# SECOND RECORDED EPISODE OF MASS CORAL BLEACHING IN THE NORTHWESTERN HAWAIIAN ISLANDS

BY

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## ABSTRACT

Mass coral bleaching involves multiple species over large areas. A second known episode of mass bleaching was documented in the Northwestern Hawaiian Islands (NWHI) during September/October 2004. Bleaching was observed in 10 species of the three dominant genera (*Porites, Pocillopora, Montipora*). Spatial and taxonomic patterns of bleaching in 2004 bore many similarities to a 2002 bleaching event, the first ever recorded from this region. The incidence of bleaching was higher at the three northern atolls (Pearl and Hermes, Midway, Kure) than at Lisianski and reefs farther south in the NWHI. At these northern atolls, the incidence of bleaching was higher in shallow backreef and patch reef habitats than on the deeper forereef. In both years, the combined influence of depth and the relative abundance/differential susceptibility of coral taxa underlay the salient spatial patterns of bleaching. In both years, the backreef habitat at Pearl and Hermes Atoll experienced the highest levels of bleaching. *Montipora*, among the genera most susceptible to bleaching, experienced extensive mortality and algal overgrowth in backreef habitats at the three northern atolls following the 2002 event. *In situ* subsurface temperature recorders, which registered water temperatures at 22 shallow backreef and lagoon sites, indicate corals experienced temperatures exceeding local bleaching thresholds for substantially longer periods of time in 2004 than in 2003, when only low levels of bleaching were observed. The occurrence of two episodes of mass bleaching over a period of three calendar years lends credence to predictions that the frequency of bleaching events will increase.

## INTRODUCTION

The prevalence of mass coral bleaching events, in which multiple coral species are affected over large areas, has increased worldwide during the past 25 years (Hoegh-Guldberg, 1999; Wilkinson, 2002). These large-scale events are associated with heightened sea-surface temperatures (SSTs), which in turn have been linked to climate change driven by increased atmospheric concentrations of greenhouse gases (Wellington et al., 2001; Hughes et al., 2003; Bellwood et al., 2004; Jokiel and Brown, 2004). The aftermath of bleaching can range from nearly complete recovery of affected corals (Jokiel

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and Brown, 2004) to widespread mortality (Aronson et al., 2002), algal overgrowth (McClanahan et al., 2001), and phase shifts (Ostrander et al., 2000).

Despite predictions that reefs in the central Pacific would be among the last in the world to bleach (Hoegh-Guldberg, 1999; Turgeon et al., 2002), reefs throughout the Northwestern Hawaiian Islands (NWHI) experienced a mass coral bleaching event in late summer 2002 (Aeby et al., 2003; Kenyon et al., 2004; Kenyon et al., in press). This event, in which the three northern atolls (Pearl and Hermes, Midway, and Kure) were more severely affected than reefs farther south in the NWHI, was the first ever recorded from this remote area (reviewed in Kenyon et al., in press). At these northern atolls, shallow backreef and patch reef habitats were more severely affected than deeper forereefs; the spatial patterns of bleaching were related to the combined factors of depth and the relative abundance of the dominant coral genera (*Montipora, Pocillopora, Porites*) in different atoll habitats, coupled with their differential susceptibility to bleaching (Kenyon et al., 2004; Kenyon et al., in press). Bleaching coincided with a period of prolonged, elevated SST, detected by satellite remote sensing and *in situ* moorings, which was particularly intense at the three northern atolls (Hoeke et al., 2004).

Resurveys of backreef sites at Midway Atoll in December 2002 revealed that colonies of *Montipora capitata*, a dominant component of the northern backreef, were still bleached or were becoming overgrown with turf and macroalgae; in contrast, pocilloporids, which predominate along other backreef exposures, had experienced low mortality and were recovering normal pigmentation (Kenyon and Aeby, unpublished data). Surveys in July/August 2003 further revealed the decline through mortality and algal overgrowth of *Montipora capitata* and the comparatively high recovery of pocilloporids at Midway as well as other northern atoll sites (G. Aeby, personal communication). In preparing for 2004 survey activities, scientists were alerted to the probability of again encountering substantial bleaching by a bleaching warning issued by National Oceanic and Atmospheric Administration's (NOAA) Coral Reef Watch for Pearl and Hermes Atoll, as well as by reports from NOAA personnel engaged in marine debris removal activities at Pearl and Hermes Atoll of widespread bleaching along the southwest backreef (J. Asher, personal communication). This paper is focused on the spatial and taxonomic patterns of coral bleaching documented throughout much of the NWHI using quantitative surveys conducted in September/October 2004. We show that this episode, while of more moderate intensity than the 2002 event, was of sufficient magnitude and spatial extent to be considered the second mass bleaching event to affect this region within three years. This second documented episode of mass bleaching corresponded to another period of prolonged, elevated SSTs in shallow waters, which were registered using *in situ* temperature recorders during deployments that included the warmest months in both 2003 and 2004. In both 2002 and 2004, bleaching was most intense on the backreef at Pearl and Hermes Atoll, a finding that may warrant special research and management attention to this habitat as the NWHI move through a sanctuary designation process for possible inclusion in the U.S. National Marine Sanctuary system.

## METHODS AND MATERIALS

### Study Area

The NWHI consist of ten island/banks and atolls, as well as numerous deeper submerged banks. From southeast to northwest the shallow-water reefs include: Nihoa, Necker, French Frigate Shoals, Gardner Pinnacles, Maro Reef, Laysan, Lisianski, Pearl and Hermes, Midway, and Kure (Fig. 1). Nihoa and Necker are small basalt islands, each surrounded by a shallow (<50 m) shelf. French Frigate Shoals (FFS) is an open atoll with a small basaltic pinnacle in the interior. Gardner Pinnacles constitutes the last basaltic outcrop in the Hawaiian Archipelago, consisting of three small rocks on an extensive submerged bank. Maro Reef is a complex of shallow reticulated reefs with no associated island. Laysan and Lisianski are low carbonate islands that crest shallow, submerged banks. Northwest of these are three atolls: Pearl and Hermes, Midway, and Kure Atolls (NOAA, 2003). Surveys spanned a latitudinal/longitudinal range between 23°63' N latitude, 166°14' W longitude (French Frigate Shoals), and 28°45' N latitude, 178°38' W longitude (Kure Atoll).

### Benthic Surveys

In 2003, 73 sites were selected for long-term monitoring by a group of biologists experienced in surveys of fish, algae, corals, and other macro-invertebrates in the NWHI. These long-term monitoring sites were selected from a pool of 391 sites that had been surveyed during annual research cruises in 2000, 2001, and 2002. Criteria for selection of long-term monitoring sites included representation of a range of habitats and biological communities at each location and a high probability of accessibility to divers on annual research cruises under prevalent sea conditions. Belt-transect (25 m x 2 m) surveys were conducted at 66 of these 73 long-term monitoring sites (Table 1) between 16 September and 11 October 2004 according to the methods described by Maragos et al. (2004) for 2002 Rapid Ecological Assessments (REA). The species and size class of each coral colony whose center fell within 1 m of each side of the transect line were recorded as well as the number of bleached colonies of each species. A colony was tallied as "bleached" if more than half of its live tissue had lost an estimated 75% or more of its normal pigmentation (Cook et al., 1990; Bruno et al., 2001; Cumming et al., 2002). For species in which clonal propagation (e.g. *Porites compressa*) or fissioning (e.g. *Porites lobata*) is an important part of the life history pattern, consideration was given to tissue color, interfaces with neighboring conspecifics, and distance between conspecifics in determining the number of colonies. Either 50 $m^2$ or 100 $m^2$ was surveyed at each site. Identical protocols were used as during 2002 surveys (Kenyon et al., in press), with the exception that most corals were tallied at the genus level in 2002.

### Temperature Recorders

In order to monitor *in situ* temperature regimes at the major reef systems between French Frigate Shoals and Kure, inclusive, 12 subsurface temperature recorders (STRs)

(SBE 39; SeaBird Electronics, Inc.) were fastened to the benthos between 12 September and 3 December 2002. Between 15 July and 3 August 2003, these were retrieved and replaced with fresh STRs; nine more STRs were fastened to the benthos at additional sites, and one STR was attached to the cable of a moored buoy in the central lagoon at Kure Atoll (Table 2). Benthic STR deployments at the atoll locations targeted backreef and lagoon patch reef habitats, which had experienced the highest levels of bleaching in 2002. Depths of STR sites (n = 22) ranged from 0.5 to 10.4 m. Temperature ($^{o}$C) was electronically recorded at 15- or 30-minute intervals (17 and 5 STRs, respectively). Recorders deployed in 2003 were retrieved from 19 September to 9 October 2004, and replaced with fresh STRs.

## Data Analysis

Incidence of bleaching by site, habitat, or taxon was calculated as the percentage of colonies with bleached tissue. Non-parametric tests were used for statistical analyses in which data sets were not normally distributed or had unequal variances. Statistical analyses were conducted using SigmaStat® software. The Mann-Whitney rank sum test and one-way analysis of variance (ANOVA) were used to examine spatial and habitat differences in bleaching incidence; one-way ANOVA was used to examine differences among coral taxa in bleaching incidence; and the Bonferroni t-test was used for multiple group comparisons. The relationship between incidence of bleaching and depth at each location was examined using Pearson or Spearman rank correlation methods; at each site the percentage of colonies with bleached tissue was paired with that site's depth. In comparing the incidence of bleaching in 2002 and 2004, data for the three dominant genera (*Montipora, Pocillopora, Porites*) were pooled for each location and habitat within location, and the differences between years were examined with t-tests.

For each location, the maximum monthly climatological mean (MMM) temperature over the years 1985-2001 was calculated using a single 4-km pixel from the Pathfinder version 5.0 SST dataset that best overlapped each location. MMM + 1$^{o}$C is considered the bleaching threshold, above which thermal stress to corals accumulates (Strong et al., 1997; Skirving et al., 2004). Temperature records downloaded from each STR were inspected to determine, for 2003 and 2004, the date on which SST first exceeded the bleaching threshold, the maximum temperature, and the date of maximum temperature. As a comparative indicator of accumulated thermal stress (ATS), the number of temperature observations at each STR site that exceeded MMM + 1 was tallied and normalized by the number of data points per day to yield ATS in days.

A Spearman rank correlation coefficient was calculated to examine the relationship between ATS in the backreef habitat at the three northern atolls and incidence of bleaching; for each STR within close proximity ($\leq$ 2.5 km) of a backreef REA site, ATS was paired with the percentage of colonies bleached at the corresponding site.

## RESULTS

Belt-transect Surveys

Sixty-six surveys totaling 3,900 $m^2$ were conducted at French Frigate Shoals, Gardner Pinnacles, Maro Reef, Laysan, Lisianski, Pearl and Hermes Atoll, Midway Atoll, and Kure Atoll, ranging in depth from 0.6 to 15.5 m. Nihoa and Necker were not surveyed due to foul weather. A total of 9,499 colonies belonging to 25 species within ten genera (*Pocillopora, Acropora, Montipora, Porites, Leptastrea*, *Cyphastrea, Fungi, Cycloseris, Pavona*, *Psammacora*) were counted within the belt transects. Bleaching was not observed at any location in *Acropora* (n = 257), *Leptastrea* (n = 229), *Cyphastrea* (n = 448), *Fungia* (n = 130), *Cycloseris* (n = 3), *Pavona* (n = 180), or *Psammacora* (n = 176). Bleaching was observed in ten of the 25 species recorded (Table 3), belonging to three genera (*Montipora, Pocillopora, Porites*; Fig. 2).

A low level of bleaching (< 20% of colonies) was seen in pocilloporids in shallow patch reef habitats at French Frigate Shoals. No bleaching was seen at Gardner Pinnacles. *Montipora patula* was the most frequently affected species at Maro, Laysan, and Lisianski, with bleaching recorded in 68.8%, 35.5%, and 56.3% of the colonies, respectively. More than a quarter of the colonies of *Porites evermanni* and *Pocillopora damicornis* were bleached at both Maro and Lisianski, with lesser incidences in *Porites lobata*, *P. compressa*, *Pocillopora meandrina*, and *Montipora capitata* (Table 3).

There was a significant difference between the incidence of bleaching on the northern atoll reefs ($n_1$ = 32) and on reefs at Lisianski and farther south ($n_2$ = 34)(Mann-Whitney rank sum test, T = 1225.5, p = 0.050). At the three northern atolls, differences existed among the three habitats surveyed (forereef, backreef, patch reef) in the overall incidence of bleaching (one-way ANOVA, F = 8.332 p = 0.001), though only the backreef-forereef comparison was significant (Bonferroni t-test, t = 4.049, p = 0.001). On the backreef at Pearl and Hermes Atoll, more than half the colonies of *Montipora capitata*, *M. patula*, *M. turgescens*, and *Pocillopora meandrina* were bleached, while more than half the colonies of *Montipora capitata* and *M. turgescens* on the Midway backreef were bleached (Table 3). At Kure Atoll, *Montipora capitata* in the backreef habitat was again the most severely affected species (Table 3), although the incidence of bleaching (61.5% of colonies) at Kure was less than at Pearl and Hermes and at Midway Atolls (75.5% and 100%, respectively). There was a significant difference among the backreefs at the three northern atolls in the incidence of bleaching (one-way ANOVA, F = 15.098, p <0.001), with the severity of bleaching significantly greater at Pearl and Hermes Atoll than at Midway (Bonferroni t-test, t = 3.425, p = 0.017) or Kure Atolls (Bonferroni t-test, t = 5.308, p = 0.001).

Pocilloporids on patch reef sites at the three northern atolls also sustained moderate to high levels of bleaching. More than two-thirds of the pocilloporids recorded on patch reefs at Pearl & Hermes Atoll (*P. meandrina* and *P. damicornis*) were bleached, while more than a quarter of *P. meandrina* colonies were bleached at the Midway Atoll and Kure Atoll patch reef sites surveyed (Table 3). *Pocillopora ligulata*, recorded within belt transects only on patch reefs at Kure Atoll, also sustained moderately high levels of bleaching (40% of colonies, Table 3).

Within the range of locations most affected by bleaching (Maro to Kure Atoll, inclusive) differences existed among the three dominant genera (*Montipora, Pocillopora, Porites*) in their incidence of bleaching (one-way ANOVA, F = 4.65, p = 0.027), though only the *Montipora-Porites* comparison was significant (Bonferroni t-test, t = 3.050, p = 0.024). A significant correlation between depth and the percent of coral colonies that were bleached was found at Pearl and Hermes and at Midway Atolls, but the correlation was not significant at other locations where bleaching was observed (Table 4).

Comparison to 2002 Bleaching Patterns

The incidence of bleaching at the three northern atolls is presented in Figure 3; however, the difference in bleaching incidence between the two events was not statistically significant (t-test, t = 1.777, p = 0.095). The difference in bleaching incidence between 2004 and 2002 at Maro, Laysan, and Lisianski also was not statistically significant ($|t|$ = 0.681, p = 0.570).

Temperature Records

The maximum monthly climatological mean (MMM) temperature at the eight reef systems between French Frigate Shoals and Kure ranges from 26.9 to 27.5°C (Table 5). Of the 12 STRs deployed in 2002, only one (Lisianski) registered temperatures above the bleaching threshold (MMM + 1°C) before being retrieved and replaced with a fresh STR in late July 2003. Because of the shallow depth of this STR, the high accumulated thermal stress (ATS) relative to other sites, and the low ATS registered prior to its replacement (1.6 of the total 21.3 days), it is assumed that sites where STRs were initially deployed in 2003 did not experience temperatures exceeding their bleaching threshold until after their STRs were deployed, i.e., the values calculated for these sites in 2003 accurately reflect rather than underestimate the ATS. Most STRs first registered temperatures above the bleaching threshold several days to several weeks earlier in 2004 than in 2003. All 22 STRs registered maximum temperatures in 2004 that exceeded those in 2003, with the exception of a brief, isolated spike registered at the southeast corner of Laysan in 2003 (Table 5). Differences in maximum temperature between years ranged from 0.1°C at a Kure backreef location to 1.6°C at a Midway backreef location. Except for Gardner Pinnacles, where the STR never registered temperatures exceeding this location's threshold in either year, all locations experienced higher ATS in 2004 than in 2003 (Table 5). ATS exceeding 30 days in 2004 was recorded at Lisianski, Pearl and Hermes Atoll, and Kure Atoll. The highest ATS in 2004 (49.1 days) was documented in the central lagoon at Pearl and Hermes Atoll (Table 3). There was a significant correlation ($r_s$ = 0.80, p = 0.006) between ATS and bleaching incidence in shallow (≤ 3 m) backreef habitats at the three northern atolls where STRs and REA sites were in close proximity (i.e., within 2.5 km of each other) (Table 6).

## DISCUSSION

Coral bleachings documented in the NWHI in late summer 2002 and 2004 shared numerous spatial and taxonomic features. In both years, the incidence of bleaching was greater at the three northern atolls (Pearl and Hermes, Midway, Kure) than at Lisianski and farther south (Kenyon et al., in press). Minimal or no bleaching was observed in either year at French Frigate Shoals and Gardner Pinnacles, respectively. At the three northern atolls, bleaching was most severe in shallow backreef and lagoon habitats. While studies from other regions have noted more severe bleaching in shallow than in deep habitats (Fisk and Done, 1985; Oliver, 1985), checkered patterns of statistical correlation between depth and the incidence of bleaching in 2002 (Kenyon et al., in press) and 2004 (Table 4) suggest that factors other than those associated with depth *per se* (e.g., thermal stratification, penetration of UV radiation) contributed to the observed spatial patterns in the NWHI. In both years, significant differences existed among the three dominant coral genera (*Montipora, Pocillopora, Porites*) in their incidences of bleaching, and the average incidence of coral bleaching experienced in different reef systems and habitats closely corresponded to the composition of the dominant coral fauna coupled with its susceptibility to bleaching (Kenyon et al., in press; Fig. 2). Hence, the combined influences of depth and the relative abundance/susceptibility of coral taxa underlie salient spatial patterns. The lack of statistically significant differences in bleaching incidence between the two years throughout the range of affected reefs (Maro to Kure, inclusive) supports the conclusion that bleaching in 2004 may be of sufficient spatial extent, intensity, and taxonomic diversity to be called a mass coral bleaching event.

In both years, colonies in the genus *Montipora* sustained the highest levels of bleaching (Kenyon et al., in press; Fig. 2). At Maro, Laysan, and Lisianski, *Montipora patula* consistently showed the highest incidence of bleaching, with almost 70% of colonies affected at Maro (Table 3). *Montipora capitata* and *M. turgescens*, which along with *M. flabellata* dominate many backreef locations at the three northern atolls, showed the greatest differential susceptibility to bleaching in both years, with up to 100% of the colonies bleached (Kenyon, unpublished data; Table 3). Preliminary quantification of coral mortality from the 2002 bleaching event, as assessed through analysis of photo quadrats (Preskitt, 2004) recorded along the same lines as those used for belt transects in 2002 and 2004, indicates reduction of live *Montipora* cover by as much as 30% at backreef sites at Midway and Pearl and Hermes Atolls (Vroom and Kenyon, unpublished data). Consequently, bleaching was not as visually dramatic in 2004 as in 2002, as there was less surviving coral remaining to bleach in 2004. The shallow (1-2 m) crest of a large central patch reef system at Kure Atoll, known previous to 2002 as "the coral gardens" due to its luxuriant growth of montiporids and pocilloporids, was heavily bleached in 2002 (77.0% of colonies, n = 177; Kenyon, unpublished data); in 2004, only a few branches of *Porites compressa* remained alive, and the dead coral skeletons were thickly covered in turf and macroalgae. Live coral cover was reduced from 58.2% in 2001 to 7.3% in 2004, with a corresponding increase in algal cover from 40.4% to 91.6% (Kenyon, unpublished data). A phase shift (Done, 1992) from a system dominated by coral to a system dominated by algae occurred on this shallow reef during this interval;

such a rapid shift from coral to algae has been considered a sign of reef degradation (Done, 1992; Hughes, 1994; McCook, 1999; Nyström et al., 2000; Bellwood et al., 2004), and has been documented in the aftermath of mass bleaching in other regions (Ostrander et al., 2000).

Skirving et al. (2004) show that accumulation of thermal stress to corals exceeding four Degree Heating Weeks (DHW, in which one DHW represents 1°C above the bleaching threshold for one week) is frequently accompanied by bleaching. In 2002, regional SST around the three northern atolls reached warmer temperatures than any observed in the last 20 years, for a time period that lasted longer than any previously observed warm-water events; at Kure Atoll, regional temperatures that exceeded the bleaching threshold persisted for four weeks (Hoeke et al., in review). In 2003, surveys were conducted in July/early August, before the time of maximum temperatures (Table 5), and low levels of bleaching (< 5% of colonies) were noted at most locations (G. Aeby, personal communication). Although the extent to which bleaching increased in response to continued warming in late summer 2003 is not known, the low number of cumulative days above the bleaching threshold in 2003 determined from *in situ* temperature recorders (Table 5) suggests that bleaching was neither widespread nor severe, with the possible exception of very shallow (< 1 m) reefs off Lisianski. In 2004, all locations experienced substantially greater ATS than in 2003. The greatest ATS in 2004 was recorded at Pearl and Hermes Atoll, which experienced the highest level of bleaching in backreef and patch reef habitats during both years' bleaching events (Fig. 3). In backreef habitats at the three northern atolls, the significant positive correlation between ATS and the incidence of bleaching at REA sites within close proximity of corresponding STRs (Table 6) further demonstrates the connection between bleaching and elevated water temperatures.

Barton and Casey (2005) provide evidence from analysis of three historical SST data sets that conditions for thermally induced large-scale bleaching may have existed in the NWHI during the late 1960s. They suggest, however, that bleaching actually did not occur and that some other coral stressor acting synergistically with elevated SSTs may have brought about the large-scale bleaching observed in this region in 2002. Jokiel and Brown (2004), using one of the same data sets (HadISST) as Barton and Casey (2005), also note the absence of bleaching reports in Hawaii despite hind-cast indications that thermally-induced bleaching should have occurred during 1968 and 1974. However, rather than invoke the advent of additional, synergistic stressors as possible triggers of mass coral bleaching in the Main Hawaiian Islands and NWHI, these authors suggest the use of caution in interpreting hind-casting results on coral bleaching events. Both sets of authors, however, show an SST warming trend in the Hawaiian Archipelago that is most pronounced at the northern end of the NWHI, and other investigators (Brainard et al., 2004) have noted that maximum SSTs in the Hawaiian Archipelago are generally found at the three northern atolls. Further accounts of earlier bleaching events are documented by Kenyon et al. (in press). While contemporary methods of investigation have not provided conclusive evidence as to whether mass coral bleaching events occurred in the NWHI before 2002, the occurrence of two documented episodes of mass bleaching within a period of three calendar years lends credence to predictions of other authors that the frequency and severity of bleaching events is increasing both world-wide (Hoegh-Guldberg, 1999) and in the Hawaii region (Jokiel and Brown, 2004).

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Table 1. Position, transect depth, zone, and 2004 survey date of long-term monitoring sites in the Northwestern Hawaiian Islands. Position coordinates are given in decimal degree units. Sites are categorized by zone according to a benthic habitat classification scheme developed for the NWHI (NOAA, 2003): B = backreef, F = forereef, L = lagoon, LP = La Perouse Pinnacles, S = shelf. Within each location, sites are listed in chronological order of 2004 surveys. NS = not surveyed.

| Site # | Latitude (N) | Longitude (W) | Transect depth, m | Zone | Survey date, 2004 |
|---|---|---|---|---|---|
| **Necker** | | | | | |
| R6 | 23.5752 | 164.7058 | 13.7 | S | NS |
| 4 | 23.5740 | 164.7038 | 12.2 | S | NS |
| 2 | 23.5782 | 164.7064 | 12.2 | S | NS |
| **French Frigate Shoals** | | | | | |
| H6 | 23.8805 | 166.2737 | 11.3 | F | 9/16 |
| 21 | 23.8479 | 166.3264 | 10.7 | B | 9/16 |
| 23 | 23.8669 | 166.2418 | 1.5 | L | 9/16 |
| R46 | 23.7694 | 166.2612 | 6.1 | L (LP) | 9/17 |
| 32 | 23.8063 | 166.2309 | 8.4 | L | 9/17 |
| 33 | 23.8358 | 166.2660 | 7.6 | L | 9/17 |
| R30 | 23.8666 | 166.2145 | 1.5 | B | 9/18 |
| 30 | 23.8496 | 166.2973 | 5.8 | L | 9/18 |
| 34 | 23.6278 | 166.1358 | 10.7 | F | 9/19 |
| 12 | 23.6378 | 166.1800 | 10.7 | B | 9/19 |
| R29 | 23.6785 | 166.1464 | 6.9 | L | 9/19 |
| 22 | 23.8659 | 166.2554 | 2.7 | L | NS |
| **Gardner Pinnacles** | | | | | |
| R6 | 25.0006 | 168.0015 | 17.4 | S | 9/20 |
| R3 | 24.9969 | 167.9987 | 16.5 | S | 9/20 |
| R5 | 24.9984 | 168.0000 | 15.2 | S | 9/20 |
| **Maro Reef** | | | | | |
| R8 | 25.3342 | 170.5252 | 13.7 | S | 9/21 |
| R6 | 25.3406 | 170.5005 | 11.6 | S | 9/21 |
| R5 | 25.3684 | 170.5021 | 7.3 | S | 9/21 |
| R9 | 25.4713 | 170.6434 | 10.7 | S | 9/22 |
| R12 | 25.4615 | 170.6836 | 16.8 | S | 9/22 |
| R3 | 25.4192 | 170.6694 | 18.3 | S | 9/22 |
| 22 | 25.3782 | 170.5675 | 14.3 | S | 9/23 |
| 6 | 25.3982 | 170.5747 | 6.1 | S | 9/23 |
| 8 | 25.4171 | 170.5841 | 12.8 | S | 9/23 |
| **Laysan** | | | | | |
| R12 | 25.778 | 171.7471 | 12.2 | S | 9/24 |
| R9 | 25.754 | 171.7414 | 9.6 | S | 9/24 |
| R11 | 25.766 | 171.7442 | 9.8 | S | 9/24 |
| **Lisianski** | | | | | |
| R14 | 26.0781 | 173.9971 | 14.6 | S | 10/9 |
| 12 | 26.0658 | 174.0017 | 7.9 | S | 10/9 |
| R9 | 26.0396 | 174.0126 | 7.9 | S | 10/9 |
| 10 | 25.9409 | 173.9222 | 9.0 | S | 10/10 |
| R10 | 25.9445 | 173.9535 | 12.6 | S | 10/10 |
| R7 | 25.9538 | 173.9708 | 11.0 | S | 10/10 |
| 18 | 26.0042 | 173.9943 | 7.5 | S | 10/11 |
| 16 | 25.9869 | 173.9945 | 12.2 | S | 10/11 |
| 17 | 25.9707 | 173.9642 | 10.8 | S | 10/11 |

Table 1 (Con'td)

| Site # | Latitude (N) | Longitude (W) | Transect depth, m | Zone | Survey date, 2004 |
|---|---|---|---|---|---|
| **Pearl and Hermes Atoll** | | | | | |
| R26 | 27.7858 | 175.7803 | 12.2 | F | 9/26 |
| R32 | 27.8391 | 175.7528 | 2.0 | B | 9/26 |
| R31 | 27.8267 | 175.7922 | 10.4 | L | 9/26 |
| R39 | 27.9405 | 175.8616 | 13.6 | F | 9/27 |
| 26 | 27.9578 | 175.8024 | 2.4 | B | 9/27 |
| 24 | 27.9198 | 175.8617 | 8.8 | L | 9/27 |
| 33 | 27.7857 | 175.8238 | 12.2 | F | 9/28 |
| 22 | 27.7954 | 175.8666 | 1.8 | B | 9/28 |
| 30 | 27.7794 | 175.8953 | 2.7 | B | 9/28 |
| R42 | 27.7534 | 175.9488 | 13.7 | F | 9/29 |
| 31 | 27.7759 | 175.9733 | 2.4 | B | 9/29 |
| 32 | 27.7729 | 175.9392 | 5.5 | L | 9/29 |
| R44 | 27.9109 | 175.9047 | 13.4 | F | 9/30 |
| R22 | 27.8993 | 175.9148 | 4.1 | B | 9/30 |
| 23 | 27.8811 | 175.9328 | 7.6 | L | NS |
| **Midway Atoll** | | | | | |
| R15 | 28.2374 | 177.3951 | 2.1 | L | 10/1 |
| 1 | 28.2693 | 177.3862 | 0.9 | B | 10/1 |
| H21 | 28.2774 | 177.3661 | 1.1 | B | 10/1 |
| H10 | 28.2140 | 177.4259 | 13.0 | F | 10/2 |
| R25 | 28.1938 | 177.4021 | 2.1 | B | 10/2 |
| R20 | 28.2319 | 177.3184 | 1.1 | B | 10/3 |
| R3 | 28.1906 | 177.3999 | 13.3 | F | 10/4 |
| R7 | 28.1965 | 177.3752 | 14.5 | F | 10/4 |
| 2 | 28.1976 | 177.3462 | 12.3 | F | 10/4 |
| 3 | 28.2180 | 177.3439 | 7.6 | L | NS |
| H11 | 28.2178 | 177.4033 | 7.6 | L | NS |
| **Kure Atoll** | | | | | |
| R33 | 28.4167 | 178.3786 | 14.3 | F | 10/5 |
| 2 | 28.4535 | 178.3443 | 12.2 | F | 10/5 |
| R36 | 28.4204 | 178.3711 | 2.4 | B | 10/5 |
| 12 | 28.3826 | 178.3248 | 10.1 | F | 10/6 |
| 9 | 28.4058 | 178.3427 | 4.9 | L | 10/6 |
| R35 | 28.3931 | 178.3495 | 4.1 | B | 10/6 |
| 18 | 28.4187 | 178.3450 | 6.4 | L | 10/7 |
| 17 | 28.4321 | 178.3662 | 3.0 | B | 10/7 |
| 14 | 28.4537 | 178.3283 | 1.1 | B | 10/7 |

Table 2. Position of subsurface temperature recorders (STRs) in the Northwestern Hawaiian Islands. Position coordinates are given in decimal degree units. *STR initially deployed in 2002; STRs at other sites initially deployed in 2003.

| Location/habitat | Latitude (N) | Longitude (W) |
|---|---|---|
| **French Frigate Shoals** | | |
| Northeast backreef* | 23.8661 | 166.2197 |
| South backreef | 23.6448 | 166.1735 |
| La Perouse* | 23.7689 | 166.2614 |
| Central lagoon | 23.7382 | 166.1669 |
| **Gardner** | | |
| West central | 24.9988 | 167.9995 |
| **Maro** | | |
| South central* | 25.3842 | 170.5397 |
| South | 25.3670 | 170.5137 |
| **Laysan** | | |
| Northwest | 25.7795 | 171.7389 |
| Southeast | 25.7589 | 171.7294 |
| **Lisianski** | | |
| East of island* | 26.0634 | 173.9610 |
| **Pearl & Hermes** | | |
| Northwest backreef* | 27.9119 | 175.8943 |
| North backreef* | 27.9577 | 175.7808 |
| Southeast backreef | 27.8027 | 175.7793 |
| Southwest backreef* | 27.7747 | 175.9787 |
| Central lagoon | 27.8980 | 175.8313 |
| **Midway** | | |
| North backreef* | 28.2777 | 177.3679 |
| North backreef* | 28.2711 | 177.3860 |
| East backreef* | 28.2445 | 177.3234 |
| Southwest backreef | 28.1936 | 177.4018 |
| **Kure** | | |
| Northeast backreef* | 28.4474 | 178.3060 |
| West backreef* | 28.4293 | 178.3685 |
| Central lagoon | 28.4186 | 178.3446 |

Table 3. Frequency of bleaching in affected species throughout the NWHI, September/October 2004. n = number of colonies tallied within belt transects; % = percentage of colonies bleached; NT = not tallied.

| Species | FFS | | | | | | | | Gardner | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Forereef | | Backreef | | Patch reef | | La Perouse | | | |
| | n | % | n | % | n | % | n | % | # | % |
| *Montipora patula* | 14 | 0.0 | 4 | 0.0 | 11 | 0.0 | 19 | 0.0 | 0 | |
| *Montipora capitata* | 9 | 0.0 | 3 | 0.0 | 26 | NT | 0 | | 14 | 0.0 |
| *Montipora flabellata* | 3 | 0.0 | 0 | | 0 | | 3 | 0.0 | 0 | |
| *Montipora turgescens* | 0 | | 0 | | 0 | | 0 | | 0 | |
| *Porites evermanni* | 3 | 0.0 | 12 | 0.0 | 35 | 0.0 | 0 | | 0 | |
| *Porites compressa* | 5 | 0.0 | 8 | 0.0 | 80 | 0.0 | 0 | | 0 | |
| *Porites lobata* | 176 | 0.0 | 67 | 0.0 | 198 | 0.0 | 40 | 0.0 | 906 | |
| *Pocillopora damicornis* | 0 | | 13 | NT | 106 | 23.6 | 2 | 0.0 | 1 | 0.0 |
| *Pocillopora ligulata* | 13 | 0.0 | 7 | NT | 26 | 0.0 | 0 | | 0 | |
| *Pocillopora meandrina* | 49 | 0.0 | 4 | NT | 21 | 9.5 | 45 | 0.0 | 222 | 0.0 |

| Species | Maro | | Laysan | | Lisianski | |
|---|---|---|---|---|---|---|
| | n | % | n | % | n | % |
| *Montipora patula* | 93 | 68.8 | 20 | 35.5 | 190 | 56.3 |
| *Montipora capitata* | 193 | 6.2 | 38 | 13.2 | 205 | 2.4 |
| *Montipora flabellata* | 0 | | 0 | | 0 | |
| *Montipora turgescens* | 0 | | 0 | | 0 | |
| *Porites evermanni* | 32 | 35.2 | 10 | 0.0 | 154 | 52.6 |
| *Porites compressa* | 92 | 6.5 | 11 | 0.0 | 77 | 9.1 |
| *Porites lobata* | 227 | NT | 146 | NT | 91 | 23.1 |
| *Pocillopora damicornis* | 40 | 27.5 | 2 | 0.0 | 172 | 27.3 |
| *Pocillopora ligulata* | 2 | 0.0 | 1 | 0.0 | 3 | 0.0 |
| *Pocillopora meandrina* | 87 | 8.0 | 13 | 0.0 | 15 | 20.0 |

| Species | Pearl and Hermes Atoll | | | | | | Midway Atoll | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Forereef | | Backreef | | Patch reef | | Forereef | | Backreef | | Patch reef | |
| | n | % | n | % | n | % | n | % | n | % | n | % |
| *Montipora patula* | 1 | 0.0 | 1 | 100.0 | 0 | | | | 0 | | 0 | |
| *Montipora capitata* | 2 | 0.0 | 237 | 75.5 | 1 | 100.0 | 2 | 50.0 | 18 | 100.0 | 0 | |
| *Montipora flabellata* | 0 | | 81 | 1.2 | 0 | | 0 | | 68 | 7.4 | 0 | |
| *Montipora turgescens* | 0 | | 31 | 83.9 | 0 | | 0 | | 15 | 66.7 | 0 | |
| *Porites evermanni* | 2 | 0.0 | 1 | 0.0 | 0 | | | | 3 | 33.3 | 0 | |
| *Porites compressa* | 3 | 0.0 | 1 | 0.0 | 96 | 9.4 | | | 0 | | 0 | |
| *Porites lobata* | 540 | 0.0 | 91 | 1.1 | 0 | | 456 | 0.0 | 52 | 1.9 | 25 | 0.0 |
| *Pocillopora damicornis* | 5 | 0.0 | 98 | 43.9 | 6 | 66.7 | | | 16 | 18.8 | 33 | 9.1 |
| *Pocillopora ligulata* | 0 | | 0 | | 0 | | 0 | | 0 | | 0 | |
| *Pocillopora meandrina* | 145 | 4.1 | 279 | 60.2 | 123 | 74.8 | 73 | 0.0 | 9 | 11.1 | 16 | 31.3 |

| Species | Kure Atoll | | | | | |
|---|---|---|---|---|---|---|
| | Forereef | | Backreef | | Patch reef | |
| | n | % | n | % | n | % |
| *Montipora patula* | 0 | | 0 | | 0 | |
| *Montipora capitata* | 0 | | 91 | 61.5 | 0 | |
| *Montipora flabellata* | 0 | | 73 | 1.4 | 0 | |
| *Montipora turgescens* | 0 | | 7 | 0.0 | 0 | |
| *Porites evermanni* | 0 | | 0 | | 0 | |
| *Porites compressa* | 0 | | 0 | | 24 | 0.0 |
| *Porites lobata* | 169 | 0.0 | 18 | 0.0 | 0 | |
| *Pocillopora damicornis* | 2 | 0.0 | 80 | 3.7 | 7 | 6.7 |
| *Pocillopora ligulata* | 0 | | 2 | 0.0 | 5 | 40.0 |
| *Pocillopora meandrina* | 253 | 4.1 | 258 | 6.2 | 35 | 42.9 |

Table 4. Correlation between depth and incidence of bleaching. FFS = French Frigate Shoals; P & H = Pearl and Hermes Atoll; NB = no bleaching observed

| Location | # sites | r | p |
|---|---|---|---|
| FFS | 11 | -0.10 | 0.76 |
| Gardner | 3 | NB | - |
| Maro | 8 | 0.42 | 0.30 |
| Laysan | 3 | -0.41 | 0.74 |
| Lisianski | 9 | -0.44 | 0.24 |
| P&H | 14 | -0.68 | 0.01 |
| Midway | 9 | -0.88 | 0.00 |
| Kure | 9 | -0.40 | 0.24 |

Table 5. Summary of data extracted or calculated from subsurface temperature recorder (STR) data. *STR initially deployed in 2002; STRs at other sites initially deployed in 2003. ATS = accumulated thermal stress. See Methods for details.

| | | | 2003 | | | | 2004 | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| **Location/habitat** | **Depth, m** | **MMM** | **First date >MMM+1** | **Max. temp. °C** | **Date of max. temp.** | **ATS (days)** | **First date >MMM+1** | **Max. temp. °C** | **Date of max. temp.** | **ATS (days)** |
| **French Frigate Shoals** | | 27.2 | | | | | | | | |
| Northeast backreef* | 2.1 | | 7/29 | 28.6 | 9/27 | 1.1 | 7/10 | 29.3 | 8/21 | 6.0 |
| South backreef | 2.1 | | 9/13 | 28.6 | 9/21 | 0.8 | 7/26 | 28.7 | 9/3 | 2.7 |
| La Perouse* | 4.0 | | 9/20 | 28.2 | 9/20 | 0.0 | 8/16 | 28.6 | 8/18 | 2.0 |
| Central lagoon | 2.1 | | 7/29 | 28.6 | 9/20 | 3.0 | 7/10 | 29.5 | 9/5 | 13.5 |
| **Gardner** | | 26.9 | | | | | | | | |
| West central | 10.4 | | -- | 27.4 | 9/21 | 0 | -- | 27.9 | 8/22 | 0 |
| **Maro** | | 27.3 | | | | | | | | |
| South central* | 1.5 | | 9/17 | 28.5 | 9/18 | 1.6 | 8/18 | 29.1 | 9/7 | 28.9 |
| South | 4.3 | | 9/17 | 28.4 | 9/22 | 0.8 | 8/20 | 28.9 | 9/7 | 25.0 |
| **Laysan** | | 27.1 | | | | | | | | |
| Northwest | 1.2 | | 8/5 | 29.0 | 9/21 | 12.8 | 8/6 | 29.4 | 8/21 | 21.2 |
| Southeast | 1.0 | | 8/6 | 30.2 | 9/14 | 5.3 | 8/18 | 29.0 | 9/21 | 16.2 |
| **Lisianski** | | 27.5 | | | | | | | | |
| East of island* | 0.6 | | 7/17 | 31.0 | 8/1 | 21.3 | 7/1 | 31.2 | 8/23 | 35.9 |
| **Pearl & Hermes** | | 26.9 | | | | | | | | |
| Northwest backreef* | 2.4 | | 8/6 | 28.4 | 8/10 | 2.5 | 7/28 | 29.5 | 9/3 | 37.8 |
| North backreef* | 0.5 | | 8/3 | 29.4 | 8/10 | 6.0 | 7/10 | 30.0 | 8/20 | 34.8 |
| Southeast backreef | 1.5 | | 8/1 | 28.0 | 8/10 | 0.1 | 8/12 | 28.9 | 9/2 | 28.3 |
| Southwest backreef* | 1.5 | | -- | 27.8 | 9/5 | 0 | 8/12 | 28.7 | 9/3 | 18.4 |
| Central lagoon | 2.0 | | 8/3 | 29.1 | 8/12 | 16.9 | 7/10 | 30.1 | 8/23 | 49.1 |
| **Midway** | | 27.0 | | | | | | | | |
| North backreef* | 0.9 | | 8/9 | 29.0 | 9/7 | 3.4 | 8/8 | 30.4 | 8/16 | 22.1 |
| North backreef* | 1.5 | | 8/3 | 29.1 | 8/15 | 2.9 | 7/13 | 30.6 | 8/17 | 24.6 |
| East backreef* | 0.9 | | 8/11 | 28.7 | 9/16 | 0.6 | 8/12 | 30.3 | 8/20 | 16.5 |
| Southwest backreef | 0.9 | | -- | 27.9 | 9/18 | 0 | 8/15 | 28.8 | 9/2 | 13.4 |
| **Kure** | | 26.9 | | | | | | | | |
| Northeast backreef* | 0.8 | | 8/3 | 28.4 | 8/31 | 1.5 | 7/30 | 29.5 | 8/19 | 7 |
| West backreef* | 0.6 | | 7/30 | 29.2 | 9/2 | 5.3 | 7/14 | 29.3 | 8/19 | 11.8 |
| Central lagoon | 1.2 | | 8/10 | 29.3 | 8/11 | 14.4 | 7/11 | 30.6 | 8/17 | 30.7 |

Table 6. Summary of accumulated thermal stress (ATS) calculated from subsurface temperature recorders (STRs) and bleaching incidence (% of colonies bleached) at REA sites within 2.5 km of STR, in backreef habitats at the three northern atolls, NWHI.

| STR location | Site #, closest REA site | Distance (km) between STR and REA site | STR depth, m | REA transect depth, m | ATS (days), 2004 | Bleaching incidence at REA site |
|---|---|---|---|---|---|---|
| **Pearl & Hermes** | | | | | | |
| Northwest backreef | R22 | 2.5 | 2.4 | 4.1 | 37.8 | 55.6 |
| North backreef | 26 | 2.0 | 0.5 | 2.4 | 34.8 | 45.7 |
| Southwest backreef | 31 | 0.5 | 1.5 | 2.4 | 18.4 | 56.2 |
| **Midway** | | | | | | |
| North backreef | 1 | 0.2 | 0.9 | 0.9 | 22.1 | 24.0 |
| North backreef | H21 | 0.2 | 1.5 | 1.1 | 24.6 | 35.1 |
| East backreef | R20 | 1.5 | 0.9 | 1.1 | 16.5 | 26.7 |
| Southwest backreef | R25 | 0.0 | 0.9 | 2.1 | 13.4 | 7.4 |
| **Kure** | | | | | | |
| Northeast backreef | 14 | 2.2 | 0.8 | 1.1 | 7 | 0.9 |
| West backreef | 17 | 0.3 | 0.6 | 3.0 | 11.8 | 6.5 |

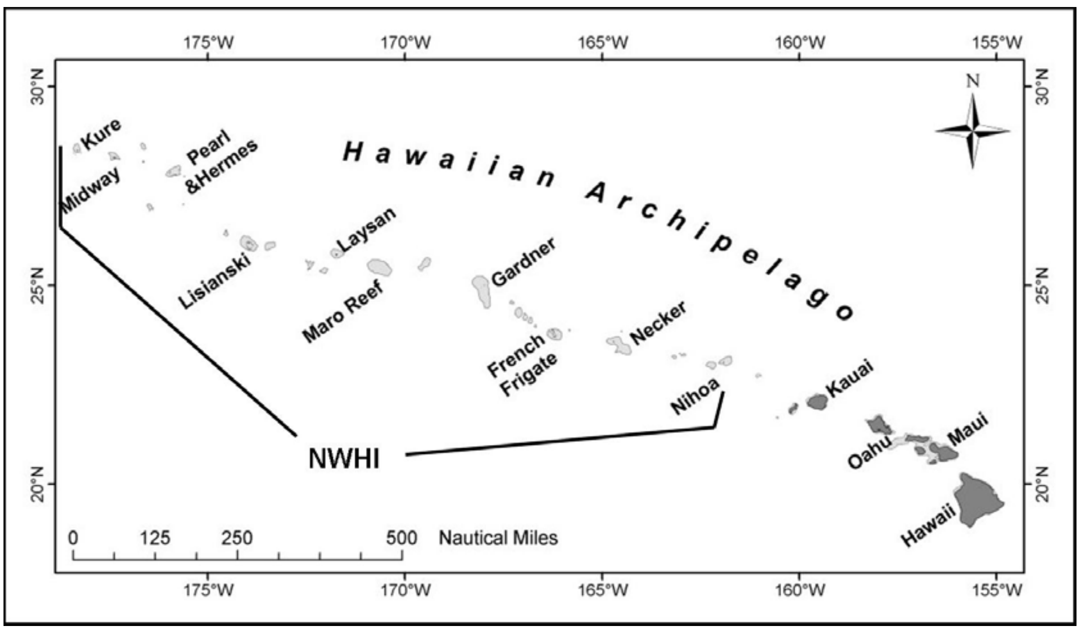


**Figure 1**. The Hawaiian Archipelago. Lightly shaded areas represent 100-fathom isobaths. The NWHI extend northwestward from Nihoa Island to Kure Atoll.

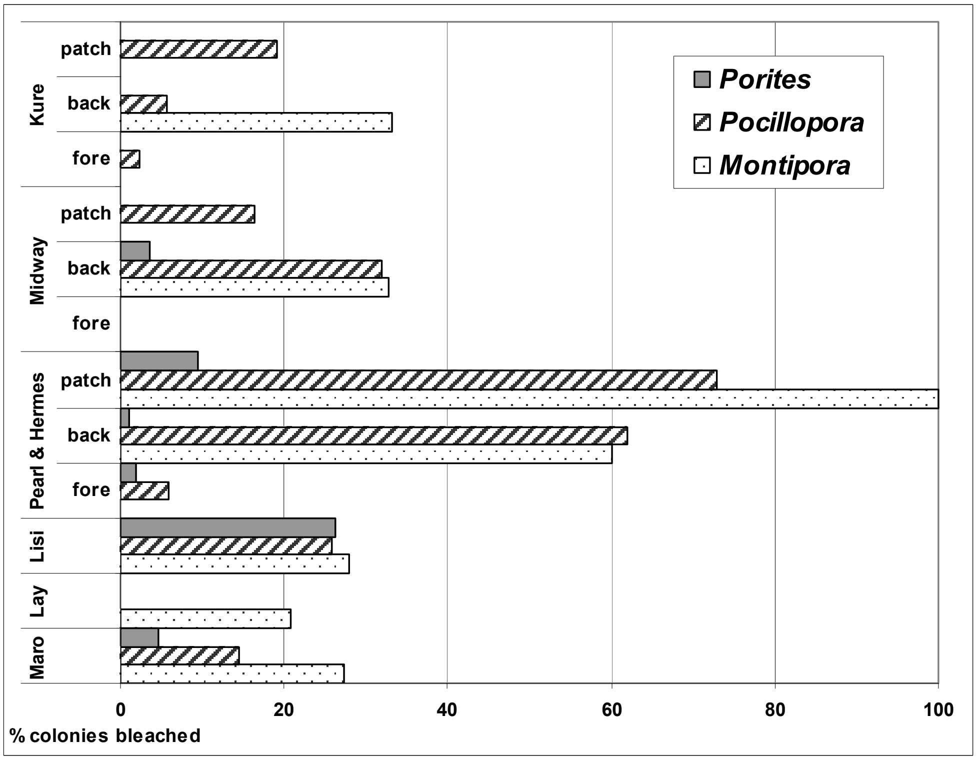


**Figure 2.** Incidence of bleaching within belt transects by location, habitat, and genus, September/October 2004. Lay = Laysan; Lisi = Lisianski. Gardner Pinnacles and French Frigate Shoals are not shown to reduce the complexity of the figure.

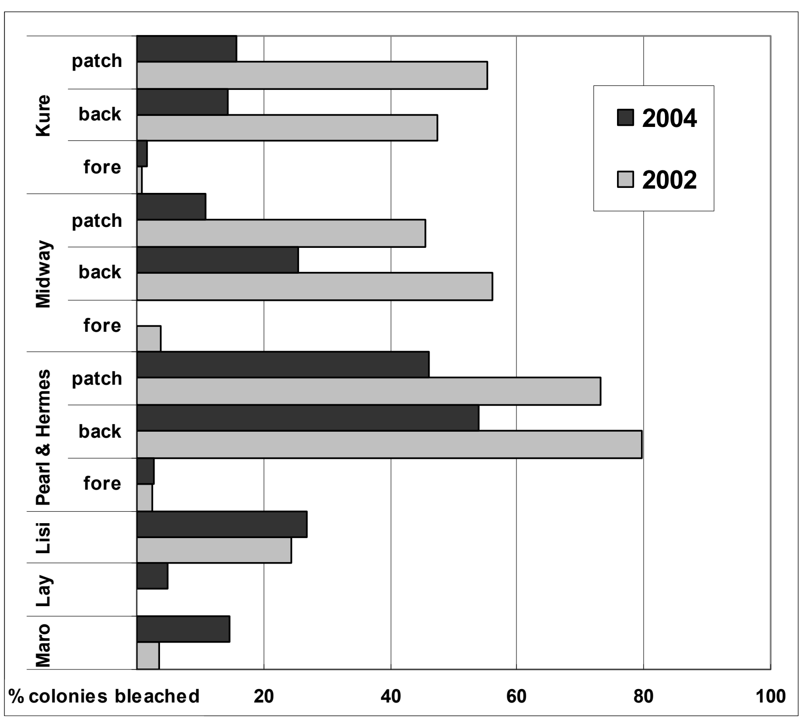


**Figure 3.** Incidence of bleaching in 2002 and 2004. Colony count data for the three dominant genera (Montipora, Pocillopora, Porites) are pooled for each location and habitat within location. Lay = Laysan; Lisi = Lisianski. Gardner Pinnacles and French Frigate Shoals are not shown to reduce the complexity of the figure.

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