

Mass coral bleaching on high-latitude reefs in the Hawaiian Archipelago

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Abstract The first mass coral bleaching ever recorded in the remote Northwestern Hawaiian Islands (NWHI), a chain of small islands, atolls, and banks that span ~1800 kilometers over more than five degrees of latitude in the northern part of the Hawaiian Archipelago, was documented in late summer 2002. Between 9 September and 5 October 2002, towed-diver surveys covering more than 195 km of benthic habitat and belt-transect surveys at 118 sites were conducted at 10 banks and atolls in the NWHI and included assessment of coral bleaching across latitude, depth, zone, and taxon. Incidence of bleaching was quantified as percent cover of coral that was bleached from analysis of towed-diver survey videotapes, and as the percentage of colonies with bleached tissue from colonies counted within belt transects. Both methods indicated that the incidence of bleaching was greatest at the three highest-latitude atolls in the Hawaiian Archipelago (Pearl and Hermes, Midway, and Kure), with lesser incidences of bleaching on reefs at Lisianski and farther south in the NWHI. At the three northern atolls, bleaching was most severe on the backreef, moderate in the lagoon, and low on the deeper forereef. The average incidence of coral bleaching experienced in different geomorphic systems and zones closely corresponds to the composition of the dominant coral fauna coupled with its susceptibility to bleaching. Sea surface temperature (SST) data suggest that prolonged, elevated SST is a likely explanation for the bleaching response.

Keywords Mass coral bleaching, Northwestern Hawaiian Islands, High-latitude reefs, Towed diver, Differential susceptibility

Introduction

Coral bleaching, the loss of symbiotic zooxanthellae or pigmentation in response to physical stress, was first described nearly a century ago (Vaughan 1914). In the decades since elevated seawater temperature was first

linked to coral bleaching (Yonge and Nichols 1931), field reports of bleaching events have expanded from those occurring at local scales (Goreau 1964, Egana and DiSalvo 1982) to those at geographic scales involving entire reef systems and geographic realms, a phenomenon known as "mass bleaching" (e.g. Glynn 1984, Goreau 1990, Williams and Williams 1990, Hoegh-Guldberg and Salvat 1995). Eight major periods of mass bleaching have been reported between 1979 and 2002, inclusive; there are no reports of mass bleaching events before 1979 (Hoegh-Guldberg 2000, Wellington et al. 2001). Coral bleaching in 1998 was the most geographically extensive and severe on record (Reaser et al. 2000, Wilkinson 2000), killing an estimated 16% of the world's corals (Hughes et al. 2003). Many of the affected reefs were widely regarded as among the most "pristine" in the world (Wilkinson 2000, Hughes et al. 2003). Many reefs across southwestern Pacific Islands that escaped the destructive 1998 event experienced mass bleaching in 2000 (Cumming et al. 2002), as did those around Easter Island (Wellington et al. 2001). Information compiled by ReefBase (www.reefbase.org) indicates that 2002 was the second worst year for globally widespread bleaching after the major events of 1998.

While diverse agents including the synergistic effect of ultraviolet (UV) radiation (Coles and Jokiel 1978) have been shown to induce bleaching (reviewed in Fitt et al. 2001), the most widely-reported proximate factor common to recent mass bleaching episodes is a temperature excursion of 1° to 2° C above the mean summer monthly maximum that persists for more than several consecutive weeks (e.g. Cook et al. 1990, Aronson et al. 2000, Bruno et al. 2001, Mumby et al. 2001, Cumming et al. 2002). Over the past decade, the perspective on the underlying drivers responsible for the accelerated pace and scale of mass bleaching has shifted from one in which explanations of global change (e.g. greenhouse warming) have not been convincing (Glynn 1993), to one in which the contribution of anthropogenic

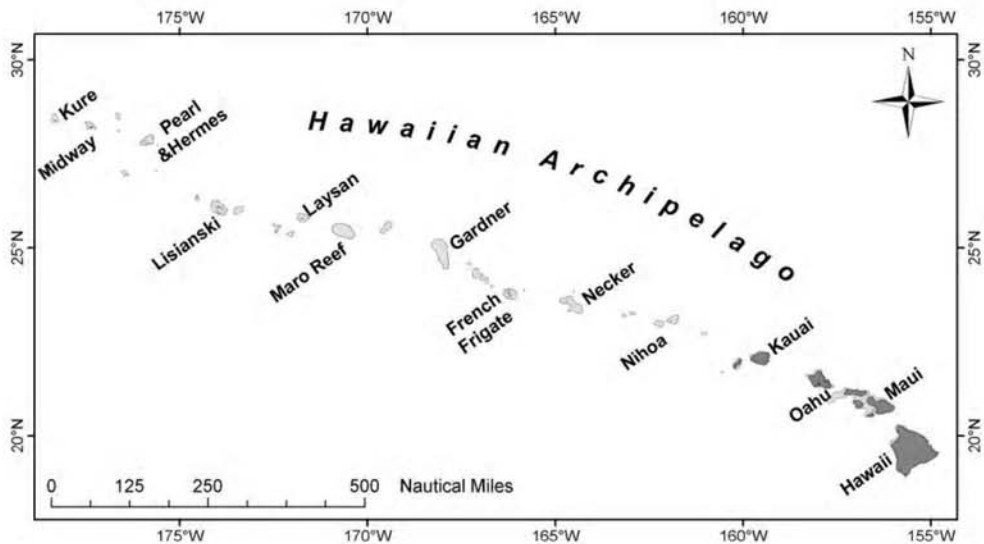


Fig. 1. The Hawaiian Archipelago. Lightly shaded areas represent 100-fathom isobaths.

global warming is probable (Aronson et al. 2000, Reaser et al. 2000), to one in which the link appears certain (Pockley 2000, Wellington et al. 2001, Hughes et al. 2003).

The Hawaiian Archipelago consists of the inhabited main Hawaiian Islands (MHI) and the more remote Northwestern Hawaiian Islands (NWHI), which span ~1800 kilometers across more than five degrees of latitude in the northern part of the Archipelago (Fig. 1). Hawaiian reefs were unaffected by 1998 mass bleaching events (Hoegh-Guldberg 1999, Reaser et al. 2000, Wilkinson 2002, Jokiel and Brown 2004). Reports of bleaching in the MHI before 1998 are limited to localized occurrences (Jokiel and Coles 1974, 1990) and a larger-scale event in several shallow bays in late summer 1996 (Jokiel and Brown 2004). In the NWHI, most coral reef research since the conclusion of early baseline surveys (1979-1983) (e.g. Grigg 1981, 1982) has revolved around endangered or commercially important species, with relatively few *in situ* observations of corals conducted by divers. Although the NWHI were historically exploited for consumptive and strategic purposes, their remoteness from population centers coupled with protection under federal and state legislation since 1909 has spared them from considerable modern anthropogenic disturbance. With an estimated 11,550 km² of shallow-water (<30 m) habitat, about 65% of the United States' coral reefs are located in the NWHI (Miller and Crosby 1998). Corals in three genera – *Porites*, *Pocillopora*, and *Montipora* – dominate most NWHI reefs (Maragos et al. 2004). The only previous observations of bleaching in the NWHI were made by Grigg and Dollar at Midway Atoll in very shallow water in the late 1970s and early 1980s (pers. comm.).

Based on comparing historical thermal bleaching thresholds to future trends in sea surface temperatures simulated by three models of global climate change, Hoegh-Guldberg (1999) predicted that the frequency of bleaching is set to rise rapidly, with the rate being slowest in the central Pacific. Other writers have speculated that Hawaiian reefs would be among the last to experience major bleaching events due to the Archipelago's subtropical and north-central location in regard to existing oceanic gyres and the broad expanse of deep water surrounding the islands (Turgeon et al. 2002).

The purpose of this paper is to present details of the first report of mass coral bleaching in the Northwestern Hawaiian Islands (Aeby et al. 2003) that was observed during late summer 2002 and is consistent with observations from other regions showing the phenomenon is related to elevated sea surface temperature (SST) (Hoeke et al. 2004). We assessed the bleaching event using belt transects at numerous sites and towed-diver surveys accompanied by digital video documentation over extensive areas. We quantified the incidence of coral that was bleached using both *in situ* colony counts and analysis of tow-survey videotapes to determine the spatial extent and taxonomic composition of bleaching across latitude, zone, and depth.

Materials and Methods

Study Area

The NWHI consists of ten island/banks and atolls, as well as numerous deeper submerged banks. From southeast to northwest the shallow-water reefs include: Niihau, 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 northernmost 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°03'N, 161°55'W (Nihoa), and 28°27'N, 178°19'W (Kure Atoll).

Benthic Surveys

Locations of towed-diver and belt-transect surveys were determined on the basis of (1) filling gaps in the locations of baseline assessments conducted during two expeditions to the NWHI in 2000 and 2001, (2) depths that allowed 3 dives/day/diver, (3) constraints imposed by other ship-supported operations, and (4) sea conditions. Locations of some towed-diver surveys in the present study were specifically directed to the shallow back reef zone to examine the extent of bleaching in this zone. No towed-diver surveys were conducted at Nihoa, Necker, or Gardner Pinnacles.

Towed-diver surveys (Hill and Wilkinson 2004, Kenyon et al. 2004) were conducted between 11 September and 4 October 2002. Habitat videotapes were quantitatively analyzed for coral percent cover (Kenyon et al. 2004), in which the categories that could be distinguished were *Pocillopora* Lamarck 1816, massive and encrusting *Porites* Link 1807, *Porites compressa* Dana 1846, *Montipora* Blainville 1830, and other coral (e.g. *Pavona* Lamarck 1801, *Acropora* Oken 1815, *Fungia* Lamarck 1801). For each category, bleached and unbleached percent cover were measured and tallied separately. Coral was considered to be bleached when its coloration was obviously pale or white in appearance (Cook et al. 1990, Bruno et al. 2001) relative to that recorded on videotaped surveys during the previous two years, during which bleaching was not observed. The depth of each sampled video still frame was determined using the closest matching time stamp on an SBE 39 recorder (Sea-Bird Electronics, Inc.) mounted on the habitat towboard, which recorded time, temperature, and depth at 5-second intervals.

Belt-transect (25 m x 2 m) surveys were independently conducted by two separate teams of divers between 9 September and 5 October 2002 according to the methods described by Maragos et al. (2004). The genus 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 colonies in each taxon with bleached tissue. For species in which clonal propagation (e.g. *Porites compressa*) or fissioning (e.g. *Porites lobata* Dana 1846) 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 m² or 100 m² was surveyed at each site.

Data Analysis

Towed-diver and belt-transect surveys at each of the 10 locations were spatially grouped according to the geomorphic system (atoll or bank) and zone (forereef, backreef, lagoon, channel, or shelf) in which they were conducted, based upon a benthic habitat classification scheme designed for the NWHI (NOAA 2003). For towed-diver surveys, incidence of bleaching was calculated for each sampled video frame that contained coral by dividing the percent cover of bleached coral by the total coral percent cover, and an average was calculated for each zone at each location. Similar calculations were conducted for each coral taxon that contributed >2% of the coral cover in each zone to determine its incidence of bleaching, a measure of relative susceptibility. Coral taxa contributing < 2% of the coral cover in each zone were excluded from this calculation as the rarity of their occurrence skews the meaningfulness of this result. For belt-transect surveys, the percentage of colonies with bleached tissue was used as the incidence of bleaching by site, zone, or taxon.

Neither percent cover data from towed-diver surveys nor bleaching incidence data from belt-transect surveys were normally distributed, even with transformations; consequently, non-parametric tests were used for all statistical analyses. Kruskal-Wallis one-way analysis of variance was used to test for main effects in spatial patterns of bleaching and differences among coral taxa in bleaching incidence, and Bonferroni correction was used to test for multiple group comparisons. The relationship between incidence of bleaching and depth at each location was examined using Spearman rank correlation methods. For towed-diver surveys, each sampled video frame that contained coral was matched with depth using the closest time stamp on the SBE 39 instrument. For belt-transect surveys, at each site the percentage of colonies with bleached tissue was paired with that site's depth.

Results

Towed-diver Surveys

More than 195 km of benthic habitat were surveyed during towed-diver surveys at FFS, Maro Reef, Laysan, Lisianski, Pearl and Hermes Atoll, Midway Atoll, and Kure Atoll, with average depths ranging from 1.4 to 18.2 m (Table 1). Average total coral cover is generally low throughout the 4.8 degrees of latitude spanned by the surveys, ranging from 3.3% (sd 2.6%) in atoll channels (9.23 km surveyed) to 17.3% (sd 10.2%) in lagoons (16.09 km surveyed).

The relative abundance of coral taxa varied by zone and, over latitudinal scales of several degrees, by

Table 1. Summary of towed-diver surveys conducted in the Northwestern Hawaiian Islands from 11 September to 04 October 2002. Percent cover data is generated from whole-image analysis of digital videotapes sampled at 30-sec intervals. For each coral taxon contributing >2% of the coral fauna, "average % cover that is bleached" represents a relative measure of susceptibility to bleaching. P&H = Pearl and Hermes Atoll; FFS = French Frigate Shoals; NS = not sampled. See Methods for details.

Zone	Atoll/Bank	Distance surveyed, km	Range of average depths, m	Average % coral cover	Average % coral bleached	average % of total coral fauna (average % cover that is bleached)				
						<i>Pocillopora</i>	Massive and encrusting <i>Porites</i>	<i>Porites compressa</i>	<i>Montipora</i>	Other coral
Backreef	Kure	12.26	1.8 - 3.2	10.2	64.1	31.0 (76.7)	12.1 (1.0)	0.8	56.0 (86.6)	0.1
	Midway	8.66	1.4 - 2.8	11.3	77.4	19.5 (89.9)	1.5	0.1	79.0 (80.7)	0.0
	P&H	35.22	1.5 - 5.0	10.2	66.1	26.4 (93.5)	25.3 (13.9)	5.9 (46.0)	40.7 (74.4)	1.7
	FFS	4.65	7.1 - 9.3	23.7	3.8	1.9	53.6 (0.3)	1.6	0.1	42.8 (0.1)
Forereef	Kure	10.56	12.3 - 17.5	6.7	14.4	33.1 (61.7)	66.3 (0.1)	0.0	0.0	0.6
	Midway	21.95	10.0 - 14.7	1.6	15.0	23.1 (63.7)	76.0 (8.5)	0.8	0.0	0.2
	P&H	4.88	5.6 - 6.0	5.9	75.4	56.4 (96.3)	16.8 (11.8)	0.4	4.5 (74.9)	21.9 (39.5)
	FFS	27.15	9.1 - 14.2	6.0	19.3	49.6 (32.4)	44.6 (1.4)	1.4	0.5	4.0 (36.7)
Lagoon	Kure	1.63	2.2	18.6	37.3	9.4 (96.1)	1.8	84.2 (4.2)	3.0 (100)	1.5
	Midway	0	NS	NS	NS	NS	NS	NS	NS	NS
	P&H	9.42	4.2 - 6.3	26.9	36.8	0.0	0.3	99.3 (31.4)	0.1	0.4
	FFS	5.04	3.5 - 13.4	6.6	4.2	5.6 (22.2)	67.7 (0.8)	25.6 (16.2)	0.1	1.0
Channel	Kure	0	NS	NS	NS	NS	NS	NS	NS	NS
	Midway	6.58	7.5 - 16.8	1.5	32.4	11.2 (88.6)	83.1 (17.9)	0.5	0.4	4.8 (37.7)
	P&H	2.65	10.4	5.2	73.1	68.4 (87.4)	19.3 (8.3)	0.2	10.4 (100)	1.8
Shelf, Inner (shallow)	Lisianski	7.86	3.4 - 6.3	16.1	39.5	0.4	6.9 (0.8)	6.1 (18.2)	86.6 (24.8)	0
Shelf, Outer (deeper)	Lisianski	13.09	11.6 - 15.1	22.3	22.8	1.2	42.7 (9.1)	31.3 (18.2)	24.8 (27.0)	0.5
	Laysan	7.31	10.6 - 18.2	5.4	13.2	13.1 (39.2)	79.0 (0.0)	6.9 (0.9)	1.0	0.1
	Maro	16.37	10.5 - 16.6	8.8	24.8	2.8 (57.8)	33.2 (2.2)	21.9 (12.7)	41.2 (14.4)	0.9

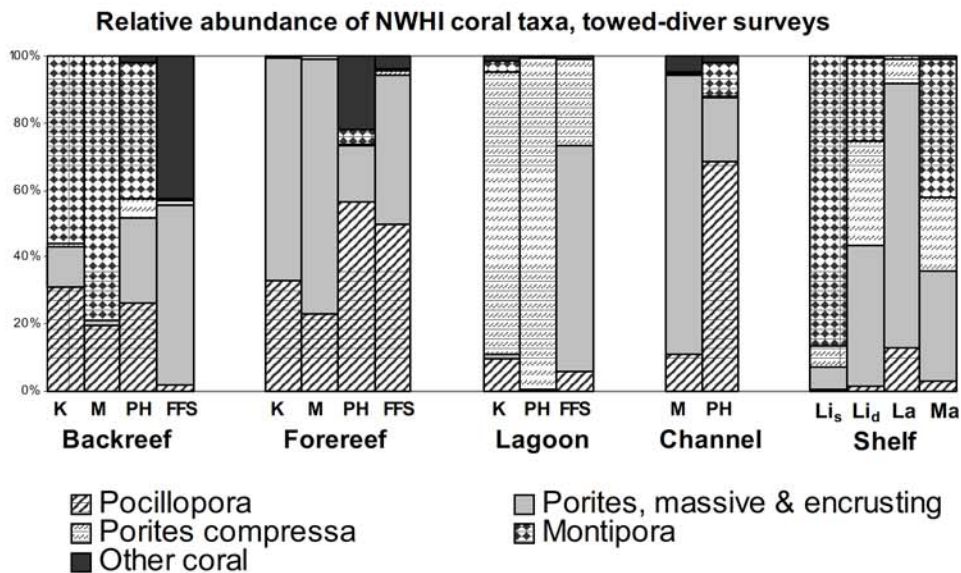


Fig. 2. Relative abundance of coral taxa on major reefs in the NWHI, based on analysis of videotapes recorded during towed-diver surveys in September/October 2002. Length of bar segment represents proportion of total coral percent cover at each zone/location. K = Kure; M = Midway; PH = Pearl and Hermes; FFS = French Frigate Shoals; Li_s = Lisianski, shallow (< 6.3 m); Li_d = Lisianski, deep (>11.6 m); La = Laysan; Ma = Maro Reef

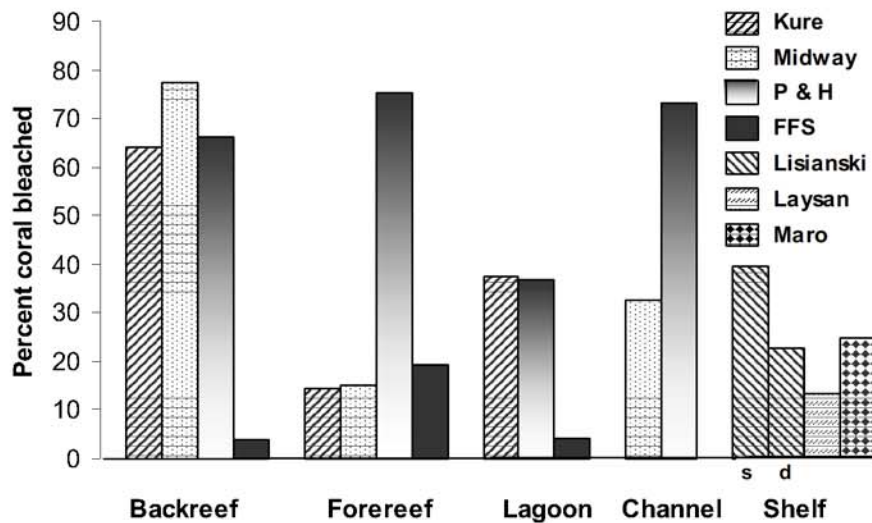


Fig. 3. Incidence of coral bleaching in the NWHI, derived from analysis of videotapes recorded during towed-diver surveys. s = shallow (< 6.3 m), d = deep (>11.6 m); see Table 1 for range of depths.

latitude within zones (Table 1, Fig. 2). In atoll geomorphic systems, backreef zones at the three highest-latitude atolls (Kure, Midway, Pearl and Hermes) were dominated by montiporids and to a lesser extent pocilloporids, whereas at French Frigate Shoals the backreef was dominated by massive and encrusting *Porites* (e.g. *P. lobata*, *P. evermanni* Vaughan 1907) and other coral (predominantly *Acropora*). At all four atolls the forereef zone was co-dominated by pocilloporids and by massive and encrusting *Porites*. In the lagoon zone, branching *Porites compressa* dominated the coral fauna at Kure and at Pearl and Hermes, whereas massive and encrusting *Porites* along with *Porites compressa* co-dominated the lagoon zone at French Frigate Shoals. Sparsely covered channel areas at Midway and at Pearl and Hermes were largely populated by massive and encrusting *Porites* and by pocilloporids.

Bleaching was documented in all zones at all atolls and banks surveyed by towed divers in the NWHI (Table 1, Figs. 3,4). The greatest overall incidence of bleaching was observed at the three highest-latitude atolls in the Hawaiian Archipelago: Kure, Midway, and Pearl and Hermes. There was a significant difference between the incidence of bleaching (average percent coral bleached) on these northern atoll reefs and on reefs at Lisianski and farther south ($H = 13.47$, $df = 1$, $p = 0.000$). At these three atolls, the highest levels of bleaching (> 64%) were consistently found in the shallow (< 5 m) backreef zone, and the lowest levels of bleaching (~15%) were found in the deeper (10 – 17.5 m) forereef zone (Table 1, Fig. 3-4). The shallow forereef (~6 m) was sampled only at Pearl and Hermes Atoll, on which 75% of the total coral cover was bleached. Moderate levels of bleaching (~37%) occurred in the shallow (< 6.3 m) lagoon zone at

Kure and at Pearl and Hermes. Channel areas at Midway and at Pearl and Hermes ranging in depth from 7.5 to 16.8 m varied in their average incidence of bleaching from 32.4% to 73.1%, respectively. The difference in the incidence of bleaching among the four zones at the three northern atolls was significant ($H = 21.46$, $df = 3$, $p = 0.000$). At Midway and Kure Atoll, a significant negative correlation was found between depth and the incidence of bleaching, but the correlation was not significant at Pearl and Hermes Atoll. On the more southerly reefs, a significant negative correlation was also found between depth and the incidence of bleaching at Lisianski and Laysan, whereas a significant positive correlation was found at French Frigate Shoals; no significant relationship was found at Maro Reef (Table 2).

Table 2. Correlation between depth and incidence of bleaching, using percent cover or colony count data from towed-diver surveys and belt transects, respectively. FFS = French Frigate Shoals; P&H = Pearl and Hermes Atoll; NB = no bleaching observed

Atoll/Bank # frames	Towed-diver surveys		Belt transects		
	r_s	p	# sites	r_s	p
FFS	1244	0.09 0.00	19	NB	-
Maro	347	0.01 0.79	9	0.56	0.12
Laysan	184	-0.21 0.00	7	NB	-
Lisianski	666	-0.19 0.00	15	0.27	0.35
P&H	1713	-0.04 0.07	25	-0.72	0.00
Midway	1129	-0.50 0.00	20	-0.73	0.00
Kure	844	-0.38 0.00	15	-0.66	0.00

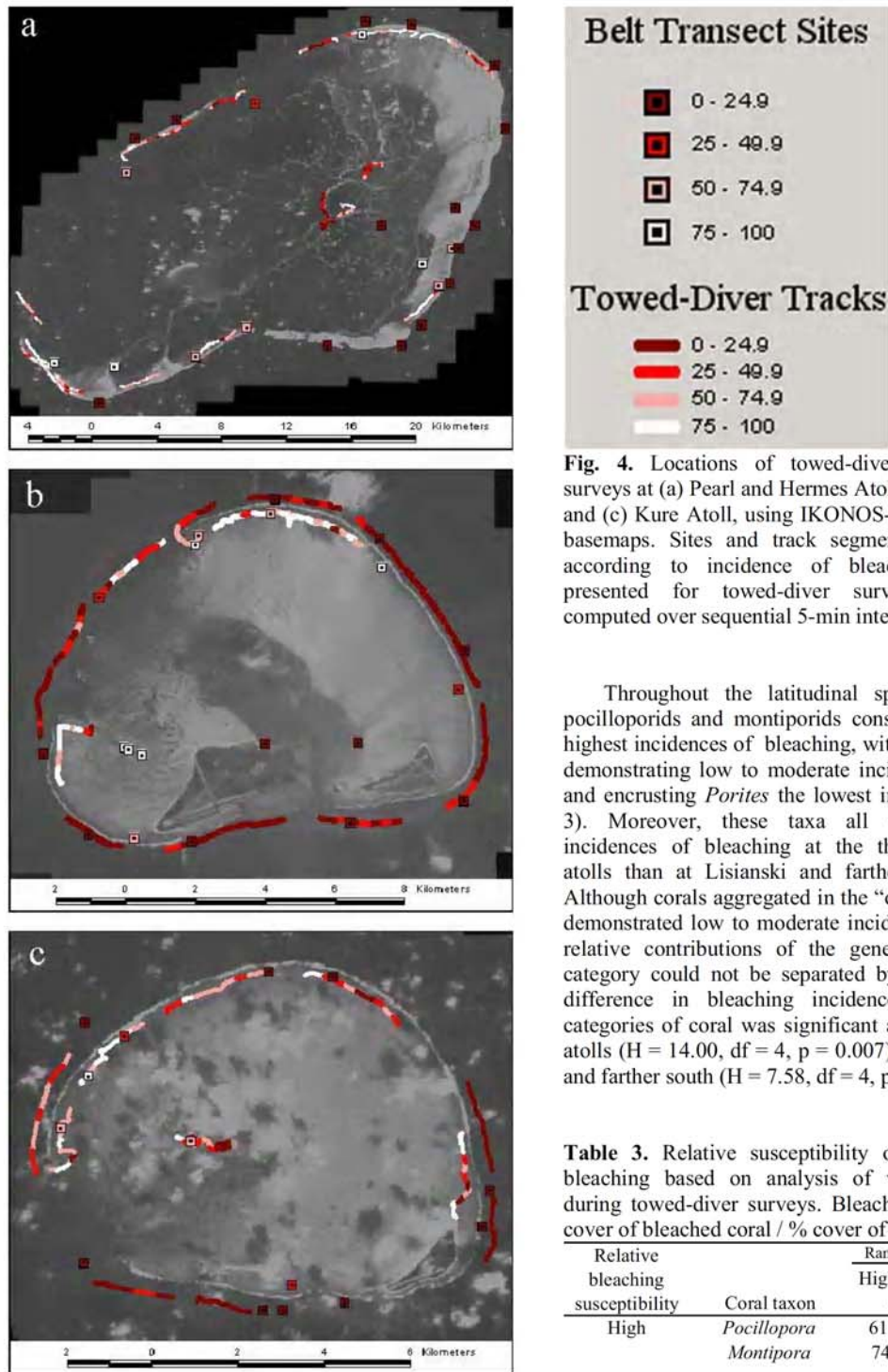


Fig. 4. Locations of towed-diver and belt-transect surveys at (a) Pearl and Hermes Atoll, (b) Midway Atoll, and (c) Kure Atoll, using IKONOS-acquired imagery as basemaps. Sites and track segments are color-coded according to incidence of bleached coral; values presented for towed-diver surveys are averages computed over sequential 5-min intervals.

Throughout the latitudinal span of the NWHI, pocilloporids and montiporids consistently showed the highest incidences of bleaching, with *Porites compressa* demonstrating low to moderate incidences and massive and encrusting *Porites* the lowest incidences (Tables 1, 3). Moreover, these taxa all experienced higher incidences of bleaching at the three highest-latitude atolls than at Lisianski and farther south (Table 3). Although corals aggregated in the “other coral” category demonstrated low to moderate incidences (Table 1), the relative contributions of the genera grouped in this category could not be separated by this analysis. The difference in bleaching incidence among the five categories of coral was significant at the three northern atolls ($H = 14.00$, $df = 4$, $p = 0.007$) but not at Lisianski and farther south ($H = 7.58$, $df = 4$, $p = 0.108$).

Table 3. Relative susceptibility of NWHI corals to bleaching based on analysis of videotapes recorded during towed-diver surveys. Bleaching incidence = (% cover of bleached coral / % cover of total coral) x 100

Relative bleaching susceptibility	Coral taxon	Range of bleaching incidence	
		High-latitude atolls	Lisianski and south
High	<i>Pocillopora</i>	61.7 - 96.3	22.2 - 57.8
	<i>Montipora</i>	74.4 - 100	14.4 - 27.0
Moderate	<i>Porites compressa</i>	4.2 - 46.0	0.9 - 18.2
Low	<i>Porites lobata</i>	0.1 - 17.9	0.0 - 9.1
	<i>Porites evermanni</i>		

Table 4. Correspondence between overall bleaching incidence (average percent coral bleached) and the susceptibility of dominant coral groups in each area surveyed by towed divers. P&H = Pearl and Hermes; FFS = French Frigate Shoals; *Porites* = massive and encrusting *Porites*; *P. compressa* = *Porites compressa*

Bleaching Incidence	Area	Dominant coral groups	Bleaching susceptibility
High (>64%)	Kure backreef	<i>Montipora/Pocillopora</i>	High/high
	Midway backreef	<i>Montipora/Pocillopora</i>	High/high
	P&H backreef	<i>Montipora/Pocillopora</i>	High/high
	P&H forereef	<i>Pocillopora/other coral</i>	High/moderate
	P&H channel	<i>Pocillopora</i>	High
Moderate (22% - 40%)	Kure lagoon	<i>P. compressa</i>	low
	P&H lagoon	<i>P. compressa</i>	moderate
	Midway channel	<i>Porites</i>	low
	Lisianski shelf, shallow	<i>Montipora</i>	moderate
	Lisianski shelf, deeper	<i>Porites/P. compressa/Montipora</i>	low/moderate/moderate
	Maro shelf	<i>Porites/P. compressa/Montipora</i>	low/low/low
Low (<20%)	Kure forereef	<i>Porites</i>	low
	Midway forereef	<i>Porites</i>	low
	FFS backreef	<i>Porites/other coral</i>	low/low
	FFS forereef	<i>Pocillopora/Porites</i>	moderate/low
	FFS lagoon	<i>Porites/P.compressa</i>	low/low
	Laysan shelf	<i>Porites</i>	low

Table 5. Summary of belt-transect surveys conducted in the Northwestern Hawaiian Islands from 09 September to 05 October 2002. N = # of colonies counted within belt transects. Number in parentheses is percentage of colonies with bleached tissue. P&H = Pearl and Hermes Atoll; FFS = French Frigate Shoals; OR = outside geographic range of distribution

Zone	Atoll/Bank	# sites	Area surveyed m ²	Depth range, m	# sites with bleached coral	N (% colonies with bleached tissue)					
						All taxa	<i>Pocillopora</i>	<i>Porites</i>	<i>Montipora</i>	<i>Cyphastrea / Leptastrea</i>	<i>Acropora</i>
Backreef											
	Kure	6	650	1.2 - 3.4	6	526 (48.4)	190 (67.4)	148 (0)	89 (83.2)	76 (0)	OR
	Midway	6	550	1.2 - 2.4	6	408 (56.1)	74 (83.8)	59 (0)	266 (61.3)	2 (0)	OR
	P&H	8	700	1.5 - 10.7	7	497 (73.0)	210 (95.2)	95 (17.9)	130 (100)	56 (28.6)	OR
	FFS	7	450	9.1 - 15.2	0	1775 (0)	243 (0)	1155 (0)	55 (0)	35 (0)	257 (0)
Forereef											
	Kure	7	500	8.8 - 20.4	2	1937 (1.0)	360 (5.3)	1552 (0)	2 (0)	19 (0)	OR
	Midway	8	550	12.5 - 16.5	6	1258 (3.7)	159 (29.6)	1065 (0)	2 (0)	9 (0)	OR
	P&H	13	850	11.3 - 20.4	9	2581 (1.9)	707 (6.1)	1358 (0.2)	34 (14.7)	295 (0)	OR
	FFS	5	500	11.9 - 13.1	0	1433 (0)	564 (0)	582 (0)	20 (0)	68 (0)	133 (0)
Lagoon											
	Kure	2	200	1.8 - 7.9	2	323 (55.1)	165 (93.9)	141 (5.0)	16 (100)	0	OR
	Midway	5	350	6.1 - 11.3	3	303 (38.9)	128 (92.2)	132 (0)	0	0	OR
	P&H	4	400	3.4 - 11.6	4	346 (66.8)	142 (92.3)	162 (55.6)	4 (100)	36 (16.7)	OR
	FFS	7	550	1.5 - 3.4	0	1371 (0)	309 (0)	768 (0)	53 (0)	151 (0)	30 (0)
Channel											
	Midway	1	50	9.4	1	67 (32.8)	12 (66.7)	26 (0)	8 (0)	21 (66.7)	OR
Shelf											
	Lisianski	15	1150	11.3 - 19.5	13	4002 (19.5)	188 (9.0)	1487 (14.1)	1371 (37.9)	360 (9.7)	OR
	Laysan	7	500	11.0 - 17.1	0	1090 (0)	122 (0)	784 (0)	114 (0)	54 (0)	0
	Maro	9	650	9.1 - 18.2	2	2221 (2.9)	202 (0)	1330 (3.3)	364 (5.8)	66 (0)	112 (0)
	Gardner	3	150	15.2 - 18.3	0	1099 (0)	55 (0)	990 (0)	9 (0)	22 (0)	1 (0)
	Necker	4	250	11.0 - 15.2	0	1017 (0)	226 (0)	736 (0)	50 (0)	5 (0)	0
	Nihoa	1	50	15.2	1	215 (7.9)	56 (30.4)	102 (0)	38 (0)	19 (0)	OR

The average incidence of overall coral bleaching experienced in different geomorphic systems and zones closely corresponded to the composition of the dominant coral fauna coupled with its susceptibility to bleaching (Table 4), which for each faunal category was lower at more southerly latitudes in the NWHI (Table 3).

Belt-transect Surveys

One hundred and eighteen belt-transect surveys totaling 9050 m² were conducted at Nihoa, Necker, French Frigate Shoals, Gardner Pinnacles, Maro Reef, Laysan, Lisianski, Pearl and Hermes Atoll, Midway Atoll, and Kure Atoll, ranging in depth from 1.2 to 20.4 m (Table 5). A total of 22,469 colonies belonging to nine genera (*Pocillopora*, *Acropora*, *Montipora*, *Porites*, *Leptastrea* Milne Edwards and Haime 1848, *Cyphastrea* Milne Edwards and Haime 1848, *Fungia*, *Pavona* Lamarck 1801, *Psammacora* Dana 1846) were counted within the belt transects. Bleaching was not observed at any location in *Acropora* (N = 533), *Pavona* (N = 652), or *Psammacora* (N = 111) and was recorded in <1% of fungiids (N = 470).

Bleaching was not seen at Necker, French Frigate Shoals, Gardner Pinnacles, or Laysan (Table 5). A low level of bleaching (7.9% of colonies) was observed at the single site surveyed at Nihoa. A low level (2.9% of colonies) of bleaching was detected at Maro Reef, where bleached colonies were recorded at only two of nine sites surveyed. Moderate levels of bleaching (19.5% of colonies) were found at Lisianski, where bleached colonies were recorded at 13 of 15 sites surveyed. The greatest incidence of bleaching was observed at the three highest-latitude atolls (Fig. 5). There was a significant difference between the incidence of bleaching on these northern atoll reefs and on reefs at Lisianski and farther south ($H = 8.55$, $df = 1$, $p = 0.004$). A significant correlation between depth and the percent of coral colonies that were bleached was found at Kure, Midway, and Pearl and Hermes Atolls, but the correlation was not significant at Lisianski and Maro Reef (Table 2).

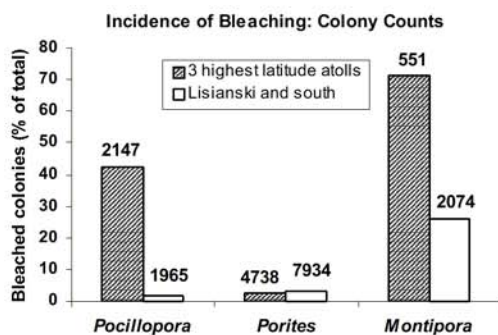


Fig. 5. Incidence of bleaching of predominant coral taxa surveyed within belt transects in the NWHI, 2002. Histograms represent the percent of colonies counted within belt transects that had bleached tissue. The total number of colonies counted is indicated.

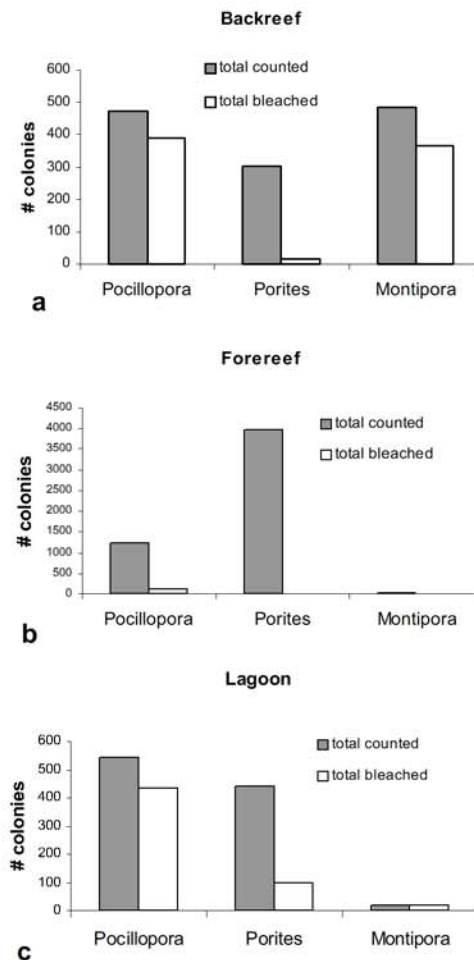


Fig. 6. Incidence of bleaching of predominant coral taxa surveyed within belt transects in the three primary zones of the three highest-latitude atolls (Kure, Midway, Pearl and Hermes) in the NWHI, 2002. Histograms represent number of colonies.

At the three northern atolls, significant differences existed among the three zones surveyed in the overall incidence of bleaching ($H = 36.69$, $df = 2$, $p = 0.000$); only the backreef-lagoon comparison was not significant. The backreef zone was largely populated by *Pocillopora* and *Montipora*, both of which had a high proportion of bleached colonies (Table 5, Fig. 6a). Deeper forereef environments were numerically dominated by *Porites*, in which bleaching was rarely noted, and to a lesser extent by *Pocillopora*, which was less impacted by bleaching than in other atoll zones (Table 5, Fig. 6b). Lagoon sites were co-dominated by pocilloporids, most of which were bleached, and *Porites*, of which 22% of colonies had bleached tissue (Table 5, Fig. 6c). Significant differences existed among these

three predominant genera in their incidence of bleaching ($H = 27.70$, $df = 2$, $p = 0.000$); only the *Pocillopora-Montipora* comparison was not significant.

Discussion

Although towed-diver and belt-transect surveys covered different spatial scales and used different parameters to quantify bleaching in the NWHI (percent cover vs. colony counts, respectively), the spatial patterns of bleaching and differential generic susceptibility revealed by the two methods were highly congruent. The results of both methods showed that the scope of bleaching was greater at the three highest-latitude atolls (Kure, Midway, and Pearl and Hermes) than at Lisianski and farther south, as evidenced by (1) the higher bleaching incidences calculated using tow-survey percent cover data (Tables 1, 3), (2) the greater proportion of colonies that had bleached tissue (Fig. 5), and (3) the absence of bleached colonies recorded at Laysan, Gardner Pinnacles, French Frigate Shoals, or Necker during belt-transect surveys (Table 5). The detection of low levels (< 20%) of bleaching by towed-diver surveys at Laysan and French Frigate Shoals was likely a result of the more extensive area covered by these surveys (Table 1). Both percent cover data and colony count data showed that at the three highest-latitude atolls, *Montipora* and *Pocillopora* were the genera most susceptible to bleaching, while *Porites* was significantly less affected (Table 3, Fig. 5). Both methods demonstrated that the backreef zone at the three northern atolls was dominated by the two genera that were most susceptible to bleaching (Tables 1, 5, Fig. 6a), accounting for the high levels of bleaching documented in this zone. Both methods revealed that the lagoon zone in the three northern atolls was dominated or co-dominated by the genus *Porites* (Tables 1, 5, Fig. 6c), whose members had low to moderate susceptibility to bleaching (Tables 3, 5, Fig. 6c), accounting for the more moderate levels of bleaching in this zone (Tables 4, 5). Both methods documented that the deeper (> 9.8 m) forereef in the northern atolls was dominated by *Porites* (Tables 1, 5, Fig. 6b). As *Porites compressa* was rarely found in the forereef zone (Table 1 and Kenyon, unpublished data), the low susceptibility of massive and encrusting *Porites* coupled with their dominance on the deeper forereef accounted for the low levels of bleaching quantified in this zone (Tables 4, 5, Fig. 4). The significant negative correlation between depth and the incidence of bleaching found at Kure Atoll, Midway Atoll, Pearl and Hermes Atoll, Lisianski, and Laysan using at least one of the two survey methods (Table 2) agreed with reports by some investigators in other regions of more severe bleaching in shallow than in deep habitats (e.g. Fisk and Done 1985, Oliver 1985). However, the disparate correlation statistics at Pearl and Hermes Atoll and Lisianski, the lack of significant correlation at Maro Reef, and the significant positive correlation at French Frigate Shoals (Table 2) suggested that factors other than those associated with depth *per se* contributed to observed spatial patterns. Both data sets

supported the conclusion that spatial variation in bleaching across zones could be largely attributed to the differential susceptibility of the coral fauna composing the assemblages, a linkage previously suggested to explain bleaching patterns around inshore islands of the Great Barrier Reef (Marshall and Baird 2000).

Anomalously high and prolonged sea surface temperatures (SST) across a large portion of the subtropical central Pacific accompanied the bleaching event (Hoeke et al. 2004), a causal linkage that has been widely associated with other mass bleaching events (e.g. Cook et al. 1990, Bruno et al. 2001, Skirving et al. 2004). Local SSTs within lagoon and backreef areas at the three northern atolls were further elevated over the already anomalously high regional SST (Hoeke et al. 2004). Divers' gauges generally registered water temperatures one degree Fahrenheit cooler on the forereef than inside the atoll at comparable depths over the several days spent at each of the three northern atolls. Wave-induced mixing and improved circulation along the more exposed reefs outside the atoll barriers may have contributed to the lower levels of bleaching in addition to the lower susceptibility of the dominant coral fauna and cooler water temperatures, as experiments have shown that coral colonies growing in high waterflow environments are more resistant to bleaching than colonies in low waterflow environments under the same SST and irradiance regimes (Nakamura and van Woesik 2001). This effect may be mediated through a higher rate of passive diffusion of destructive oxygen radicals and their derivatives caused by high SST and irradiance (Jones et al. 1998) or the higher concentration of UV-protective micosporine-like amino acids (MAAs) found in corals growing in high water motion environments irrespective of irradiance (Jokiel et al. 1997, Kuffner 2002). The reduced proportion of colonies that were bleached on the forereef relative to their congeners in other atoll zones (Fig. 6) may in part reflect this influence.

Differences among species in susceptibility to bleaching have been reported from numerous field and experimental studies throughout the Indo-Pacific. Pocilloporids are well documented in both laboratory studies (Edmondson 1928, Coles et al. 1976, Jokiel and Coles 1977, Hueerkamp et al. 2001) and field surveys throughout the Indo-Pacific (Jokiel and Coles 1974, Marshall and Baird 2000, Edwards et al. 2001, Jimenez et al. 2001, McClanahan et al. 2001, Mumby et al. 2001, Obura 2001, Turner et al. 2001, Wellington et al. 2001, Stimson et al. 2002, Jokiel and Brown 2004) to be highly susceptible to thermal stress and bleaching, a response that is congruent with the high levels of bleaching in pocilloporids documented in the present study (Table 3, Fig. 5). Relative to other coral faunas, thermal and bleaching susceptibility of several species of *Montipora* have been ranked as high (Edmondson 1928, Jokiel and Coles 1974, Coles et al. 1976, Jokiel and Coles 1977, Marshall and Baird 2000, Celliers and Schleyer 2002, Hughes et al. 2003, Jokiel and Brown 2004) or moderate (Obura 2001, Rajasuriya and Karunaratna 2001, Jokiel

and Brown 2004). In backreef zones in the three highest-latitude atolls in the NWHI where several prevalent species of *Montipora* co-occur (*M. capitata* Dana 1846, *M. turgescens* Bernard 1897, *M. flabellata* Studer 1901), bleaching was more widespread and severe in *M. capitata* than in its two congeners (Kenyon and Aeby, unpublished data). Massive species of *Porites* have consistently ranked as the most resistant to thermal stress and bleaching, with little to no mortality if they do bleach during field events (Edmondson 1928, Jokiel and Coles 1974, Coles et al. 1976, Gleason 1993, Hoegh-Guldberg and Salvat 1995, Marshall and Baird 2000, Edwards et al. 2001, Hueerkamp et al. 2001, Turner et al. 2001, Rajasuriya and Karunaratna 2001, Wellington et al. 2001, Stimson et al. 2002, Jokiel and Brown 2004), which agrees with both towed-diver and belt-transect survey results for massive and encrusting *Porites* (chiefly *P. lobata* and *P. evermanni*) in the present study. Despite their generally low susceptibility to bleaching, however, numerous massive, and presumably old, *Porites* colonies were found entirely bleached along the northwestern backreef at Pearl and Hermes Atoll, an unusual taxonomic response also reported by Mumby et al. (2001) at Rangiroa Atoll in French Polynesia. In studies where they co-occur, branching species of *Porites* have been relatively more affected than their massive congeners (McClanahan et al. 2001, Stimson et al. 2002). The endemic Hawaiian branching species *Porites compressa*, which could be analyzed separately from massive and encrusting *Porites* species in towed-diver survey videotapes because of its distinctive morphology, was more susceptible to bleaching than its congeners throughout the NWHI (Table 3). The low levels of bleaching in the faviid genera *Leptastrea* and *Cyphastrea* (Table 5), its absence in *Pavona* and *Psammacora*, and its negligible occurrence in *Fungia* within belt transects in the NWHI, agreed with observations of their resistance to thermal stress experimentally (Edmondson 1928, Coles et al. 1976, Jokiel and Coles 1977, Hueerkamp et al. 2001) and in field studies (Jokiel and Coles 1974, Marshall and Baird 2000, Stimson et al. 2002, Hughes et al. 2003, Jokiel and Brown 2004). Numerous field studies have indicated that acroporids are among the taxa most sensitive to bleaching (e.g. Gleason 1993, Hoegh-Guldberg and Salvat 1995, Marshall and Baird 2000, McClanahan et al. 2001, Mumby et al. 2001, Fisk and Birkeland 2002, Stimson et al. 2002, Hughes et al. 2003). In the NWHI, *Acropora* has a restricted distribution and has been found only between Necker and Laysan; it is most abundant at French Frigate Shoals and Maro Reef (Grigg 1981, Maragos et al. 2004). The absence of bleaching in *Acropora* when observed within its known range (Table 5) was a further indication of the lower incidence of bleaching on reefs at Lisianski and farther south in the NWHI. Inter- and intraspecific differences in bleaching susceptibility have been variously attributed to (1) architectural differences that influence tissue shading (Hoegh-Guldberg 1999), (2) acclimatization (bleaching history), because the thermal tolerance of corals can be

increased by pre-exposure to high sublethal temperatures (Coles and Jokiel 1978, Jokiel and Coles 1990), (3) presence and concentration of fluorescent pigments that can dissipate excess light energy through fluorescence and light scattering (Salih et al. 2000), and (4) dynamic communities of zooxanthellae symbionts that can respond selectively to thermal stress (Rowan et al. 1997, Baker 2001).

Recovery is dependent in part on few or no repeats of extreme bleaching events, with estimates of 10 to 50 years given as the time for many reefs affected by 1998 bleaching events to recover (Hughes 1994, Done 1999, Wilkinson 2000). Because the NWHI are relatively protected from anthropogenic pollution, recovery is unlikely to be impeded by pollutants such as heavy metals, oils, or pesticides, which can delay or halt recovery (Brown 2000). However, high levels of toxic contaminants including DDT, PCBs, arsenic, and nickel have been reported from sediments collected at several nearshore sites at Midway and Kure Atolls (Maragos and Gulko 2002, Turgeon et al. 2002). In the absence of additional bleaching episodes, other short-term (< 2 yr) responses to bleaching can include diminished reproductive capacity (e.g. Michalek-Wagner and Willis 2001, Omori et al. 2001) and reduced recruitment (e.g. Obura 2001, Turner et al. 2001), while longer-term community effects can include phase shifts (e.g. McClanahan et al. 2001, Ostrander et al. 2000), strategy shifts (e.g. Gleason 1993, Edwards et al. 2001), or local extinction of species (Glynn 1988). Despite the absence of observations of large-scale bleaching before 2002, a review of three historical SST data sets collected since 1871 suggested that conditions favorable for thermally induced coral bleaching may have existed in the NWHI prior to 1979 (Barton and Casey 2004). A previous mass bleaching event, or series of preceding events, would be expected to have influenced community patterns observed since the relatively recent advent of documented reef surveys in this remote region.

By comparing computer-simulated SSTs to thermal bleaching thresholds of corals from several regions globally, Hoegh-Guldberg (1999) suggested that bleaching events are likely to increase in frequency until they become annual by 2050 in most tropical oceans, including the central Pacific; at this frequency, corals would not recover from bleaching-related mortality, and a phase shift to algal-dominated communities was predicted. High-latitude reefs in the Hawaiian Archipelago may be particularly retarded in their pace of recovery from bleaching-induced mortality due to their relative genetic isolation from more central, interconnected populations (Hughes et al. 2003), the slow pace of coral growth at high-latitude Hawaiian atolls (Grigg 1982), and the potential weakening of coral skeleton accretions resulting from projected increases in atmospheric CO₂, particularly on high-latitude reefs (Kleypas et al. 1999). Moreover, Jokiel and Brown (2004) demonstrated a trend of increasing temperature in Hawaiian waters over the past several decades and predicted that, if the warming trend continued, bleaching

events would continue to occur in the Hawaiian region with increasing frequency and severity.

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