Temporal changes in the polychaete infaunal community surrounding a Hawaiian mariculture operation

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ABSTRACT: Benthic monitoring efforts in the vicinity of a Pacific threadfin *Polydactylis sexfilis* mariculture venture have allowed us to examine eutrophic effects on the infaunal community. Polychaete infaunal communities from 2 sites near the point source were compared to 2 control stations beyond the range of fish feed and wastes. Regression analysis indicated significant decreases in Shannon-Weiner diversity over time and near the effluent source. Non-metric multidimensional scaling (nMDS) showed a progression of species succession and turnover at impacted sites but relatively unchanging polychaete communities at control sites. An analysis of similarity (ANOSIM) indicated significant differences between community structures at impacted and control sites but less obvious differences over time. An abundant and regionally widespread polychaete *Pionosyllis heterocirrata* had disappeared from impacted sites. Increasing abundances of 2 opportunistic polychaetes, *Capitella capitata* (complex) and *Ophryotrocha adherens*, resulted in decreasing Shannon-Weiner diversity values (*H'*) at impacted stations. Expanding populations of *C. capitata* and *O. adherens* seem to be preceded by high densities of *Myriochele oculata*. These 3 species may represent an order of succession due to attrition by anoxia in Hawaiian waters. Deviation of the infaunal polychaete community at impacted sites resulting from the appearance of polychaete pollution indicators, low species richness resulting from the disappearance of ambient polychaete species and depressed community abundance reflect the effects of fish mariculture on the benthic community. Such effects may be diluted by the open-ocean location on the south shore of O'ahu, Hawai'i.

KEY WORDS: Aquaculture · Environmental monitoring · Eutrophication · Hawai'i · Indicator species · Polychaetes

INTRODUCTION

The environmental effects of open-water mariculture have been reported from studies conducted internationally, including the UK (Henderson & Ross 1995), Eastern Canada (Pocklington et al. 1994, Pohle et al. 2001), Australia (Ritz et al. 1989, Crawford 2003) and Japan (Tsutsumi 1995, Yokoyama 2002). Mariculture operations produce fecal matter and excess food that leads to organic enrichment of the surrounding benthos, creating reducing conditions in the sediment and oxygen depletion of the bottom water (Hargrave 1994,

Tsutsumi 1995, Pohle et al. 2001). Microbial degradation of surplus organics often leads to benthic conditions characterized by anoxic conditions, low redox potential and elevation of the redox potential discontinuity (RPD) layer (Henderson & Ross 1995). Previous aquaculture operations have been operated in embayments (e.g. Tsutsumi 1987, 1995, Pohle et al. 2001, Yokoyama 2002), which usually contain low energy environments with reduced dilution effects from currents. Open-ocean mariculture operations are relatively new and provide a location in which enrichment effects can be buffered by increased current activity

and dilution as well as a deeper operation site (Fernandes et al. 2001, Henderson et al. 2001).

Commercial culturing of the Pacific threadfin *Polydactylus sexfilis* was recently introduced to open-ocean waters of Hawai'i. Known locally as moi, this popular finfish was once reserved for Hawaiian royalty (Titcomb 1972) and is a popular item on restaurant menus (Chambers et al. 2001). Experimental phases of a mariculture operation culturing the Hawaiian moi began in April 1999 with 1 cage 2 km offshore from Ewa Beach in Mámala Bay, O'ahu, Hawai'i (Bybee & Bailey-Brock 2003). The commercial phases of mariculture began with 1 cage in November 2001 and increased to 3 cages in subsequent years. The amount of nutrient input into the system has increased with additional open-water enclosures installed over the past 5 yr (Fig. 1).

Like most aquaculture ventures, the effects of nutrient enrichment from the fish cages on the macrobenthic environment are evident in monitoring studies. Regulatory and pollution control authorities have used benthic community structure in the past to gauge organic enrichment (Pearson & Rosenberg 1978, Henderson & Ross 1995). Analysis of faunal community changes has reportedly been more sensitive than geochemical parameters in detecting organic enrichment (Carroll et al. 2003). Infaunal community analyses supplemented by measurement of geochemical properties are used to assess enrichment intensity and benthic health for this mariculture operation. Benthic sampling data collected from the area surrounding the mariculture cage over a 36 mo period has been examined within the context of several long-term studies conducted at similar depths in the surrounding area of Mámala Bay, O'ahu (Swartz et al. 2001, Bailey-Brock et al. 2002).

From infaunal community data, univariate measures such as species diversity and evenness are calculated and correlated with changes in organic levels (Gray et al. 1990). Declining species richness especially coupled with increasing infaunal abundance, as well as decreasing diversity and evenness values, are associated with pollution (Krassulya 2001). Comparisons of species composition between native, unaffected communities and communities from impacted or polluted environments may be performed using multivariate analyses such as a non-metric multidimensional scaling (nMDS, Clarke & Warwick 2001). All these techniques are useful and often combined for monitoring sewage outfall effluent and effects of organic enrichment on infaunal community succession (Pearson & Rosenberg 1978).

Designating species that thrive in disturbed environments as indicators of organic enrichment is another measure that has gained acceptance. While the concept of indicator species is widely applicable, ubiquitous usage of indicator taxa has been questioned (Bustos-Baez & Frid 2003). Polychaetes such as *Capitella capitata* and *Ophryotrocha* spp. have shown potential as enrichment indicators in temperate environments and in Hawai'i (Grassle & Grassle 1974, Tsutsumi 1987, 1990, 1995, Henderson & Ross 1995, Bailey-Brock 1996, Paavo et al. 2000, Bailey-Brock et al. 2002, Bybee & Bailey-Brock 2003, Simonini 2002, Brooks et al. 2003). High abundances of invertebrate indicator species coupled with low numbers of ambient or native species in the community is a signal of disturbance. Low numbers of indicators may reflect their natural population density in the unperturbed community. Anoxic conditions also affect the distribution of indicator species such as *C. capitata* (Gamenick et al. 1998). This study illustrates a change in macrobenthic community composition from a native assemblage to one dominated by indicator species in response to mariculture activity.

MATERIALS AND METHODS

Study sites. The mariculture cages were moored at a designated site about 2 km offshore and 13 km west of Honolulu Harbor. Four sampling sites were at the cage and at varying distances from it (Fig. 2). The Sea Station cage system developed by Ocean Spar Technologies is a biconical structure enclosing ca. 3000 m^3 and sus-
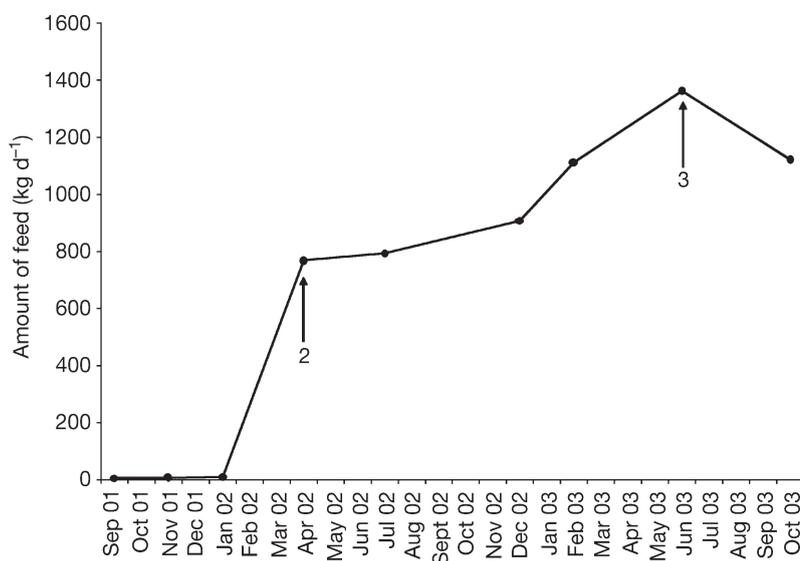

Fig. 1. Feed data as reported by Cates International. New cages were added in March 2002 and June 2003
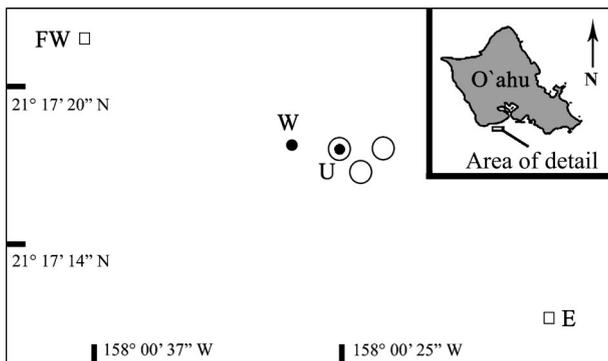
Fig. 2. Map of study area including latitudinal and longitudinal coordinates. Site U is located under western lip of enclosure, Site W is 80 m from center of enclosure, Site FW is 390 m distant, and Site E is 360 m away. Control sites: (□), impacted sites: (●), mariculture enclosures on map: (○)

pended ca. 10 m above a sand bottom. New fry were added to an inner netted area, while fish ready for harvest occupied the outer sector. Up to 130 000 moi of 2 age classes could be enclosed within each cage. Solid sections of the lower conic mesh helped direct falling food pellets toward a catch basin where they decomposed, and residue was dispersed by currents.

SCUBA divers collected samples from sediments between 31 and 35 m depths over 12 sampling periods between November 2001 and November 2004. Two stations under (U) and 80 m west (W) of the fish cages were designated as impacted, while 2 stations 390 m westward (FW) and 360 m eastward (E) of the cages were control sites. Sites were selected on the premise that currents move predominantly westward. Hydrodynamic properties were characterized by project divers and oceanographic models created for the nearby Barbers Point and Sand Island sewage outfalls. Bottom currents measured at the Barber's Point outfall (less than 1 km from Site E) never exceeded 50 cm s^{-1} (Roberts 1995).

Sampling methods: environmental variables. SCUBA divers collected 3 replicate 125 ml sediment cores in clear plastic Nalgene bottles from each of the 4 stations for qualitative measurements of electrochemical oxidation reduction potential (ORP) and granulometric analyses. The ORP of each core's surface was measured using a handheld Oakton ORP meter with direct electrode contact to sediment cores. Presence of sulfide in sediment cores was determined by olfactory detection. Total organic carbon analyses of carbonate sand samples were measured using the HCl vapor digestion method (Hedges & Stern 1984). However, results did not meet QA/QC requirements, were not interpretable, and are not presented here.

Sediment grain sizes and distributions were assessed using a wet sieve gravimetric procedure (McCarthy 1996). A fraction was removed to a nested sieve series suspended over a clean white bucket. The collected slurry was drawn off and filtered to remove the finest silt fraction. All grain size fractions were dried for a minimum of 12 h at 80°C before weighing. This process lost any information on sedimentary stratification. McCarthy's (1996) detailed sedimentary study did not find any evidence of grain size stratification in sediments from east Mámala Bay. The major grain size fractions agreed within 11% of their respective values, supporting an assumption of uniform processing.

Sampling methods: benthic invertebrates. SCUBA divers collected 100 cm^2 sediment cores 5 cm deep from 4 stations over 12 sampling dates. Three replicates per sampling were taken from within a 2 m^2 area previously undisturbed by diving activities at each site. Cores for infaunal analyses were preserved in 10% buffered formalin and elutriated over 0.5 mm sieve according to procedures detailed by Sanders (1958). Infauna were sorted, identified to lowest possible taxa according to Bailey-Brock (1987) and enumerated.

Data analysis. Shannon-Wiener diversity (log e; H') and Pielou's evenness (J) were calculated for each sediment core for all sampling dates. Spatial and temporal variation in H' was analyzed by polynomial regression, using distance (m) from the effluent source and time (d) since the first sampling as independent variables.

Changes in community composition were analyzed using a matrix of multivariate ecological similarity coefficients. Bray-Curtis similarity coefficients between samples were calculated based on the similarity of infaunal community structure. Each species' contribution to the Bray-Curtis coefficient was determined by those species' abundances in the compared samples. Samples with many species in common at similar abundances had high Bray-Curtis similarity coefficients. Construction of the Bray-Curtis similarity matrix utilized polychaete abundance data that were pooled for the 3 sediment cores from each site during each sampling period and then 4th root transformed.

The Bray-Curtis similarity matrix was used in the construction of a 2-dimensional non-metric multidimensional scaling (nMDS). This ordination plot is a visualization of a 2-factor analysis of similarities (ANOSIM, Clarke & Warwick 2001) crossed between sites and sampling dates. This procedure allowed us to test for significant differences in polychaete community structure between sampling periods using average site values and between sites using average sampling date values. Each ANOSIM procedure entailed the use of 999 permutations.
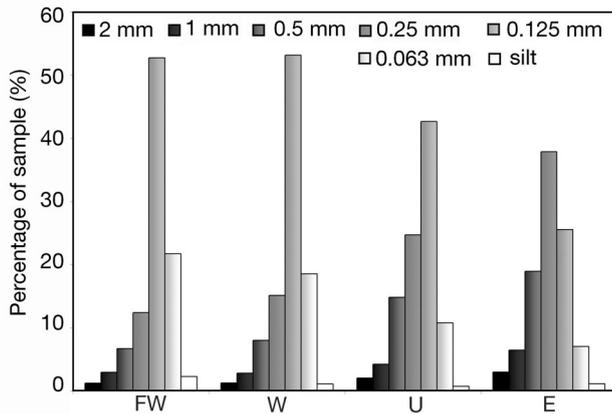
Fig. 3. Average percentages of each grain size from 8 samplings. Fractions of smaller grain sizes increase toward west while fractions of larger grain sizes increase toward east

PRIMER's similarity percentage (SIMPER, Clarke & Warwick 2001) analysis identifies discriminating and typifying species in a comparison of infaunal communities (Clarke & Warwick 2001). This analysis ranked each species' contribution to community structure based on abundances found in replicates for each site. Common species with similar abundances between replicates contributed most to Bray-Curtis similarity within a sample. Low standard deviations of these coefficients suggested consistency in the species' abundances across replicates. Characteristic species were identified by a high ratio of Bray-Curtis similarity contribution to a coefficient's standard deviation. Discriminating species were identified using the Bray-Curtis dissimilarity coefficient, which was calculated using differences in species abundances between samples (Clarke & Warwick 2001).

Analyses were performed with MINITAB 13.32 for Windows (Minitab 2000) and PRIMER 5 for Windows v. 5.2.9 (PRIMER-E 2002).

RESULTS

Granulometry

A general trend indicated that grains found in western sampling sites were finer than grains found in eastern sites (Fig. 3). Since smaller grain sizes would be carried down current more easily than larger sand grains, average grain sizes decreased from Site E to FW. The greatest separation of grain sizes was between 0.125 and 0.25 mm. Although sediment compositions showed slight variations between sites, granulometric profiles were still highly similar (Fig. 2).

Oxidation-reduction potential. ORP measurements at impacted sites were consistently lower than measurements at control sites (Fig. 4). The difference between ORP measurements from control and impacted sites increased since the initial sampling. Site U samples had redox potentials consistently below the range of the meter used, which coincided with sulfuric odors detected by collectors. Such effects are not observed at other sites.

Infaunal data. Shannon-Weiner diversity values at Site U decreased from (2.85 average) the November 2001 sampling to the lowest levels found during this study (1.02 average) in December 2002. Diversity values at Site W fluctuated between 0.96 (November 2004) and 2.61 (April 2002). In contrast, diversity values at Site FW never decreased below 1.78 and had a peak level of 2.67 in January 2002. Site E had even higher diversity, ranging from 2.19 to 2.81 (Fig. 5). Decreases in Pielou's evenness (Fig. 6) and Shannon-Weiner diversity values (Fig. 5) at Sites U and W were primarily attributed to increased dominance of opportunistic polychaetes *Capitella capitata* (complex) and *Ophryotrocha adherens* (Fig. 5) and a concomitant decrease in species richness (Fig. 7). Percent abundance of these 2 opportunists at impacted sites ranged from 8.4 to 84.9% of all polychaetes. Fluctuations in their respective percent abundances were roughly inversely related to fluctuations in Shannon-Weiner diversity values. Only 10 species of polychaetes were found at Site U in December 2002, resulting in the lowest average Shannon-Weiner values found during the study period. Except for a few data points, Pielou's evenness values at impacted sites were depressed relative to control sites.
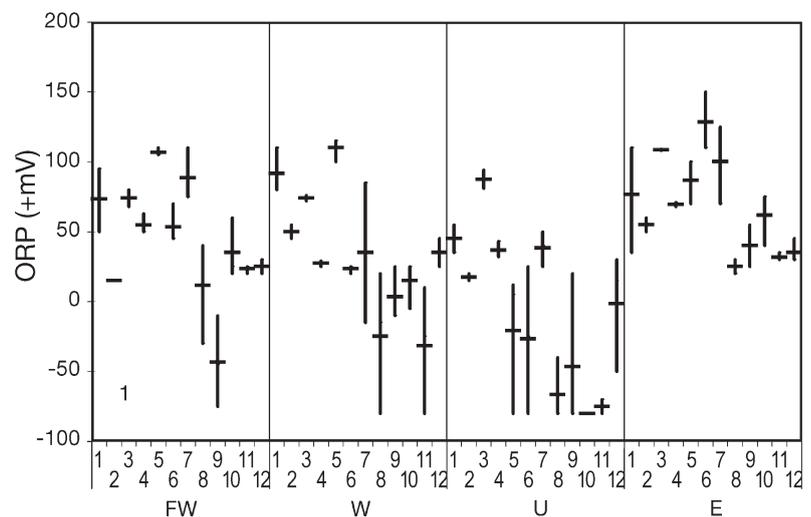

Fig. 4. Range of ORP measurements and their averages as shown by a ▬. Numbers on *x*-axis correspond to sampling period for each station. 1: Nov. 2001; 2: Jan. 2002; 3: Apr. 2002; 4: Jul. 2002; 5: Dec. 2002; 6: Feb. 2003; 7: Jun. 2003; 8: Oct. 2003; 9: Feb. 2004; 10: May 2004; 11: Sep. 2004; 12: Nov. 2004

Fig. 5. Abundances of indicator species as fraction of total polychaete abundance for each station. Numbers on *x*-axis correspond to sampling period for each station. *Ophryotrocha adherens* and *Capitella capitata* are found in impacted stations and rarely found in reference stations. A line graph of Shannon-Wiener diversity values for each site is plotted on secondary *y*-axis. 1: Nov. 2001; 2: Jan. 2002; 3: Apr. 2002; 4: Jul. 2002; 5: Dec. 2002; 6: Feb. 2003; 7: Jun. 2003; 8: Oct. 2003; 9: Feb. 2004; 10: May 2004; 11: Sep. 2004; 12: Nov. 2004
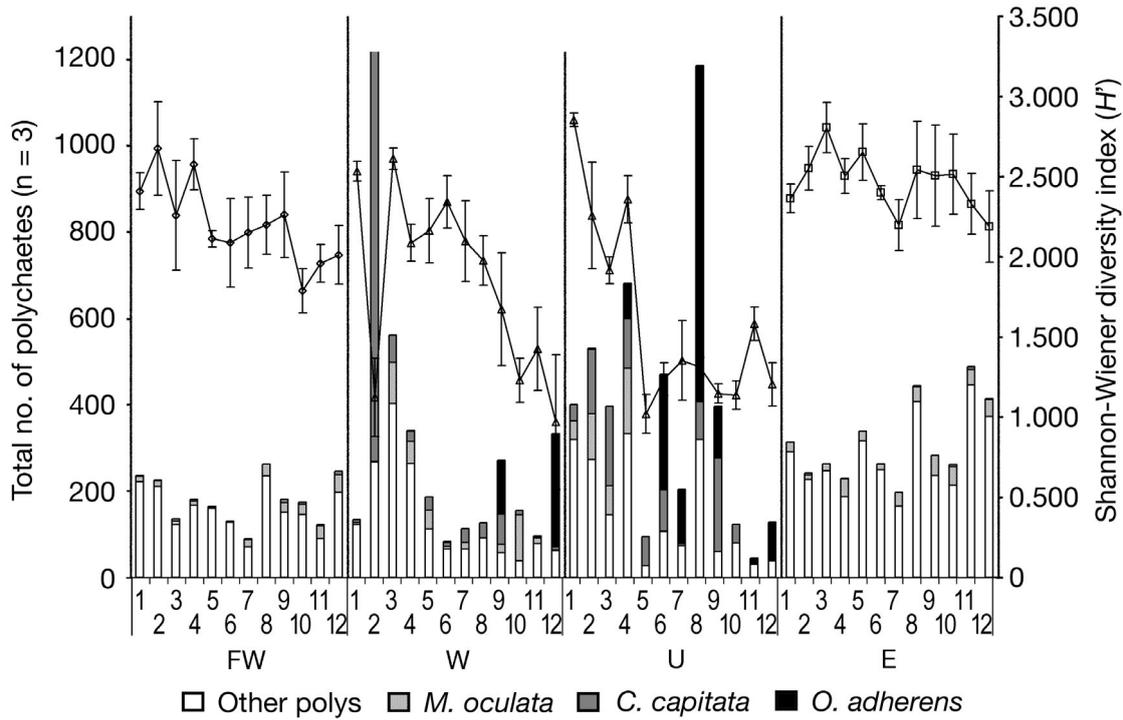
Shannon-Weiner diversity varied significantly both over time and with distance from the cages (Table 1). Because one control station was up-current from the cages (negative distance) and the other was down-current (positive distance), the positive coefficient for distance squared indicated increasing diversity with greater distance from the effluent source in either direction. The negative coefficient for time reflected a decrease over the course of the study in diversity, averaging across the sites. The positive coefficient for the interaction of time and distance² indicated that the difference between the impacted stations under or near the cages and the control stations further away increased over time. Higher-order terms were included to decrease lack of fit, but we were not able to construct a model without significant lack of fit. The principal lack of fit was the 3 replicates from Site W in January 2002, which had unusually high density of *Capitella capitata* and low diversity despite species richness comparable to the previous sampling of the same site.

The relatively close grouping in the nMDS of E and FW across all sampling dates showed consistent infaunal communities found through time (Fig. 8). These communities represented ambient communities that would be found in the absence of artificial influxes of
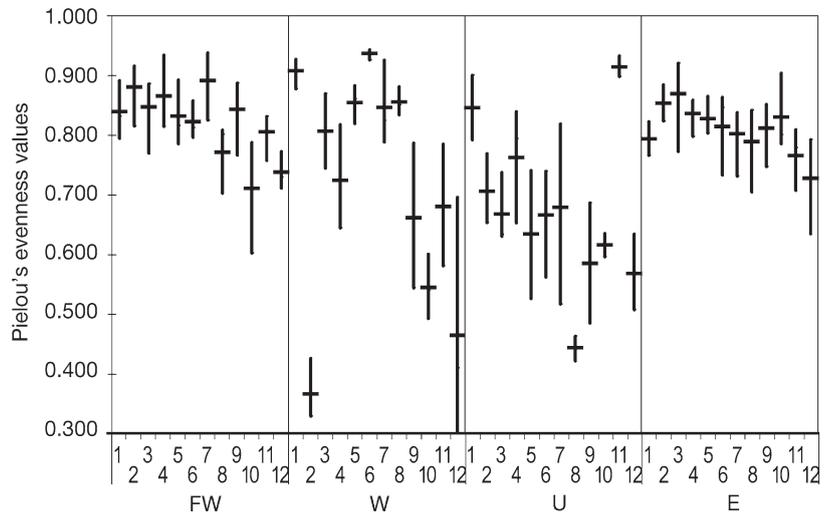

Fig. 6. Pielou's evenness levels for each site over the course of our samplings. Site U consistently has lowest levels of community evenness. 1: Nov. 2001; 2: Jan. 2002; 3: Apr. 2002; 4: Jul. 2002; 5: Dec. 2002; 6: Feb. 2003; 7: Jun. 2003; 8: Oct. 2003; 9: Feb. 2004; 10: May 2004; 11: Sep. 2004; 12: Nov. 2004
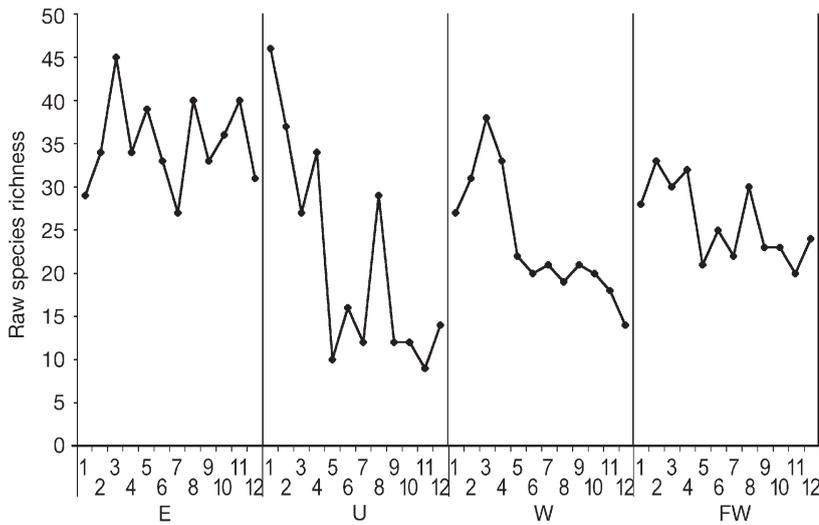
Fig. 7. Total numbers of polychaete species found based on pooled data for each sampling date. 1: Nov. 2001; 2: Jan. 2002; 3: Apr. 2002; 4: Jul. 2002; 5: Dec. 2002; 6: Feb. 2003; 7: Jun. 2003; 8: Oct. 2003; 9: Feb. 2004; 10: May 2004; 11: Sep. 2004; 12: Nov. 2004

controls. Two-way crossed ANOSIM determined significant differences between sites averaged across all dates as well as significant differences between dates averaged across all sites. However, separate ANOSIMs using only the first and last 6 dates yielded no significant differences (Table 2).

The 3 species that best typified their respective sites (i.e. had the greatest ratio of contribution to Bray-Curtis similarity: standard deviation) were designated with A, B and C (Table 3). Species that best typified control sites were *Pionosyllis heterocirrata* (Family Syllidae), *Euchone* sp. (Family Sabellidae) and *Litocorsa acuminata* (Family Pilargidae). *L. acuminata* was once a prevalent species in the infaunal communities at impacted sites, but its abundance decreased over the course of the study. None were found in impacted site samples after June 2003. *P. heterocirrata* and *Euchone* sp. were consistently found at Sites E and FW, respectively.

Species that most characterized impacted infaunal communities include *Ophryotrocha adherens* (Family Dorvilleidae), *Capitella capitata* (Family Capitellidae) species complex and *Myriochele oculata* (Family Oweniidae). *C. capitata* has been consistently present at impacted sites since the beginning of this study. Of the 1875 *O. adherens* counted in this study, 78.8% were found in Site U samples and 95.1% were found in samplings after December 2002. While SIMPER may indicate *M. oculata* as one of the most characteristic polychaetes of impacted samples, data also show it as a member of the ambient infaunal community. It was consistently present at control sites and had elevated abundances at both impacted sites until December 2002, after which it had nearly disappeared from Site U.

organic matter. Initial samplings of impacted sites yielded infaunal communities relatively similar to those found at control sites. In successive samplings, a gradual infaunal species turnover at Site U resulted in a deviation from the ambient infaunal community. Until the June 2003 sampling, infaunal communities sampled at Site W were more similar to Sites E and FW than to Site U. Over time, the community structure at Site W began to resemble Site U samples more than

Table 1. Results of regression analysis of Shannon-Weiner diversity values with centered predictor variables

Predictor	Coeff	df	Seq SS	p
Constant	1.5248		0.000	
Distance	2.7519	1	1.2905	0.000
Days	−0.34335	1	9.1036	0.000
Days × Distance	−0.02626	1	0.2242	0.718
$Distance^2$	0.28664	1	12.8425	0.000
$Days^2$	0.17025	1	0.0733	0.000
$Days × Distance^2$	0.12736	1	1.9973	0.000
$Distance × Days^2$	−1.9832	1	0.0097	0.000
$Distance^3$	−1.4475	1	1.094	0.000
$Days^3$	−0.0227	1	0.0308	0.576
$Days^2 × Distance^3$	1.0239	1	4.4845	0.000
$Distance × Days^3$	0.00185	1	0.0002	0.964
R-Sq = 70.7% R-Sq(pred) = 65.74%		R-Sq(adj) = 68.3%		
ANOVA				
Source	df	MS	*F*	p
Regression	11	2.8319	28.98	0.000
Residual error	132	0.0977		
Lack of fit	36	0.2531	6.41	0.000
Pure error	96	0.0395		
Total	143			

Table 2. Results of 2-way crossed ANOSIM where tests (999 permutations per test) for site groups were averaged over sampling groups and vice versa. *Significance level at α = 0.05

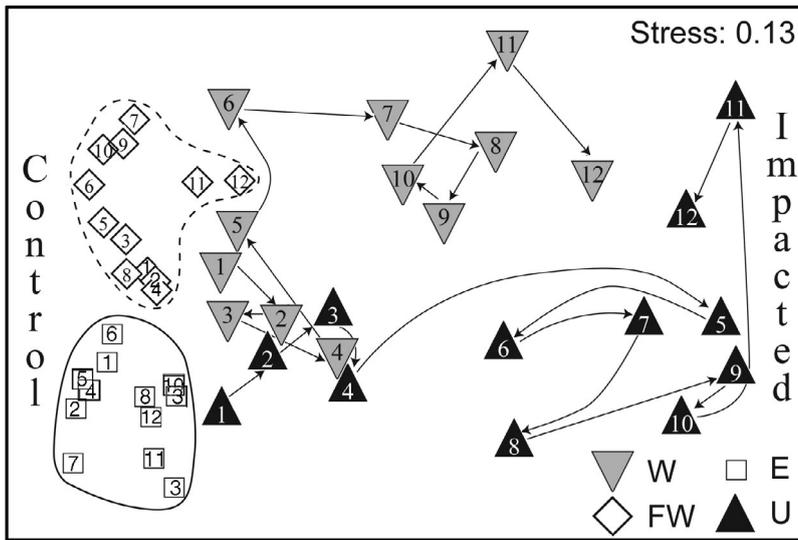|	Rho
November 2001–November 2004	
Site	0.542*
Sampling	0.317*
November 2001–February 2003	
Site	0.436*
Sampling	0.047
June 2003–November 2004	
Site	0.726*
Sampling	0.044

Fig. 8. A non-metric multi-dimensional scaling illustrates a (dis)similarity matrix on a 2-dimensional plot. Distances between points on map indicate relative similarity between infaunal communities of those 2 points. Control samples showed little variation between samplings. This plot illustrates development of Site U from an enriched site (Nov 01–Jan 02) with high species richness and abundance to a grossly impacted site dominated by a few opportunistic species (Dec 02–May 04). Site W from June 2003 has also diverged from W group toward grossly impacted U group

The 5 species with the highest contribution to the Bray-Curtis dissimilarity and lowest standard deviation of that coefficient are listed in Table 4. *Armandia intermedia* (Family Ophelidae) was found in elevated abundances in impacted samples but fewer numbers in control samples (Table 4) and may be a discriminating species between the 2 sample groups. Species that were found to characterize control or impacted sites had generally high discriminatory potential as well. *Capitella capitata*, *Ophryotrocha adherens*, *Pionosyllis heterocirrata* and *Euchone* sp. were the top 4 discriminatory species between control and impacted sites. The 2 opportunistic species *C. capitata* and *O. adherens* were more abundant at impacted sites, while *P. heterocirrata* and *Euchone* sp. were more abundant at control sites.

Table 3. Results of SIMPER analyses identifying species that contribute most to the similarity of compared replicates within a site as well as the similarity between group samples. [A,B,C] indicate rank of each characteristic species based on similarity for each site

Species	Avg. abundance	Avg. similarity	Contrib. (%)	Ratio	Species	Avg. abundance	Avg. similarity	Contrib. (%)	Ratio
Group E					**Group U**				
Avg. similarity = 57.64					Avg. similarity = 27.18				
Pionosyllis heterocirrata[A]	73.33	13.58	23.57	6.20	*Capitella capitata*[A]	93.75	10.49	38.59	11.40
Litocorsa acuminata[C]	35.25	9.15	15.88	3.30	*Ophryotrocha adherens*[B]	137.92	5.86	21.55	10.85
Myriochele oculata[B]	29.67	7.33	12.71	3.44	*Hesionidae* sp.	15.00	2.19	8.07	1.38
Prionospio cirrifera	22.75	5.34	9.26	2.63	*Neanthes arenaceodentata*	13.17	1.69	6.22	2.11
Heteropodarke sp.	18.33	4.90	8.50	1.63	*Capitellidae* sp.	24.17	1.56	5.73	1.61
					Myriochele oculata[C]	30.75	1.11	4.07	3.58
Group FW					**Group W**				
Avg. similarity = 51.04					Avg. similarity = 25.78				
Litocorsa acuminata[B]	30.58	11.48	22.49	7.04	*Capitella capitata*[B]	103.50	5.91	22.91	5.28
Euchone sp.[A]	36.58	9.48	18.57	8.70	*Myriochele oculata*[A]	30.00	4.55	17.65	5.91
Myriochele oculata[C]	17.42	5.97	11.70	4.23	*Prionospio steenstrupi*	10.50	2.65	10.30	3.01
Prionospio cirrobranchiata	15.58	5.44	10.65	3.78	*Armandia intermedia*	23.17	2.56	9.93	4.34
Prionospio steenstrupi	14.75	5.09	9.97	3.01	*Litocorsa acuminata*	17.92	1.38	5.36	2.76
					Ophryotrocha adherens[C]	33.00	0.79	3.05	4.94
Group Control					**Group Impact**				
Avg. similarity = 44.88					Avg. similarity = 24.80				
Litocorsa acuminata[C]	32.92	10.23	22.80	5.47	*Capitella capitata*[B]	98.63	7.50	30.26	8.06
Myriochele oculata	23.54	6.47	14.41	3.92	*Ophryotrocha adherens*[A]	85.46	3.21	12.94	9.44
Euchone sp.[B]	22.54	4.06	9.05	5.80	*Myriochele oculata*[C]	30.38	2.55	10.29	5.20
Pionosyllis heterocirrata[A]	37.63	3.82	8.51	6.26	*Armandia intermedia*	21.00	1.79	7.23	3.65
Prionospio cirrobranchiata	13.29	3.44	7.67	3.34	*Hesionidae* sp.	11.54	1.59	6.42	1.39

Table 4. Results of SIMPER analyses identifying species that contribute most to dissimilarity of compared samples within a group as well as dissimilarity between group samples. [A,B,C] indicate rank of each discriminating species based on dissimilarity for each site

Species	Avg. abundance		Avg. dissim.	Contrib. (%)	Ratio	Species	Avg. abundance		Avg. dissim.	Contrib. (%)	Ratio
Groups	**E**	**FW**				**Groups**	**U**	**W**			
Avg. dissimilarity = 63.78						Avg. dissimilarity = 76.74					
Pionosyllis heterocirrata	73.33[A]	1.92	13.63	21.38	7.57	*Ophryotrocha adherens*	137.92[A]	33.00	17.85	23.26	19.19
Euchone sp.	8.50	36.58[B]	6.37	9.98	5.95	*Capitella capitata*	93.75	103.50[B]	16.88	22.00	15.78
Litocorsa acuminata	35.25	30.58[C]	3.87	6.07	2.91	*Myriochele oculata*	30.75[C]	30.00	7.31	9.52	8.12
Myriochele oculata	29.67	17.42	3.62	5.67	2.62	*Armandia intermedia*	18.83	23.17	5.33	6.95	7.51
Prionospio cirrifera	22.75	6.58	3.46	5.43	2.10	*Litocorsa acuminata*	9.75	17.92	3.18	4.14	3.83
Groups	**E**	**W**				**Groups**	**U**	**FW**			
Avg. dissimilarity = 78.46						Avg. dissimilarity = 88.07					
Pionosyllis heterocirrata	73.33[C]	4.42	12.38	15.79	8.14	*Ophryotrocha adherens*	137.92[A]	0.17	16.81	19.09	19.32
Capitella capitata	2.08	103.50[A]	9.35	11.92	16.40	*Capitella capitata*	93.75[B]	3.08	14.97	16.99	12.37
Litocorsa acuminata	35.25	17.92	5.63	7.18	3.99	*Euchone* sp.	0.33	36.58[C]	7.55	8.57	7.78
Myriochele oculata	29.67	30.00	5.57	7.10	4.76	*Litocorsa acuminata*	9.75	30.58	6.37	7.24	5.35
Ophryotrocha adherens	0.00	33.00[B]	5.44	6.94	12.65	*Myriochele oculata*	30.75	17.42	6.35	7.21	4.96
Armandia intermedia	8.58	23.17	3.99	5.08	5.96	*Neanthes arenaceodentata*	13.17	0.08	3.29	3.73	5.77
Groups	**E**	**U**				**Groups**	**W**	**FW**			
Avg. dissimilarity = 85.65						Avg. dissimilarity = 73.40					
Ophryotrocha adherens	0.00	137.92[A]	14.09	16.45	16.98	*Capitella capitata*	103.50[A]	3.08	10.93	14.90	17.92
Capitella capitata	2.08	93.75[B]	12.26	14.32	10.13	*Euchone* sp.	8.75	36.58	8.48	11.55	8.15
Pionosyllis heterocirrata	73.33[C]	12.67	9.72	11.35	7.97	*Litocorsa acuminata*	17.92	30.58	6.88	9.38	4.99
Myriochele oculata	29.67	30.75	6.06	7.08	3.86	*Ophryotrocha adherens*	33.00[B]	0.17	6.84	9.32	15.55
Litocorsa acuminata	35.25	9.75	5.46	6.37	3.93	*Myriochele oculata*	30.00	17.42	6.63	9.04	7.37
						Armandia intermedia	23.17[C]	2.75	5.41	7.37	8.45
Groups	**Control**	**Impacted**									
Avg. dissimilarity = 81.39											
Capitella capitata	2.58	98.63[B]	11.88	14.59	14.67						
Ophryotrocha adherens	0.08	85.46[A]	10.80	13.27	16.88						
Pionosyllis heterocirrata	37.63[C]	8.54	6.19	7.61	7.64						
Myriochele oculata	23.54	30.38	6.15	7.56	5.39						
Litocorsa acuminata	32.92	13.83	6.09	7.48	4.65						
Euchone sp.	22.54	4.54	4.85	5.96	6.55						
Armandia intermedia	5.67	21.00	3.70	4.55	6.07						

DISCUSSION

Granulometric profiles have shown slight variation over the course of the study, but the general trends are apparent (Fig. 3). Sediment compositions between the 4 study sites are highly similar and would not likely affect infaunal community structure. Lowered ORP values resulting from microbial degradation of accumulated organic detritus may be indicative of geochemical factors affecting infaunal composition. Changes in sediment color as well as ORP may be an indication of detrimental effects of nutrient influx from the fish enclosure. Organic matter loading creates anoxic conditions due to excessive microbial oxygen consumption. Microbial sulfate reduction leads to accumulated sulfides in sediments and creates a chemical oxygen demand (Hargrave 1994). We observed a general trend of increasing difference between the average ORP values of control and impacted sites over time, indicating a shift toward anaerobic conditions

due to carbon influx from the fish cages. Anaerobic conditions may influence ecological dynamics of the benthic system. Organisms with varying defenses against sulfide toxicity can tolerate microbial sulfide metabolites or leave the affected area. Consequently, the sulfide concentration in the sediment will shape the infaunal community structure by displacing non-tolerant species (Vismann 1991).

The change in the infaunal community found under the fish enclosure over time follows the model progression for organic enrichment (Pearson & Rosenberg 1978). Due to organic enrichment from the fish enclosure, impacted sites had diversity values that were initially higher than control sites. Diversity decreased (Fig. 5) as the buildup of organic material continued (Fig. 1), following a pattern illustrated by Pearson & Rosenberg (1978). Infaunal communities under the cages were severely depressed in December 2002 when average Shannon-Weiner diversity values were among the lowest of the study and one Site U replicate

was nearly devoid of infauna. The Site U sediments from November 2001 had an enriched benthic environment with high Shannon-Weiner diversity values. At 13 mo after the initial sampling (November 2001), Site U from sampling 5 (December 2002) had evolved into a grossly polluted site with a severely depressed polychaete community (Fig. 5). The polychaete community found underneath the enclosure at Site U was the first to respond to changing environmental conditions. The polychaete community found 80 m down-current at site W followed, indicating that the footprint of effect had spread from beyond the immediate vicinity of the enclosure to nearby environments. By the November 2004 sampling, Sites U and W had become highly similar in polychaete community structure.

The nMDS ordination illustrates relatively little species turnover occurring in control sites compared to high species turnover in impacted sites. The relative lack of species turnover at control sites indicates that there may not be a noticeable seasonal trend in species composition or a natural cycle of succession in the area, a stark contrast to the communities found at impacted sites. Polychaete communities at impacted sites that were initially relatively similar to control site communities shifted in response to decreasing redox potential, possibly due to decreasing oxygen concentrations. This is evident in both univariate and multivariate statistical analyses. Regression analyses of univariate Shannon-Weiner diversity values indicate that diversity has decreased over time but increases with distance away from the effluent source. ANOSIM results also indicate significant differences in polychaete community structure over both space and time. However, when we break down the analysis by using subsets of data involving only the first 6 samplings, trends found in time are non-significant. This result is repeated by an analysis involving only the last 6 samplings. Concurrently, significant differences can be found between impacted and control sites in all analyses indicating significant effect of mariculture enrichment on polychaete community structure. This suggests that species turnover may occur over time in the absence of enrichment, but such a process is more gradual and only evident if we perform low-resolution analyses.

While species composition changed with each sampling, a few opportunistic polychaete species have consistently held the top rank of species abundance at impacted sites. The nearly exclusive presence of opportunistic polychaetes *Capitella capitata* and *Ophryotrocha adherens* at impacted sites suggests that they are indicative of perturbed environments. Likewise, the nearly exclusive presence of *Pionosyllis heterocirrata* and *Euchone* sp. at control sites suggests that their presence may be indicative of ambient environ-mental conditions unaffected by organic enrichment. This pattern of distribution was also found in previous benthic studies along the southern shores of O'ahu (Bailey-Brock 1996, Paavo et al. 2000, Bailey-Brock et al. 2001, Swartz et al. 2001, Bybee & Bailey-Brock 2003).

Benthic studies in the Mámala Bay region have shown that *Pionosyllis heterocirrata* is a widespread species whose presence is expected in the ambient infaunal community. *Euchone* sp. has been found to have an antithetical distribution to *Ophryotrocha adherens* in the benthos of nearby sewage outfall areas (Bailey-Brock et al. 2002, Swartz et al. 2003a,b, 2004). Having achieved high abundances during early stages of organic enrichment, a polychaete such as *Myriochele oculata* may be an early indicator of organic enrichment (Davis 1987). Its gradual disappearance with increasing intensity and duration of enrichment suggests a low tolerance of eutrophication effects. *C. capitata* populations respond to intermediate levels of organic enrichment and reach peak abundances before conditions in the environment are strongly enriched. The succession of indicators terminates with *O. adherens* that reach peak abundances when organic levels are high, anoxic conditions may be present and other species have declined. The presence of *O. adherens* and Capitellids has changed the trophic composition of the infaunal communities at impacted sites. Other studies have shown that both *C. capitata* and various *Ophryotrocha* spp. are opportunistic species tolerant of organic carbon loading (Bailey-Brock et. al. 2002, Brooks et al. 2003, Bybee & Bailey-Brock 2003, Davis 1987, Henderson & Ross 1995). We believe that *M. oculata*, *C. capitata* and *O. adherens* represent a succession of attrition to anoxia. Members of the ambient community show varying levels of tolerance to organic enrichment. Species that disappear under enriched nutrient regimes are less tolerant to attrition from anoxia. Indicator species such as *M. oculata*, *C. capitata* and *O. adherens* are increasingly more tolerant to attrition resulting from enrichment anoxia and increasingly better competitors under hypernutrification.

Infaunal communities found at control sites have been characterized by species commonly found in ambient infaunal communities unaffected by enrichment processes. Species such as *Pionosyllis heterocirrata* are ubiquitously found throughout the southern shore of O'ahu (Bailey-Brock 1996, Bailey-Brock et al. 2002, Swartz et al. 2004), which leads us to believe that it is a regional indicator of benthic health. *Litocorsa acuminata* and *Euchone* sp. are not as ubiquitously found throughout Mámala Bay but were commonly found species in nearby sewage outfall benthic studies (Swartz et al. 2003a,b). These results reflect the find-

ings of similar benthic studies conducted within Mámala Bay (Bailey-Brock et al. 2002). The relative consistency of the infaunal community structure found at control sites in this and other nearby benthic studies serves as a benchmark for benthic health in the region.

The conclusions based on these data indicate that the gradual buildup of organic detritus under the cage has drastically changed the infaunal community structure by displacing indicators of healthy benthic environments such as *Pionosyllis heterocirrata* with indicators of organic enrichment, such as *Capitella capitata* and *Ophryotrocha adherens*. Evolution of the benthic environment is illustrated by the nMDS as well as average Shannon-Weiner diversity values. The progression of Site U from a slightly enriched site in November 2001 to a grossly affected site by December 2002 is illustrated in reference to a generalized Pearson-Rosenberg model (Fig. 9). The nMDS illustrates the evolution of Site W from a normal to slightly enriched site in November 2001 to a heavily impacted site by June 2003. The comparisons display examples of both temporal and spatial applications of the Pearson-Rosenberg model. Site U, which is directly under the mariculture enclosures, reflects results of the most intense nutrient enrichment effects. At 40 m down-current Site W is influenced by a diluted nutrient enrichment regime. While the benthos at Site U had reached grossly affected conditions within 13 mo of sampling, the benthos at Site W only reached indicated heavily impacted conditions in 23 mo. Shannon-Weiner diversity values at Site W and nMDS results show that sustained changes in community structure at

Site W were evident beginning with the October 2003 sampling. Results of earlier studies showed similar responses of Capitellids and *O. adherens* to fish food and wastes (Bybee & Bailey-Brock 2002). Population abundances returned to preculture levels in less than 2 mo after feeding ended. It is not known if the infauna would return to preculture levels in the present case because both the stocking density and duration under culture conditions have increased, resulting in larger amounts of feed added and affected bottom. Although the footprint of eutrophication effects increased westward during this study, influences were localized to areas immediately surrounding the fish enclosure as neither the MDS nor Shannon-Weiner diversity levels at Site FW (390 m down-current) indicated notable changes in infaunal community structure. This may be attributed to one of the advantages of open-water mariculture over those established in embayments: more rapid dilution and dispersal of the nutrient wastes due to greater volume of water flow through the enclosure site. Despite the open-water location and alongshore currents, the effects of fish feed and waste on the benthic polychaete community were evident.

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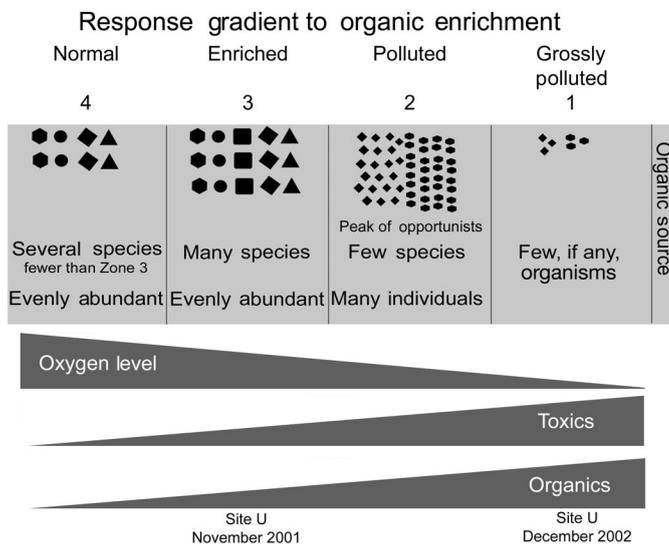
Response gradient to organic enrichment

Fig. 9. Pearson-Rosenberg's model predicts a response gradient to organic enrichment. Species richness is highest in Zone 3 where an optimal balance between organic levels and oxygen levels facilitates infaunal community growth. This model is applicable to both temporal and geographical scales

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