Fig. 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 colonies, and the presence of oocytes or spermatozoa 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 (Fig. 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 (Fig. 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 the disappearance of gametes during time-series collections (see below). Externally, none of the examined polyps contained brooded larvae or oocytes 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, $P > 0.05$). Similarly, spermatozoa stage-frequency distributions were not

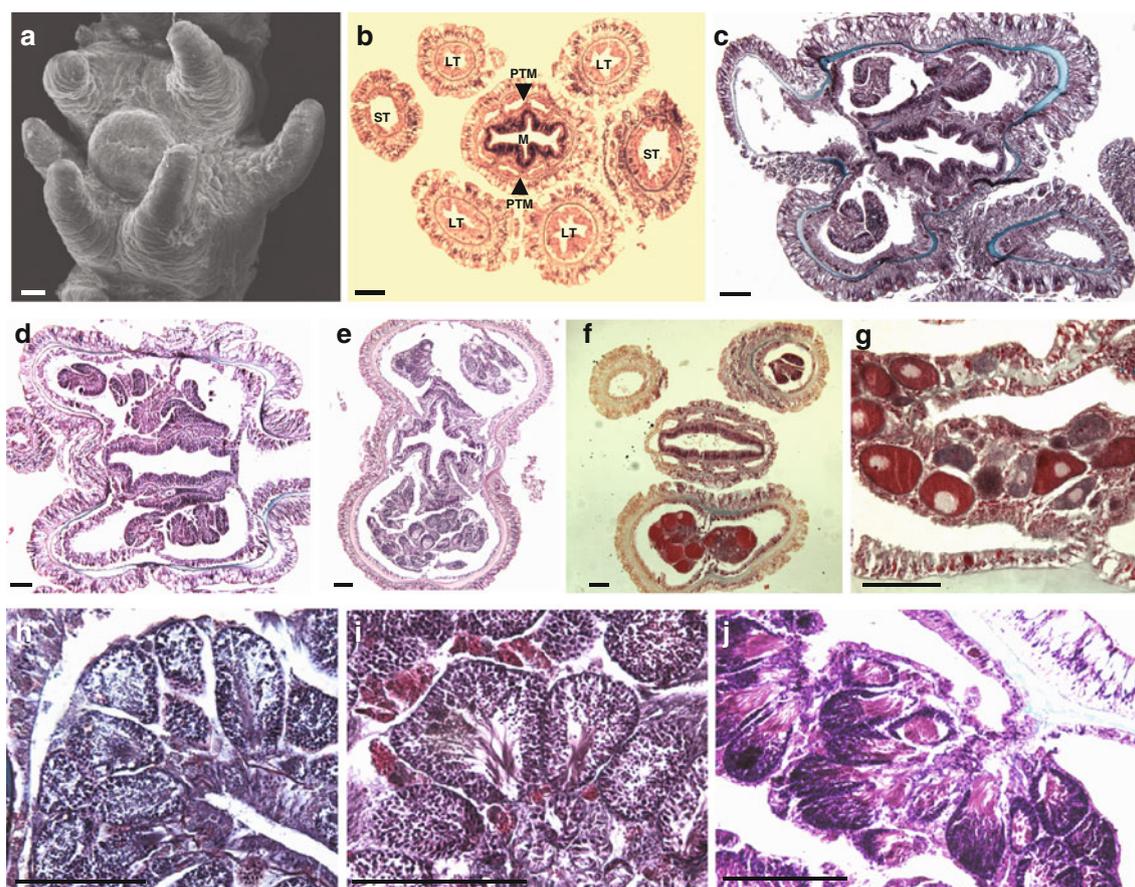


Fig. 2 **a** Scanning electron micrograph of *Antipathes griggi* polyp showing mouth surrounded by six tentacles and **b–j** histological cross-sections through polyps of *A. griggi* showing **b** locations of primary transverse mesenteries, which bear the filaments and gametes (*M* mouth, *PTM* primary 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** stage 1 spermatocysts; **i** stage 2 spermatocysts; and **j** stage 3 spermatocysts (scale bars = 100 μm)

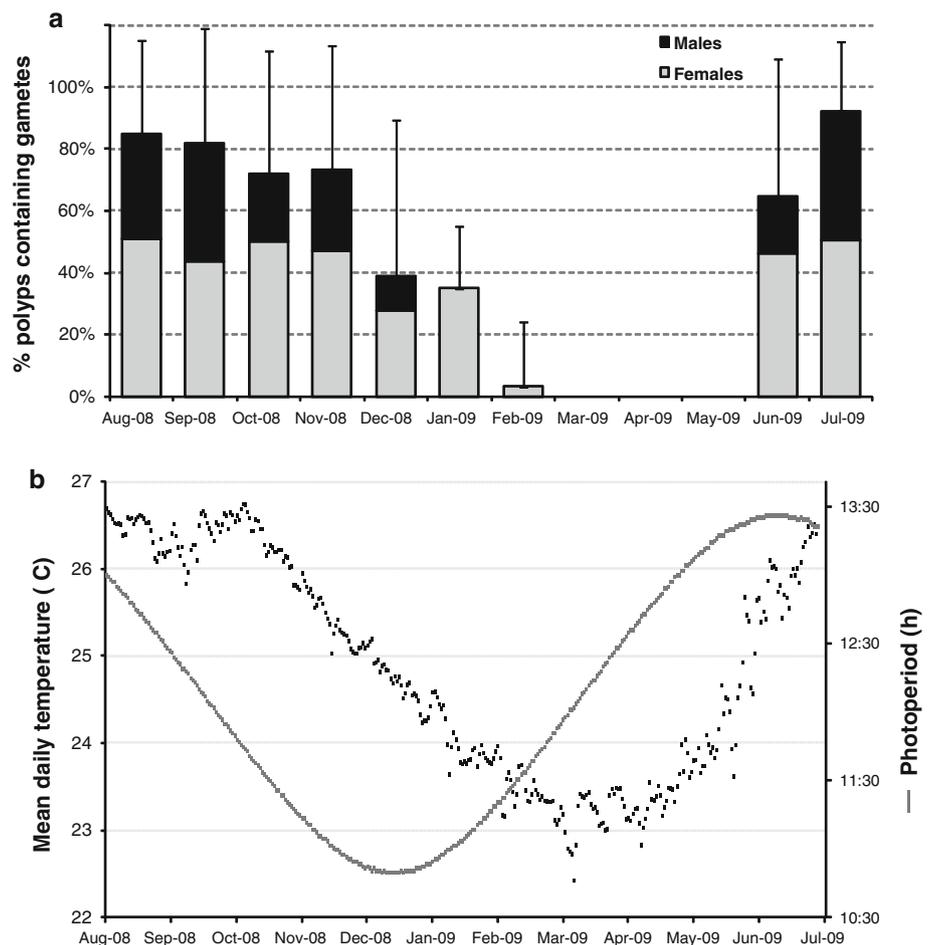
significantly different among the five male colonies across sampling dates (one-way ANOVA, $P > 0.05$). Therefore, frequency distribution data were pooled for both female and male colonies in each month. Reproductive output, measured as the proportion of polyps containing gametes, coincided with seasonal temperature fluctuations (Fig. 3). None of the samples collected in March through May contained any gametes, coinciding with the period of lowest mean temperatures ($\sim 23^\circ\text{C}$; Fig. 3). Reproductive output and mean temperatures increased from June to August and then decreased from August to March (Fig. 3). Both male and female colonies had a similar seasonal pattern of reproductive output, although there were slight temporal differences between sexes (Figs. 3, 4). All male polyps were completely void of spermatocysts by January, whereas a few female polyps (<3%) still contained oocytes through February (Figs. 3, 4). Gamete maturity stages generally increased from June through December (Fig. 4).

For male colonies, spermatocysts were mostly in early stages of development (stages 1 and 2) in June to August and then progressively became dominated by spermatocysts in late developmental stages through December (stage 3; Fig. 4). Similarly, female colonies had polyps containing a higher proportion of previtellogenic oocytes in June–August, which gradually progressed to a high proportion of vitellogenic oocytes of larger size classes in January–February (Fig. 4). However, female colonies contained oocytes of a large range of size and maturity stage throughout the reproductive season (Fig. 4), with immature oocytes often occurring within close proximity to mature oocytes even within the same mesentery (Fig. 2).

Minimum size of sexual maturity

Among colonies that were sampled during the reproductive season (June–December; $n = 128$), 39 (38.3%) did not

Fig. 3 a 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 (*gray lines*) and mean daily temperature (*black dots*) measured at the Port Allen site



contain any gametes. All colonies smaller than 40 cm ($n = 14$) did not contain any gametes and were thus considered sexually immature (Fig. 5). The proportion of mature colonies increased with increasing colony height, from 20% for colonies measuring 40–49 cm ($n = 5$) to ~60% for colonies with a height of 50–59 cm ($n = 8$) and to ~80% for colonies measuring 60–69 cm ($n = 6$) (Fig. 5). Among colonies meeting, State of Hawai'i legal harvesting limit (>90 cm) ~80% were sexually mature ($n = 75$), whereas ~90% of colonies meeting the federal harvesting limit (>120 cm) were mature ($n = 32$). All colonies that were taller than 130 cm ($n = 21$) were mature (Fig. 5).

Maximum depth of sexual reproduction

Despite intense sampling of black coral colonies at depths ranging between 75 and 130 m ($n = 76$), only five *A. griggi* colonies were sampled below 75 m, with the deepest colony occurring at 99 m. Below 75 m, most of the sampled colonies belonged to the species *Antipathes grandis* (68.4%) and *Aphanipathes verticillata* Brook, 1889 (25.0%). Despite being rare, all five *A. griggi* colonies that

were sampled below a depth of 75 m contained mature gametes.

Discussion

Reproductive strategy

Among samples containing gametes, all contained either only oocytes or spermatocysts, but never both within the same colony (Fig. 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 1 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 of all size classes (Fig. 5). Consistent with these results,

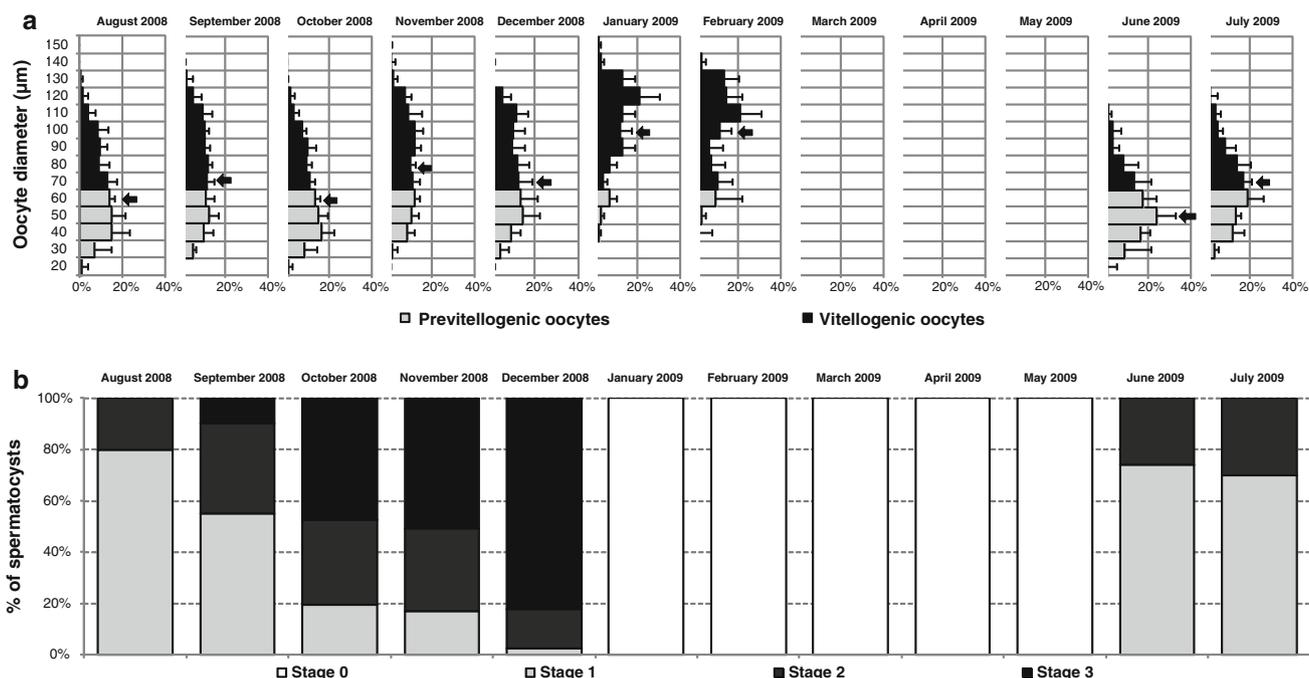


Fig. 4 **a** Percentage of oocytes per size class for five female colonies that were tagged at the Port Allen site. *Arrows* point toward mean oocyte diameter. *Error bars* represent standard deviations. **b** Percentage of spermatocysts per reproductive stage for five male colonies

tagged at the Port Allen site. (*Note:* Female colonies collected in March through May did not contain any oocytes, whereas male colonies collected in January through May did not contain any spermatocysts.)

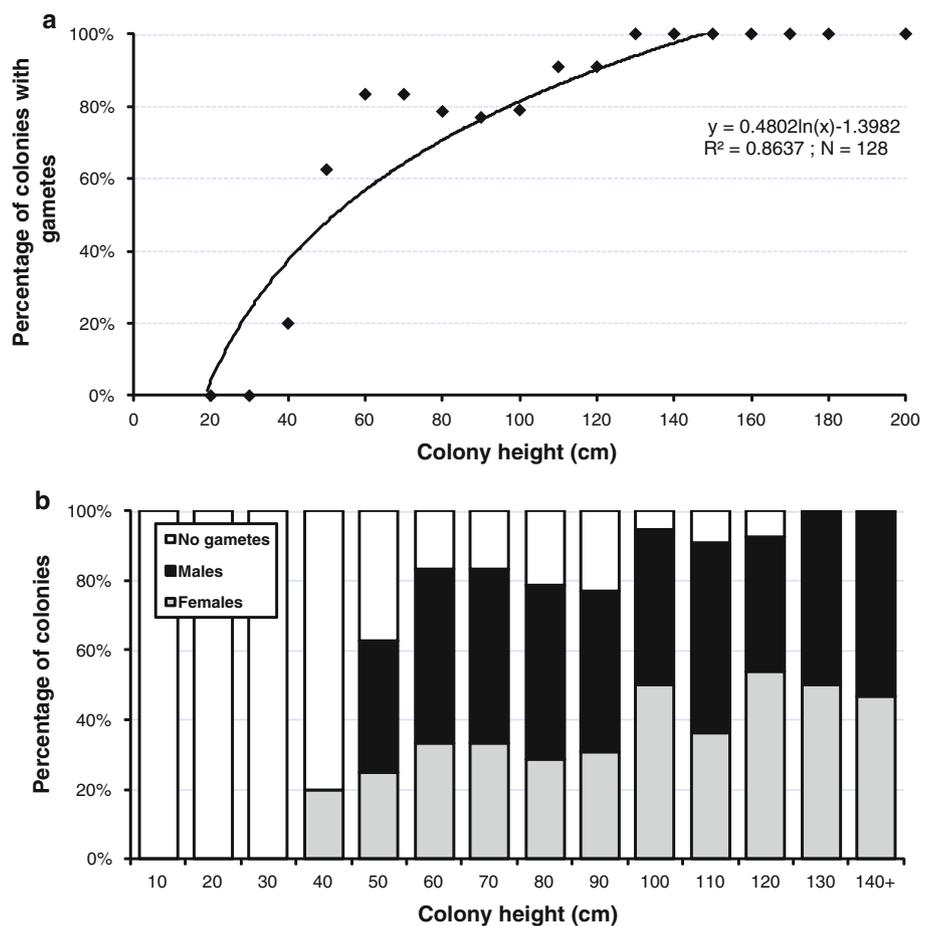
Parker et al. (1997) reported that there is no relationship between sex and colony size in *Antipathella fiordensis* populations from New Zealand. Unfortunately, both this study and that of *A. fiordensis* in New Zealand (Parker et al. 1997) only monitored sex of individual colonies over a single reproductive 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 3 years and reported that both species were gonochoric. In contrast, Bo (2008) studied the sexuality of *Cirrhopathes* sp. in Indonesia over 2 years and noted that some colonies changed sex over the course of the study and were thus sequential hermaphrodites. Other than these two studies that have monitored the sexuality of individual colonies over multiple years, 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; Opresko and Genin 1990; Opresko 2003, 2005; Molodtsova and Pasternak 2005; Molodtsova 2006; Gaino and Scoccia 2008, 2009, 2010; Gaino et al. 2008; Moon and Song 2008; Bo et al. 2009; Wagner et al. 2011b). All of these short-term studies report finding oocytes or

spermatocysts but never both within the same colony. To date, Bo (2008) is the only study documenting sex changes in an antipatharian coral, but the paucity of long-term studies makes it impossible to determine whether sequential hermaphroditism is widespread within the order Antipatharia.

While this study does not conclusively resolve whether *A. griggsi* is gonochoric or sequentially hermaphroditic, our results clearly indicate that *A. griggsi* is not a simultaneous hermaphroditic species, because none of the examined specimens contained both oocytes and spermatocysts (Fig. 2). Likewise, most previous examinations of antipatharians have failed to detect simultaneous hermaphroditic colonies (reviewed by Wagner et al. 2011b). 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. griggsi*, they were always found in association with the primary transverse mesenteries, which reached into the cavity of lateral tentacles in many cases (Fig. 2). Acknowledging that the transverse and sagittal planes may have not been correctly defined within the Antipatharia (Schultze 1896), we continue to use the terminology used by most previous authors (Brook 1889; Van Pesch 1914; Pax 1918; Hyman 1940;

Fig. 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. *Number* of colonies per size category: 20 cm = 11; 30 cm = 3; 40 cm = 5; 50 cm = 8; 60 cm = 6; 70 cm = 6; 80 cm = 14; 90 cm = 13; 100 cm = 19; 110 cm = 11; 120 cm = 11; 130 cm = 5; and 140 + cm = 16



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 (Fig. 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. 2011b). These previous reports are consistent with the observations of this study, and collectively suggest that gamete location is evolutionarily 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. 2011b). Additionally, none of the samples examined as part of this study contained brooded larvae or oocytes on their surfaces, thus indicating that *A. griggi* is not a brooding species. Consequently,

A. griggi must be 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 sensu Kahng et al. 2008). Interestingly, none of the male polyps collected in January contained any spermatocysts, whereas a small number of female polyps (<3%) still contained oocytes through February (Figs. 3, 4). These observations may indicate that oocytes are retained for a brief period following internal fertilization. However, distinguishing whether *A. griggi* spawns both spermatocysts and oocytes for external fertilization or retains oocytes for internal fertilization will require sampling either right before or during a spawning event (Harrison and Wallace 1990; Vermeij et al. 2004). 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 (Figs. 3, 4). To date, there are very few direct observations of the spawning behavior of antipatharians (Goenaga 1977; Miller 1996; Gaino and 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 and 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 h 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 maturation) from their mouths. 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. Beyond these few direct observations of antipatharian spawning, indirect evidence of spawning comes from histological examinations (Cooper 1909; Opresko 2005; Gaino et al. 2008; Gaino and Scoccia 2010). In histological sections of male *Cirripathes* 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 and Scoccia 2010). Such signs of spawning were not apparent in any of the *A. griggi* polyps examined as part of this study. This could reflect 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 and Wallace 1990; Richmond and Hunter 1990; Glynn et al. 1991; Dahan and 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) classified colonies 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 2005). In contrast, no signs of polyp deterioration were observed in any of the *A. griggi* 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 suggest that *Antipathes griggi* has an annual reproductive cycle (Figs. 3, 4). Additionally, the reproductive cycle of *A. griggi* appears to be related to 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 (Fig. 3). From July to March, the percentage of polyps containing gametes dropped continuously from >90 to 0%, a pattern that closely tracked seasonal declines in average temperatures from ~27 to ~23°C (Fig. 3). This seasonal decline in reproductive output suggests that spawning occurs continuously throughout the reproductive season of *A. griggi*, with greatest intensity between November and December when the greatest decline in gamete-containing polyps occurred. Consistent with this interpretation, immature oocytes were often observed in close proximity to mature oocytes even within the same mesentery (Fig. 2), suggesting that spawning occurs in successive events. In comparison with a single-mass spawning event, spawning over multiple episodes has the advantage that a single catastrophic event cannot eliminate the entire reproductive effort of 1 year. However, spawning over multiple episodes also decreases fertilization success due to lower gamete concentrations per event (Leviton et al. 1991, 1992). To overcome the lower fertilization success associated with multiple spawning events, *A. griggi* may rely on dense aggregations of colonies, such as those commonly

observed for *A. griggsi* around the Hawaiian Archipelago (Grigg 1976, 2001, 2004; Boland and Parrish 2005; Parrish and Baco 2007).

Both male and female colonies contained an increasingly larger proportion of gametes in late stages of maturity as the reproductive season progressed (Fig. 3), suggesting that new gametes are formed in lower numbers later in the reproductive season when water temperatures get colder. No gametes were observed in any of the samples collected during March and May when water temperatures were coldest (Fig. 3). Consistent with these results, Grigg (1976) did not find any mature gametes in *A. griggsi* colonies collected in March 1975. Collectively, these results indicate that the gametogenic cycle of *A. griggsi* tracks seasonal temperature fluctuations, and that low temperature may inhibit gametogenesis during the off-season (March–May; Figs. 3, 4). Several previous surveys have noted that the lower depth range of *A. griggsi* corresponds to the top of the thermocline in the Main Hawaiian Islands (110 m; Grigg 1984, 1993; Kahng and Grigg 2005; Kahng and Kelley 2007), suggesting that low temperatures may exclude *A. griggsi* from deeper waters (>110 m). Interestingly, mean temperatures in the time of the year when no gametes were present in the shallow-water (30–40 m) *A. griggsi* population monitored as part of this study (~23°C; Fig. 3) are similar to the maximum temperatures experienced by the deepest *A. griggsi* populations in the Main Hawaiian Islands (110 m; Grigg 1976, 1984, 1993; Kahng and Grigg 2005; Kahng and Kelley 2007). Together, these observations suggest that *A. griggsi* may be restricted from inhabiting depths below 110 m in the Main Hawaiian Islands because colder temperatures inhibit gametogenesis or other reproductive processes.

To date, few studies have examined the reproductive seasonality of black corals (Grigg 1976; Goenaga 1977; Schmidt and Zissler 1979; Parker et al. 1997; Bo 2008; Gaino and Scoccia 2008, 2010), all of which were conducted in shallow water (<70 m). These studies report seasonality in the appearances and disappearances of gametes, which at least in some cases have been correlated with seasonal temperature fluctuations (Schmidt and Zissler 1979; Parker et al. 1997; Gaino and Scoccia 2010). For example, 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 and Scoccia (2010) examined *Antipathella subpinnata* specimens collected from the Mediterranean and found no fertile colonies in September through 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 *Cirrhopathes*

reproduced in the two mid-summer months. As in previous antipatharian studies, 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 (Fig. 3). Seasonal changes in temperature have also been correlated with the reproductive seasonality of numerous species of shallow-water (<40 m) scleractinian corals (reviewed by Harrison and Wallace 1990). 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 controlled experiments in laboratory cultures. Some 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 and Eernisse 1982) and the sea urchin *Eucidaris tribuloides* (McClintock and 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 (Van Woessik et al. 2006). In this study, both *A. griggsi* oocytes and spermatocysts first appeared in June, coinciding with the longest photoperiods of the year (Fig. 3). However, determining whether these long photoperiods trigger the initiation of gametogenesis in *A. griggsi* will require manipulative experiments in laboratory culture. Regardless of the underlying cause, reproductive seasonality in *A. griggsi* tracks seasonal temperature fluctuations, as has previously been reported for several shallow-water water antipatharians (<70 m).

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%; Fig. 5). The proportion of sexually mature colonies increased with increasing colony size until a height of 130 cm at which 100% of colonies were mature. 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 state regulations prohibit commercial harvesting of *A. griggsi* colonies that are smaller than 90 cm (Boland and Parrish 2005), and federal regulations prohibit harvesting of colonies that are smaller than 120 cm (Grigg 2010; Tsounis et al. 2010). Our study indicates that most (~80 and ~90%, respectively) colonies that reach these legal harvesting limits are sexually mature (Fig. 5). Increasing the legal harvesting limits of both state and federal regulations

to 130 cm would therefore ensure that more colonies have a chance to reproduce before being exposed to fishing mortality. Given the substantial declines in population biomass of *A. griggsi* due to recent increases in harvesting pressure (Grigg 2004), increasing the legal limit of harvested colonies may be a prudent strategy to ensure continued sustainability of the fishery. In addition, setting aside no take areas may allow more colonies to continuously reproduce and reseed fished populations.

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 and 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, 2001, 2010; Oishi 1990; Parrish and Baco 2007). However, dense black coral populations exist off the islands of Hawai'i, Maui, and Kaua'i at depths down to 110 m (Grigg 1976, 2001, 2004; Grigg et al. 2002; Kahng and Grigg 2005; Kahng and Kelley 2007; Parrish and Baco 2007; Wagner et al. 2010). It had previously been thought that colonies below the harvesting depth zone (>75 m) provided a depth refuge from harvest and were capable of reseeding fished populations (Grigg 1976, 2001). The results of our study indicate that the depth refuge of *A. griggsi* colonies below the harvesting zone has been greatly overestimated. 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. griggsi* colonies were collected. Below 75 m, the majority of sampled colonies consisted of *A. grandis* (68.4%) and *Aphanipathes verticillata* (25.0%), with *A. griggsi* accounting for only 6.6% of the colonies sampled. Although all *A. griggsi* colonies collected below 75 m were sexually mature, the low occurrences predict very low fertilization success 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, 1992; Oliver and Babcock 1992; Babcock et al. 1994; Harrison and Jamieson 1999). Thus, the low occurrence of *A. griggsi* colonies below 75 m indicates that while reproduction is possible at depths up to 100 m, it does not occur frequently, and these isolated colonies presumably contribute little to the overall population. Given that the population size of *A. griggsi* colonies below the harvesting zone has been overestimated in the past, this study indicates that there is no real depth refuge from harvest. Future studies will need to reevaluate the sizes of *A. griggsi* populations that are exposed to and protected from fishing mortality.

Acknowledgments We thank D. Opresko for taxonomic assistance and J. DeMello for valuable help during this project. Special thanks to the captain and crew of *R/V Kaimikai-o-Kanaloa* and *R/V Hi'ialakai*, and to L. Marsh, J. Heacock, S. Reed, J. Leonard, K. Longenecker, R. Boland, J. Eble, Y. Papastamatiou, F. Parrish, J. Rooney, K. Ryan, R. Pyle, K. Gleason, R. Kosaki, G. McFall, C. Kane, B. Hauk and S. Kahng for help with sample collections. Additional help in the laboratory was provided by T. Carvalho, M. Bellinger, R. Macleod and E. Bates. This work was funded in part by the Western Pacific Fisheries Management Council (NA07NMF4410114 to the University of Hawai'i through NOAA's Coral Reef Conservation Grant Program), the National Oceanic and Atmospheric Administration (NOAA) Coastal Ocean Program (NA07NOS4780189 to the State of Hawai'i Department of Land and Natural Resources [DLNR]), the NOAA Coral Reef Conservation Program (NA05OAR4301108 to HURL), the NOAA Fisheries Disaster Relief Program (NA03NMF4520452 to the State of Hawai'i/DLNR), the National Science Foundation (OCE-0623678 to RJT), and the National Marine Sanctuary Program (NWHICRER MOA 2005-008/6882). Submersible support was provided by HURL. This manuscript represents SOEST contribution number 8558 and HIMB contribution number 1484. The findings and conclusions in this article are those of the authors and do not necessarily represent the views of the U.S. Fish and Wildlife Service.

References

- Babcock RC, Bull GD, Harrison PL, Heyward AJ, Oliver JK, Wallace CC, Willis BL (1986) Synchronous spawning of 105 scleractinian coral species on the Great Barrier Reef. *Mar Biol* 90:379–394
- Babcock RC, Mundy CN, Whitehead D (1994) Sperm diffusion models and in situ confirmation of long-distance fertilization in the free-spawning asteroid *Acanthaster planci*. *Biol Bull* 186:17–28
- Bo M (2008) Taxonomy and ecology of antipatharians. Ph.D. thesis, Universita Politecnica Delle Marche, p 212
- Bo M, Barucca M, Biscotti MA, Canapa A, Lapian HFN, Olmo E, Bavestrello G (2009) Description of *Pseudocirrhopathes* (Cnidaria: Anthozoa: Hexacorallia: Antipathidae), a new genus of whip black coral from the Indo-Pacific. *Ital J Zool* 76:392–402
- Boland RC, Parrish FA (2005) A description of fish assemblages in the black coral beds off Lahaina, Maui, Hawai'i. *Pac Sci* 59:411–420
- Brook G (1889) Report on the Antipatharia. Report of the scientific results of the voyage of the H.M.S. Challenger. *Zool* 32:1–222
- Carroll A, Harrison P, Adjeroud M (2006) Sexual reproduction of *Acropora* reef corals at Moorea, French Polynesia. *Coral Reefs* 25:93–97
- Castorena V, Metaca M (1979) El coral negro, una riqueza en peligro. *Tec Pesq* 139:22–27
- Cooper CF (1909) Reports of the Percy Sladen Trust Expedition to the Indian Ocean (1905) Antipatharia. *Trans Linn Soc Lond Zool Ser* 2(12):301–321
- Dahan M, Benayahu Y (1997) Reproduction of *Dendronephthya hemprichi* (Cnidaria: Octocorallia): year-round spawning in an azooxanthellate soft coral. *Mar Biol* 129:573–579
- Davis TLO (1982) Maturity and sexuality in Barramundi, *Lates calcarifer* (Bloch), in the Northern Territory and south-eastern Gulf of Carpentaria. *Aust J Mar Freshw Res* 33:529–545
- Ellis J, Solander D (1786) The natural history of many curious and uncommon zoophytes collected by the late John Ellis, systematically arranged and described by the late Daniel Solander. Benjamin White and Son, London
- Fadlallah YH (1983) Sexual reproduction, development and larval biology in scleractinian corals. *Coral Reefs* 2:129–150

- Fautin DG (2002) Reproduction of Cnidaria. *Can J Zool* 80:1735–1754
- Gage JD (1962) Two black coral stories from Maui but with vastly different sequels. *Hawai'i Shell News* 9:1 & 6
- Gaino E, Scoccia F (2008) Female gametes of the black coral *Cirrhopathes* cf. *anguina* (Anthozoa, Antipatharia) from the Indonesia Marine Park of Bunaken. *Invertebr Reprod Dev* 51:119–126
- Gaino E, Scoccia F (2009) Release of sperm clusters in spheres by the black coral *Cupressopathes pumila* (Anthozoa, Antipatharia). *Coral Reefs* 28:851–857
- Gaino E, Scoccia F (2010) Gamete spawning in *Antipathella subpinnata* (Anthozoa, Antipatharia): a structural and ultrastructural investigation. *Zoomorphology* 129:213–219
- Gaino E, Bo M, Boyer M, Scoccia F (2008) Sperm morphology in the black coral *Cirrhopathes* sp. (Anthozoa, Antipatharia). *Invertebr Biol* 127:249–258
- Glynn PW, Gassman NJ, Eakin CM, Cortes J, Smith DB, Guzman HM (1991) Reef coral reproduction in the eastern Pacific: Costa Rica, Panama, and Galapagos Islands (Ecuador). I. Pocilloporidae. *Mar Biol* 109:355–368
- Goenaga C (1977) Two new species of *Stichopathes* (Zooantharia; Antipatharia) with observations on aspects of their biology. M.S. thesis, University of Puerto Rico, p 101
- Grange KR (1988) Redescription of *Antipathes aperta*, Totton, (Coelenterata: Antipatharia), an ecological dominant in the southern fiords of New Zealand. *N Z J Zool* 15:55–61
- Grigg RW (1964) A contribution to the biology and ecology of the black coral, *Antipathes grandis* in Hawai'i. M.S. thesis, University of Hawai'i, p 74
- Grigg RW (1975) The commercial potential of precious corals in the western Caroline Islands, Micronesia. Sea Grant Technical Report. UNIHI-SEAGRANT-AR-75-03
- Grigg RW (1976) Fishery management of precious and stony corals in Hawai'i. Sea Grant Technical Report. UNIHI-SEAGRANT-TR-77-03
- Grigg RW (1984) Resource management of precious corals: a review and application to shallow water reef building corals. *Mar Ecol* 5:57–74
- Grigg RW (1993) Precious coral fisheries of Hawai'i and the U.S. Pacific Islands. *Mar Fish Rev* 55:50–60
- Grigg RW (2001) Black coral: history of a sustainable fishery in Hawai'i. *Pac Sci* 55:291–299
- Grigg RW (2003) Invasion of a deep coral bed by an alien species, *Carijoa riisei*, off Maui, Hawai'i. *Coral Reefs* 22:121–122
- Grigg RW (2004) Harvesting impacts and invasion by an alien species decrease estimates on black coral yield off Maui, Hawai'i. *Pac Sci* 1:1–6
- Grigg RW (2010) The precious corals fishery management plan of the Western Pacific Regional Fishery Management Council. *Pac Isl Fish Monogr* 1:1–9
- Grigg RW, Grossman EE, Earle SA, Gittings SR, Lott D, McDonough J (2002) Drowned reefs and antecedent karst topography, Au'au Channel, S.E. Hawaiian Islands. *Coral Reefs* 21:73–82
- Harrison PL (2011) Sexual reproduction of scleractinian corals. In: Dubinsky Z, Stambler N (eds) *Coral reefs: an ecosystem in transition*. Springer, Dordrecht, Heidelberg, London, New York, pp 59–85
- Harrison PL, Jamieson BG (1999) Cnidaria and Ctenophora. In: Adiyodi KG, Adiyodi RG (eds) *Reproductive biology of invertebrates, vol IX., Part A: Progress in male gamete ultrastructure and phylogeny* Wiley-Interscience, Chichester, pp 21–95
- Harrison PL, Wallace CC (1990) Reproduction, dispersal and recruitment of scleractinian corals. In: Dubinsky Z (ed) *Ecosystems of the world 25: coral reefs*. Elsevier, Amsterdam, Oxford, New York, Tokyo, pp 133–207
- Huang M-H, Ou C-H (2010) Precious coral fisheries management in Taiwan - Past, present & future. *Mar Policy* 34:1002–1009
- Hyman LH (1940) Order Antipatharia, the black or thorny corals. In: *The invertebrates: Protozoa through Ctenophora*. McGraw-Hill Book Company, New York and London, pp 625–628
- Kahng SE, Grigg RW (2005) Impact of an alien octocoral, *Carijoa riisei*, on black corals in Hawai'i. *Coral Reefs* 24:556–562
- Kahng SE, Kelley CD (2007) Vertical zonation of megabenthic taxa on a deep photosynthetic reef (50–140 m) in the Au'au Channel, Hawai'i. *Coral Reefs* 26:679–687
- Kahng SE, Benayahu Y, Wagner D, Rothe N (2008) Sexual reproduction in the invasive octocoral *Carijoa riisei* in Hawai'i. *Bull Mar Sci* 82:1–17
- Kenyon J (1984) Black coral off Cozumel. *Sea Front* 30:267–272
- Levitan DR (1991) Influence of body size and population density on fertilization success and reproductive output in a free-spawning invertebrate. *Biol Bull* 181:371–378
- Levitan DR, Sewell MA, Chia FS (1991) Kinetics of fertilization in the sea urchin *Strongylocentrotus franciscanus*: interaction of gamete dilution, age and contact time. *Biol Bull* 181:371–378
- Levitan DR, Sewell MA, Chia FS (1992) How distribution and abundance influence fertilization success in the sea urchin *Strongylocentrotus franciscanus*. *Ecology* 73:248–254
- Maldonado A (2003) Cuba's environment: today and tomorrow - an action plan. *Papers and Proceedings of the Thirteenth Annual Meeting of the Association for the Study of the Cuban Economy* 13:63–73
- McClintock JB, Watts SA (1990) The effects of photoperiod on gametogenesis in the tropical sea urchin *Eucidaris tribuloides* (Lamarck) (Echinodermata: Echinoidea). *J Exp Mar Biol Ecol* 139:175–184
- Miller K (1996) Piecing together the reproductive habits of New Zealand's endemic black corals. *Water Atmos* 4:18–19
- Miller K, Grange KR (1995) Population genetic studies of antipatharian black corals from Doubtful and Nancy Sounds, Fiordland, New Zealand. *Proceedings of the 6th International Conference on Coelenterate Biology*:353–363
- Molodtsova TN (2006) New species of *Hexopathes* Kinoshita, 1910 (Anthozoa, Antipatharia, Cladopathidae) from the South-West Pacific. *Zoosystema* 28:597–606
- Molodtsova TN, Pasternak FA (2005) Redescription of *Parantipathes euantha* (Pasternak, 1958) (Anthozoa: Antipatharia) from Kurile-Kamchatka Trench. *Invertebr Zool* 2:169–179
- Moon HW, Song JI (2008) Taxonomy of the black coral family Myriopathidae (Anthozoa: Antipatharia) from Korea. *Korean J Syst Zool* 24:251–263
- Noome C, Kristensen I (1976) Necessity of conservation of slow growing organisms like black coral. *CCA Ecology Conference Bonaire* 11:76–77
- Oishi FG (1990) Black coral harvesting and marketing activities in Hawai'i - 1990. Division of Aquatic Resources, State of Hawai'i
- Oliver JK, Babcock RC (1992) Aspects of the fertilization ecology of broadcast spawning corals: sperm dilution effects and in situ measurements of fertilization. *Biol Bull* 183:409–417
- Olsen DA, Wood RS (1980) Investigations on black coral in Salt River Submarine Canyon St. Croix, U.S. Virgin Islands. Final scientific report 80-12. Division of Fish and Wildlife U.S. Virgin Islands NULS-I Mission 79-5 and 80-12
- Opresko DM (1972) Redescriptions and reevaluations of the antipatharians described by L.F. de Pourtales. *Bull Mar Sci* 22: 950–1017
- Opresko DM (2003) Revision of the Antipatharia (Cnidaria: Anthozoa). Part III. Cladopathidae. *Zool Meded (Leiden)* 77:495–536
- Opresko DM (2005) New genera and species of antipatharian corals (Cnidaria: Anthozoa) from the North Pacific. *Zool Meded (Leiden)* 79-2:129–165

- Opresko DM (2009) A new name for the Hawaiian antipatharian coral formerly known as *Antipathes dichotoma* (Cnidaria: Anthozoa: Antipatharia). *Pac Sci* 63: 277–291
- Opresko DM, Genin A (1990) A new species of antipatharian (Cnidaria: Anthozoa) from seamounts in the eastern North Pacific. *Bull Mar Sci* 46:301–310
- Padilla C, Lara M (2003) Banco Chinchorro: the last shelter for black coral in the Mexican Caribbean. *Bull Mar Sci* 73:197–202
- Parker NR, Mladenov PV, Grange KR (1997) Reproductive biology of the antipatharian black coral *Antipathes fiordensis* in Doubtful Sound, Fiordland, New Zealand. *Mar Biol* 130:11–22
- Parrish FA, Baco AR (2007) State of deep coral ecosystems: in the U.S. Pacific Islands region: Hawai'i and the U.S. Pacific territories. In: Lumsden SE, Hourigan TF, Bruckner AW, Dorr G (eds) The state of deep coral ecosystems in the United States. NOAA Technical Memorandum CRCP - 3, Silver Spring, MD, pp 159–194
- Pax F (1918) Die Antipatharien. *Zool Jahrb Abt Syst Ökol Geogr Tiere* 41:419–479
- Pax F (1932) Beitrag zur Kenntnis der japanischen Dörnchenkorallen. *Zool Jahrb Abt Syst Ökol Geogr Tiere* 63:407–450
- Pax F, Van-Praët M, Doumenc D (1987) Ordre des antipathaires. In: Doumenc D (ed) *Traité de zoologie - anatomie, systématique, biologie*. Vol 3(Fasc. 3). Cnidaires anthozoaires. Masson, Paris
- Pearse JS, Eernisse DJ (1982) Photoperiodic regulation of gametogenesis and gonadal growth in the sea star *Pisaster ochraceus*. *Mar Biol* 67:121–125
- Pennington JT (1985) The ecology of fertilization of echinoid eggs: the consequences of sperm dilution, adult aggregation, and synchronous spawning. *Biol Bull* 169:417–430
- Reed JK, Pomponi SA, Weaver D, Paull CK, Wright AE (2005) Deep-water sinkholes and bioherms of south Florida and the Pourtales Terrace - habitat and fauna. *Bull Mar Sci* 77:267–296
- Richmond RH, Hunter CL (1990) Reproduction and recruitment of corals: comparisons among the Caribbean, the Tropical Pacific, and the Red Sea. *Mar Ecol Prog Ser* 60:185–203
- Romero XM (1997) Ecuador's vanishing black corals. *Aquaticus: J Shedd Aquar* 26:21–25
- Roule L (1905) Description des Antipathaires et Cérianthaires recueillis par S.A.S. le Prince de Monaco dans L'Atlantique nord (1886–1902). Fascicule XXX. Imprimerie de Monaco, Monaco
- Sakai K (1998) Effect of colony size, polyp size, and budding mode on egg production in a colonial coral. *Biol Bull* 195:319–325
- Schmidt H (1972) Die Nesselkapseln der Anthozoen und ihre Bedeutung für die phylogenetische Systematik. *Helgol Wiss Meeresunters* 23:422–458
- Schmidt H, Zissler D (1979) Die Spermien der Anthozoen und ihre phylogenetische Bedeutung. *Zoologica (Stuttg)* 44:1–97
- Schultze L (1896) Beitrag zur Systematik der Antipatharien. *Abh Senckenb Natforsch Ges* 23:1–39
- Schultze LS (1903) Die Antipatharien der deutschen Tiefsee-Expedition 1898–1899. In: Chun C (ed) *Wissenschaftliche Ergebnisse der Deutschen Tiefsee-Expedition auf dem Dampfer "Valdivia" 1898–1899*. Verlag von Gustav Fischer, Jena, Germany, pp 87–100
- Stimson JS (1978) Mode and timing of reproduction in some common hermatypic corals of Hawai'i and Enewetak. *Mar Biol* 48:173–184
- Szmant AM (1986) Reproductive ecology of Caribbean reef corals. *Coral Reefs* 5:43–54
- Torres JL, Armstrong RA, Weil E (2008) Enhanced ultraviolet radiation can terminate sexual reproduction in the broadcasting coral species *Acropora cervicornis* Lamarck. *J Exp Mar Biol Ecol* 358:39–45
- Tsounis G, Rossi S, Grigg RW, Santangelo G, Bramanti L, Gili JM (2010) The exploitation and conservation of precious corals. *Oceanogr Mar Biol Annu Rev* 48:161–212
- Van Pesch AJ (1914) The antipatharians of the Siboga Expedition. *Siboga-Expeditie*, 17. E.J. Brill, Leyden
- Van Woesik R, Lacharaise F, Köksal S (2006) Annual cycles of solar insolation predict spawning times of Caribbean corals. *Ecol Lett* 9:390–398
- Vermeij MJA, Sampayo E, Broecker K, Bak RPM (2004) The reproductive biology of closely related coral species: gametogenesis in *Madracis* from the southern Caribbean. *Coral Reefs* 23:206–214
- Von Koch G (1878) Zur Phylogenie der Antipatharia. *Morphol Jahrb* 4:74–86
- Wagner D, Brugler MR, Opresko DM, France SC, Montgomery AD, Toonen RJ (2010) Using morphometrics, in situ observations and genetic characters to distinguish among commercially valuable Hawaiian black coral species; a redescription of *Antipathes grandis* Verrill, 1928 (Antipatharia : Antipathidae). *Invertebr Syst* 24:271–290
- Wagner D, Waller RG, Toonen RJ (2011a) Sexual reproduction of Hawaiian black corals, with a review of reproduction of antipatharians (Cnidaria: Anthozoa: Hexacorallia). *Invertebr Biol* 130:211–225
- Wagner D, Papastamatiou YP, Kosaki RK, Gleason KA, McFall GB, Boland RC, Pyle RL, Toonen RJ (2011b) New records of commercially valuable black corals (Cnidaria: Antipatharia) from the Northwestern Hawaiian Islands at mesophotic depths. *Pac Sci* 65:249–255
- Wallace CC (1985) Reproduction, recruitment and fragmentation in nine sympatric species of the coral genus *Acropora*. *Mar Biol* 88:217–233
- Waller RG, Baco AR (2007) Reproductive morphology of three species of deep-water precious corals from the Hawaiian Archipelago: *Gerardia* sp., *Corallium secundum*, and *Corallium lauense*. *Bull Mar Sci* 81:533–542
- Waller RG, Tyler PA, Gage JD (2005) Sexual reproduction in three hermaphroditic deep-sea *Caryophyllia* species (Anthozoa: Scleractinia) from the NE Atlantic Ocean. *Coral Reefs* 24:594–602
- Walton WH (1948) Feret's statistical diameter as a measure of particle size. *Nature* 162:329–330
- Ward S (1995) The effect of damage on the growth, reproduction and storage of lipids in the scleractinian coral *Pocillopora damicornis* (Linnaeus) *J Exp Mar Biol Ecol* 187:193–206
- Ward S, Harrison P, Hoegh-Guldberg O (2000) Coral bleaching reduces reproduction of scleractinian corals and increases susceptibility to future stress. *Proc 9th Int Coral Reef Symp* 2:1123–1128
- WPRFMC (2006) 2006 black coral science and management workshop report. Western Pacific Regional Fishery Management Council, Honolulu, HI
- Zakai D, Levy O, Chadwick-Furman NE (2000) Experimental fragmentation reduces sexual reproductive output by the reef-building coral *Pocillopora damicornis*. *Coral Reefs* 19:185–188