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The immediate effects of Hurricane Iniki on intertidal fauna on the south shore of O'ahu

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Abstract

When Hurricane Iniki struck the Hawaiian Islands in September 1992, it provided a rare opportunity to examine the immediate effects of a hurricane on two intertidal benthic communities off the reefs of O'ahu, Hawai'i. The Niu Beach site contained large, obvious aggregations of the tube building polychaete *Diopatra dexiognatha*, and the Wailupe Beach site was without obvious tubiculous fauna at the surface. Ten replicate sediment cores were taken before and after the hurricane with a 7.6 cm PVC corer and organisms were identified to family and enumerated. There were no substantial depletions or loss of taxa after the hurricane. Oligochaetes were the most dominant taxa pre-and post-hurricane. The abundance of all dominant polychaete families increased post-hurricane. The three most abundant polychaetes were capitellids and *D. dexiognatha* (Onuphidae) at Niu Beach and *Pygospio muscularis* (Spionidae) at Wailupe Beach. We suggest that *D. dexiognatha* and *P. muscularis* help stabilize the sediments since they both form dense tube mats while capitellids and oligochaetes are considered highly adaptive surface burrowers that can take advantage of newly disturbed sediments. Overall, there was no substantial effect observed on the intertidal fauna exposed to this severe disturbance. It is suggested here that invertebrate communities in this area are adapted to survive

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and thrive in high-energy environments and possibly benefit from dense aggregations of tube building polychaetes.
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1. Introduction

On the afternoon of 11 September 1992, the Hawaiian Islands were struck by Hurricane Iniki, which was, and still is, the most powerful and destructive hurricane to hit Hawai'i in recorded history. Iniki approached from the south and after continuing around the other Hawaiian Islands, accelerated and made landfall on the island of Kaua'i, bringing wind speeds of 224 kph with gusts up to 280 kph. Although not in the direct path of the storm, O'ahu suffered substantial damage from strong winds and heavy, destructive surf (NWS, 1993). Beach erosion along the west coast of O'ahu was substantial, lessening to the south (NWS, 1993). Underwater, the impact of strong waves and storm surge moved sand into rock gullies, and overturned or partially buried coral heads.

Few studies have examined the immediate effects of hurricanes on intertidal or offshore communities. Unless prior biomonitoring was in progress when the storms hit, only post-storm sample data is generally available; any effects of disturbance can only be suggested. Even in studies where pre- and post-storm data are available, the results have varied tremendously. Dobbs and Vozarik (1983) examined benthic and water column fauna from the coast of Connecticut after Storm David and concluded there was no pre- and post-density difference of benthic infauna, although there was a large post-storm increase in the abundance of water column individuals. Barnett (1981) observed little significant change in intertidal infauna abundance after a severe storm indicating there was no substantial effect of severe storm conditions in the Humber Estuary in Northern England. In contrast, Boesch, Diaz, and Virnstein (1976) found that following Tropical Storm Agnes, dramatic reductions in salinity and available oxygen severely reduced populations of community dominant species while stimulating irruptions in opportunistic species. Yeo and Risk (1979) reported catastrophic mortalities of the shallow-burrowing intertidal fauna of Minas Basin, Bay of Fundy due to high surface sediment scouring from Hurricane Beulah and another major storm. Posey, Lindberg, Alphin, and Vose (1996) reported a significant decrease of one-third of the infauna associated with an artificial reef located off the coast of Florida after a severe storm event. However, infaunal abundances before the storm were more similar to after the storm than from samples from the same time and site in the previous year, suggesting an effect less than background annual variability. One of the few studies that examined a tropical location was performed by Moran and Reaka-Kudla (1991) who studied coral reef cryptofauna in St. Croix before and after Hurricanes David and Frederic. Their results, which included many different taxa, showed that polychaete density significantly increased from pre-hurricane values, likely attributable to recruitment of burrowing and then nestling species.

Physical disturbance is an important factor in soft-bottom community structure of intertidal organisms and storms can provide an unpredictable source of mortality for benthic organisms (Posey et al., 1996). Severity and duration of disturbance can determine whether entire populations are destroyed or reduced in abundance. Substratum stability, influenced by substratum type and sediment grain size, plays a role in the response of a community to disturbance (Sousa, 1984). Another component of the substratum is dense aggregations of polychaete tubes. These aggregations act to stabilize the sediment surface, help mitigate the effects of wave surge and ripple formation, and provide some resistance to erosion (Bailey-Brock, 1979, 1984, 1987; Bolam, 1999; Bolam & Fernandes, 2003; Fager, 1964; Featherstone & Risk, 1977; Friedrichs, Graf, & Springer, 2000; Meadows & Hariri, 1991; Morgan, 1997; Sanders, Goudsmit, Mills, & Hampson, 1962; Woodin, 1981). However, other studies have reported destabilization of the sediments by varying densities of tube aggregations (Eckman, Nowell, & Jumars, 1981; Eckman, 1983; Luckenbach, 1986; Schmager-Noji, 1988). Given the mixed results of these findings there is an obvious critical population density that separates destabilizing effects from stabilizing effects and that still remains uncertain. Dense aggregations of tubes also provide stability for a more diverse and abundant invertebrate community (Bailey-Brock, 1979, 1984; Bolam & Fernandes, 2002, 2003; Callaway, 2003; Fager, 1964; Gallager, Jumars, & Trueblood, 1983; Luckenbach, 1986; Noji, 1994; Reise, 1983; Woodin, 1981; Zühlke, 2001).

This study investigates the immediate effects of extreme disturbance caused by hurricanes on intertidal fauna in the presence of dense aggregations of polychaete tubes and discusses the potential for sediment stabilization by high densities of tubes on an intertidal reef system.

2. Materials and methods

2.1. Study sites

This study was conducted at Kawainui Beach Park near Niu Valley and at Wailupe Beach Park located on the south shore of O'ahu, Hawai'i. These two shallow sites, designated as Niu Beach (N) and Wailupe Beach (W) (Fig. 1) were sampled for intertidal fauna. SAMc, JB-B and W. Estabrooks took pre-hurricane samples mid-morning on 11 September 1992, immediately before the hurricane passed by O'ahu and before major impact was observed. The same collectors then took post-hurricane samples several days later on 15 September 1992. Wind speeds in this area were estimated at 40–80 kph at the height of the storm and wave height reached up to 6.1 m with storm surges of 6–12 m (NWS, 1993). Approximately 2.5 cm of rainfall was recorded for the day of the storm, and no rain recorded on subsequent days.

The Niu Beach site is the most shoreward part of the reef flat adjacent to a narrow, sandy beach. The fringing reef extends 700 m from the shoreline as a shallow reef flat. This feature provides some shelter from the full force of breaking waves

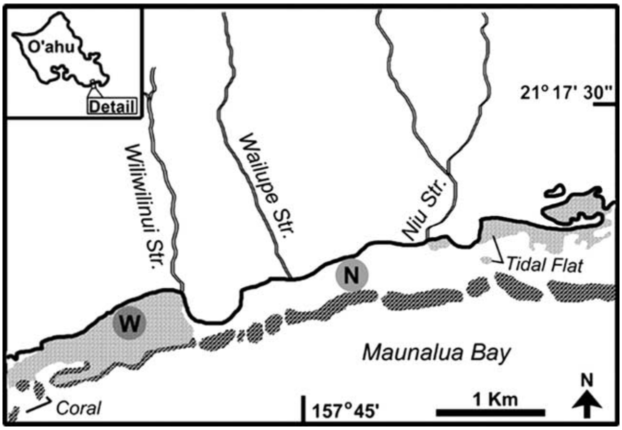

Fig. 1. Map of the SE shoreline and fringing reef of O'ahu showing study sites at Niu Beach (N) and Wailupe Beach (W) with inset of O'ahu.

along the beach. The shoreward part of the reef flat fronting the beach had extensive mounds of tubeworms, *Diopatra dexiognatha*, which provided a stable environment for other invertebrates and a diverse polychaete community (Bailey-Brock, 1984, Paxton & Bailey-Brock, 1986).

This gregarious tube-building polychaete, *D. dexiognatha*, had only been known from this location (Bailey-Brock, 1984; Paxton & Bailey-Brock, 1986), but has more recently been found at Kahala and Black Point as well (Bailey-Brock, personal observations). Densities of *D. dexiognatha* may reach 21,800/m^2. This high density leads to the formation of raised mounds of vertically oriented sand covered tubes and compacted sediment that slow water and sediment movement in front of the beach. Mounds are 15–20 cm in height, 3–5 m in width and 500 m in length (Bailey-Brock, 1984). Tubes can reach 7.5 cm long and project 1–2 cm above the surface sediment (Bailey-Brock, 1984). The vertical tubes have a buffering effect that helps reduce beach erosion and provide for sediment deposition among the tubes. After periods of heavy rain near shore salinity is reduced to 15–26 ppt at low tides due to groundwater seepage through the beach sand (Bailey-Brock, 1984). On one recent occasion the salinity at the beach park measured 1.1034 ‰ (Bailey-Brock, Brock, & Brock, 1999). Tides in Hawaiian waters are semidiurnal, from −10 cm below to +70 cm above chart datum. Mounds of *D. dexiognatha* are only typically exposed at low tides, below 0 to +6 cm, and even then mounds may be submerged by small waves generated by typical winds (Bailey-Brock, 1984).

The Wailupe Beach site is an area with muddy sediments next to a drainage channel and fronting the beach. Patches of *Pygospio muscularis* tubes forming dense mats dominate this area. These tubes are about 1 mm or less in diameter. Although they are not as large in diameter as the *D. dexiognatha* tubes, they may also serve to stabilize sediments due to high densities. The salinity at this site is reduced by the periodic freshwater input from the drainage channel and groundwater seepage. High tolerance of brackish conditions is reported for another species in the genus *Pygospio*

Table 1
Number of individuals of polychaete and non-polychaete taxa in Niu Beach samples

	Pre-hurricane values									Post-hurricane values									
Taxon	R1	R2	R3	R4	R5	R6	R7	R9	R10	R1	R2	R3	R4	R5	R6	R7	R8	R9	R10
Polychaetes																			
Amphinomidae	0	0	0	0	0	0	0	0	0	0	8	3	5	1	0	0	1	6	0
Capitellidae	2	2	0	9	19	129	32	26	14	126	144	108	52	107	138	200	375	160	293
Chaetopteridae	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Cirratulidae	7	5	7	3	10	0	7	14	1	3	21	1	2	27	4	5	8	9	17
Dorvilleidae	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Eunicidae	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0	1	0
Lumbrinereidae	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0
Nereididae	2	3	7	4	8	0	8	0	10	8	7	8	7	5	1	6	5	5	7
Onuphidae	21	36	1	46	51	73	58	1	39	53	60	87	57	53	78	78	79	57	75
Paraonidae	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Sabellidae	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Spionidae	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	1	0	1	7
Syllidae	45	54	6	0	24	57	18	33	12	60	94	20	28	34	22	39	19	48	12
Miscellaneous polychaetes	5	6	0	0	0	0	8	27	0	8	11	1	0	1	0	3	0	0	0
Non-polychaetes																			
Anthozoa	0	0	4	0	1	2	5	1	3	3	0	0	0	1	1	1	0	2	0
Crustacea	95	61	94	82	58	82	50	184	42	31	35	15	25	20	50	41	31	15	36
Hemichordata	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Oligochaeta	760	489	134	159	837	143	296	854	115	316	128	0	162	261	373	172	332	214	883
Ophiuroidea	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0
Mollusca	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Nematoda	181	387	375	45	137	201	23	757	20	139	467	0	56	198	100	228	275	201	225
Nemertea	6	1	5	2	0	0	0	5	5	1	0	0	1	1	0	2	1	0	0
Sipuncula	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Total number of polychaetes	83	106	21	63	112	259	131	101	77	260	349	228	152	228	244	332	488	287	411
Total number of non-polychaetes	1042	939	612	289	1033	428	374	1801	185	490	631	15	244	481	525	444	639	434	1144

Table 2
Number of individuals of polychaete and non-polychaete taxa in Wailupe Beach samples

	Pre-hurricane values								Post-hurricane values								
	R1	R2	R3	R6	R7	R8	R9	R10	R1	R2	R3	R4	R6	R7	R8	R9	R10
Polychaetes																	
Capitellidae	52	27	13	43	39	37	0	19	20	67	0	72	59	38	57	36	95
Cirratulidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0
Dorvilleidae	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Eunicidae	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Magelonidae	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Maldanidae	0	0	0	0	0	2	0	0	0	1	0	0	1	4	1	0	1
Nereididae	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Paraonidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0
Spionidae	234	42	23	61	101	48	4	168	90	170	70	115	100	56	133	99	94
Syllidae	9	0	0	2	2	0	1	2	6	13	2	5	9	4	8	4	4
Sabellidae	1	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0
Miscellaneous polychaetes	0	0	11	0	0	0	0	21	0	0	22	0	0	0	0	16	0
Non-polychaetes																	
Crustacea	2	1	4	3	0	2	1	0	0	3	2	1	3	0	2	1	1
Insecta	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Oligochaeta	3	9	1	1	4	0	4	0	1	0	0	10	0	0	3	4	0
Nematoda	4	3	0	4	8	3	0	1	0	1	1	3	1	3	1	1	3
Nemertea	1	0	0	0	0	2	0	0	0	0	0	0	1	0	0	0	0
Sipuncula	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Total number of polychaetes	296	72	47	106	143	87	5	210	116	251	94	194	170	102	203	155	194
Total number of non-polychaetes	10	13	5	8	12	7	5	1	1	5	4	14	5	3	6	6	4

(*P. elegans*) where high abundances were seen at salinities as low as 2 ppt (Hempel, 1957).

2.2. Sampling and analyses

Ten replicate sediment cores were collected from each site on 11 September 1992 before the hurricane and then again on 15 September 1992, at low tide using a hand held PVC corer 7.6 cm in diameter and embedded to 10 cm depth. Sediment occupied 5–10 cm of the cores, the remaining fraction was pieces of coral rubble. Samples were sieved using a 0.5 mm mesh and all organisms retained were fixed in 10% formalin with Rose Bengal stain for 48 h and transferred to 70% ethanol for long-term storage. Using a dissecting microscope, all organisms were sorted, identified, and enumerated (Tables 1 and 2). Identification was limited to family level for most polychaetes and various higher taxa for other organisms. Spionid and onuphid polychaetes were identified to species since they were very abundant and represented potential stabilizing taxa. There were individuals that could not be easily identified to family and were placed into the miscellaneous polychaete category. These comprised a small proportion of the total abundance. Our primary goal was to identify any conspicuous changes in abundance rather than describe the intertidal fauna in great detail. Some replicates at each site were excluded due to improper storage and the polychaetes could not be identified accurately. Sample sites were heterogeneous in distribution given the patchy nature of the polychaete aggregations and although some replicates were not used, the data collected is representative of this distribution without overwhelming bias. All data was normalized using a square-root transformation and two-way ANOVA analyses were computed using *R*, a statistical programming language (Ihaka & Gentleman, 1996) on oligochaete and polychaete groups. Differences in other taxa were not analyzed since we were focusing on changes in polychaetes and oligochaetes, which are very similar to capitellids in feeding and distribution.

3. Results

Two-way ANOVA results for Niu Beach showed a significant increase in the total number of individuals sampled post-hurricane ($F\,(1,17) = 7.47$, $p < 0.0067$), and a significant interaction ($F\,(1,17) = 5.408$, $p < 0.0000$) between each family/taxon and how they changed before and after the hurricane; not all families changed the same. At Niu Beach the most dominant taxon was oligochaetes pre- and post-hurricane. The oligochaetes decreased in abundance from 3787 to 2841 (Table 1) individuals but ANOVA results were not significant.

The top five most dominant polychaetes were onuphids, capitellids, syllids, cirratulids, and nereidids both pre- and post-hurricane; there were no substitutions with other families post-hurricane. All of the dominant polychaete families increased in numerical abundance post hurricane (Table 1). This was most dramatically seen in the capitellid numbers, which increased from 233 to 1703 individuals. Two-way

ANOVA results based on the mean number of individuals showed that this increase was significant (Table 3). This also represented an increase from 24% to 57% in total percent polychaete composition (Fig. 2). Capitellid densities reached a mean value of 5700/m^2 pre-hurricane increasing significantly to 37,500/m^2 post-hurricane. The onuphid, *D. dexiognatha*, increased from 326 to 677 individuals. Two-way ANOVA results based on the mean number of individuals showed that this increase was significant (Table 3). However, this represented an overall decrease from 34% to 23% of total percent polychaete composition (Fig. 2). All onuphid individuals were *D. dexiognatha* and their densities had a mean value of 8000/m^2 pre-hurricane increasing to 14,900/m^2 post-hurricane. The other dominant families also increased; syllids increased from 249 to 326 individuals, cirratulids from 54 to 97 individuals, and nereidids from 42 to 59 individuals. Amphinomids and eunicids were not dominant polychaete families but ANOVA results showed significant increases in abundance

Table 3
Summary of significant analysis of variance (ANOVA) results for polychaete families at Niu Beach and Wailupe Beach[a]

Family	df	*F*	*p*
Niu Beach			
Amphinomidae	1, 17	8.971	0.008
Capitellidae	1, 17	30.002	0.000
Eunicidae	1, 17	5.368	0.033
Onuphidae	1, 17	9.338	0.007
Wailupe Beach			
Maldanidae	1, 15	7.059	0.018
Syllidae	1, 15	10.733	0.005

$p < 0.05$ significance level.
[a] Significance values for pre- vs. post- dominant polychaete and non-polychaete abundance: $p < 0.05$.

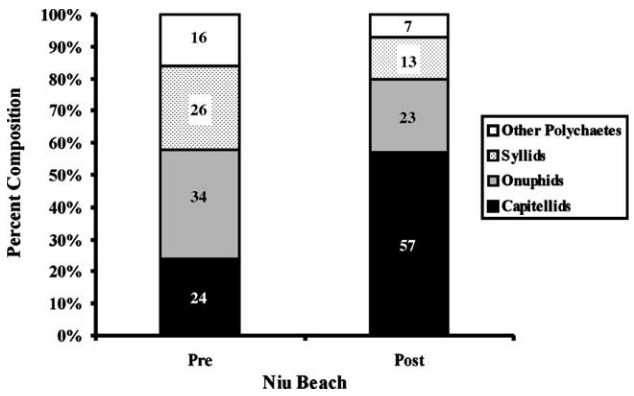

Fig. 2. Percent composition of dominant polychaete families from Niu Beach. $N = 953$ pre-hurricane and $N = 2979$ post-hurricane.

post-hurricane (Table 3). The non-polychaete numbers slightly decreased for most taxa but crustaceans were markedly less abundant going from 748 to 299 individuals.

Two-way ANOVA results for Wailupe Beach showed a significant increase in the total number of individuals sampled post-hurricane (F (1,16) = 4.2718, $p < 0.0398$), but there was no detectable difference (F (1,16) = 1.2811, $p < 0.2092$) in the familial response before and after the hurricane; all families responded the same. At Wailupe Beach the top four dominant polychaete taxa were capitellids, spionids, syllids and maldanids both pre- and post-hurricane, but there was an increase in the numerical abundance of these families post-hurricane (Table 2). Oligochaetes were in the top five dominant taxa pre-and post-hurricane but their abundance did not change much post-hurricane (22–18 individuals). The capitellids increased in number from 230 to 444 individuals and represented an increase of 24–30% in total percent polychaete composition (Fig. 3). Capitellid density reached a mean value of 6300 /m^2 pre-hurricane and increased to 10,900/m^2 post-hurricane. Spionid numbers increased from 681 to 927 individuals and represented a slight decrease of 70–63% in total percent polychaete composition (Fig. 3). The most abundant spionid present, *Pygospio muscularis*, comprised up to 95% of all spionids. *Streblospio benedicti*, the second most abundant species, was substantially lower in abundance (less than 5%). Spionid density reached a median value of 18,800/m^2 pre-hurricane and increased to 22,700/m^2 post-hurricane. The other dominant families also increased; syllids increased from 16 to 55 individuals and maldanids from 2 to 8 individuals. Two-way ANOVA results showed that these increases were the only significant results at Wailupe (Table 3). All other families did not represent a high proportion of individuals sampled and when

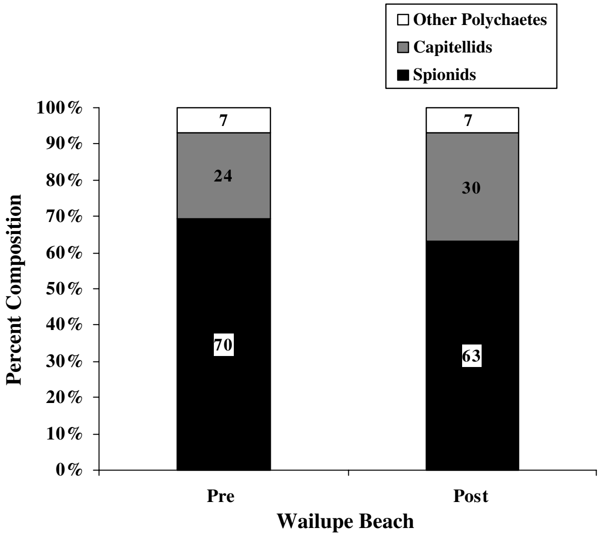

Fig. 3. Percent composition of dominant polychaete families from Wailupe Beach. $N = 966$ pre-hurricane and $N = 1479$ post-hurricane.

combined (including syllids and maldanids) only accounted for 7% of total polychaetes pre-and post-hurricane.

4. Discussion

A large reduction in total abundance was expected with the extreme disturbance caused by high winds and sea levels that developed during sampling at both sites, but none was observed. Sand was transported into the beach vegetation revealing more rubble on the beach at the post-hurricane sampling visit. Nearly all the polychaete families showed an increase in post-hurricane abundance. This can possibly be attributed to sampling irregularities due to the patchy distribution of these tubiculous polychaetes in reef habitats and sampling of slightly different parts on this narrow intertidal zone, rather than an actual increase in numbers. Given the wave activity and sand transport inshore, organisms could have also been deposited into the sampling area after the storm and settled (or were trapped) among the dense tube aggregations and algal debris. An effort was made to take post-hurricane samples close to areas sampled pre-hurricane, although exact locations were difficult to detect and would represent disturbed habitat. Storm conditions could have scoured out or smothered low-density patches and exposed high-density patches, so only high-density patches were re-sampled post-hurricane. This could add a potential bias in the sampling but because sampling methods were consistent before and after the hurricane, we feel that the comparisons are fair representations of the trends observed.

Tubiculous polychaetes that occur in dense aggregations can contribute to sediment stability and benthic community complexity (Bailey-Brock, 1979, 1984, 1987; Fager, 1964; Sanders et al., 1962; Woodin, 1981). Sediment stabilization was seen at densities of 500–1000/m^2 for *Owenia fusiformis* tubes (Fager, 1964), 400–500/m^2 for *Clymenella torquata* tubes, and 45,000–98,000/m^2 for *Spiophanes wigleyi* tubes (Featherstone & Risk, 1977). Friedrichs et al. (2000) showed that destabilization of sediments only occurred at tube densities less than 870 tubes/m^2. Previous studies also show that these tube building gregarious polychaetes have more species rich communities and retain a greater proportion of fine grains, than adjacent areas without the tube builders (Bailey-Brock, 1979, 1984; Bolam & Fernandes, 2002, 2003; Callaway, 2003; Fager, 1964; Gallager et al., 1983; Luckenbach, 1986; Noji, 1994; Reise, 1983; Woodin, 1981; Zühlke, 2001). These tubes help provide a nutritionally rich system where drifting algae and sediments are caught by projecting tube openings and compacting of sediments results in the greater abundance of burrowing and tube dwelling invertebrates (Bailey-Brock, 1984). At Fort Kamehameha reef near Pearl Harbor chaetopterid tubes reached mean densities of 80,000/m^2 and contained higher invertebrate densities and species richness than reef flats without tubeworms (Bailey-Brock, 1979). The mean density of *D. dexiognatha* in compact tube mounds at Niu Beach was previously 21,800/m^2 (Bailey-Brock, 1984) compared to the densities observed here reaching mean values of 8000/m^2 and 14,900/m^2 pre- and post-hurricane, respectively. This apparent decrease in *D. dexiognatha* density was not caused by the hurricane, but may have happened gradually over the years. A more likely cause is the frequent digging of *Diopatra* mounds and the continual removal of free-living orbiniid polychaetes from the mounds by fishermen who use them for bait (Bailey-Brock, 1984).

Large spionid populations form dense tube mats that may potentially stabilize sediments and provide refuges for other invertebrate assemblages (Blake, 1996; Bolam, 1999; Bolam & Fernandes, 2002; Bolam & Fernandes, 2003 Meadows & Hariri, 1991; Morgan, 1997; Noji, 1994; Noji & Noji, 1991; Thrush et al., 1996). Thrush et al. (1996) demonstrated that sediment instability was greater in sample plots in which dense spionid tube mats were removed. The spionid density in this study reached a moderately high mean value up to 22,700/m^2 that suggests sediment stabilization was a possibility at this site. *Pygospio muscularis* measure 5.0–5.5 mm in length and 0.5 mm in width; the tubes are 10–15 mm in length and 0.5–0.6 mm wide. *Pygospio* tubes are considerably smaller in diameter and shorter in length compared to *Diopatra* tubes (7.5 cm length, 1.5 mm width), thus have correspondingly higher densities. Spionids also tend to inhabit high exposure areas, especially species of *Pygospio* that are found high in the intertidal zone (Blake, 1996; Ward, 1981). The presence of high densities of *D. dexiognatha* at Niu Beach and similarly, *P. muscularis* at Wailupe Beach may provide a stable community for other polychaetes and small, motile invertebrates compared to areas without tubes. The robust physical nature of the mounds and turf of tubes at these two sites may provide resistance to continual physical disturbance by wave action and act as a buffer in small-scale or extreme situations.

Oligochaetes were among the most dominant taxa at both sites and appear to be very similar to capitellids in respect to their feeding and distribution and their high abundances are not surprising given the sediment disturbance and sediment deposition among the tubes. At Niu Beach capitellids contributed 24–57% of the total polychaetes and appear to be highly adapted surface burrowers able to take advantage of newly disturbed sediment with rapid recruitment. In a previous study of community structure at Niu Valley by Bailey-Brock (1984), capitellids were one of the most abundant polychaetes present and reached intermediate densities of 11,600/m^2, compared to 5700–37,500/m^2 (pre- and post-hurricane, respectively) seen in this study. As mentioned previously, Moran and Reaka-Kudla (1991) observed that burrowing polychaete species significantly increased from pre-hurricane values. Although they did not identify the polychaetes to family or species, capitellids are classically defined as burrowing polychaetes and are likely able to anchor in the sediments. Capitellids burrow and also build tubes (Fauchald & Jumars, 1979) that remain on or near the surface of sediments allowing for some increase in numbers as a result of wave action or shifting sediment sweeping them into these tube mounds (Bailey-Brock, personal communication). Other studies have shown that *Capitella capitata* has a short life cycle of approximately 30–40 days, is capable of reproducing all year round, and one female can have up to 10,000 eggs. These characters explain how species in this family are able to rapidly colonize disturbed or unoccupied sediments in large numbers (Grassle & Grassle, 1974; Rosenberg, 1973).

5. Conclusions

Overall, this study showed no dramatic depletions or loss of species/taxa/dominant groups after Hurricane Iniki. These results suggest there was no measurable effect of Hurricane Iniki on the intertidal fauna at both sites. These results are consistent with the results of previous studies by other researchers, mostly in temperate regions, demonstrating little or no substantial effects from storms.

In Hawai'i, both *D. dexiognatha* and *P. muscularis* are key species that may provide sediment stabilization for intertidal invertebrate community structure during normal, as well as severe episodic disturbances and capitellids are able to quickly colonize disturbed sediments with large numbers. Thus, severe storms appear to be a mechanism that affects community structure in a reef habitat which undergoes daily tidal fluctuations, constant and variable wave impacts, frequent foot traffic and sediment turn-over by fishermen and surfers, but may have less affect than normal background variability of this reef environment. Tubiculous polychaetes inhabiting these reef flats appear to be well adapted to survive such disturbances and may confer this benefit to other organisms living among their tubes.

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