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Partial recovery of infaunal communities during a fallow period at an open-ocean aquaculture

David T. Lin[1,*], Julie H. Bailey-Brock[1,2]

[1]Department of Zoology, University of Hawai'i at Mānoa, 2538 McCarthy Mall, Edmondson Hall 152, Honolulu, Hawai'i 96822, USA
[2]Water Resources Research Center, University of Hawai'i at Mānoa, 2540 Dole Street, Honolulu, Hawai'i 96822, USA

ABSTRACT: Open-ocean or offshore aquaculture has attracted recent controversy for its potential environmental impacts and proposed expansion in the USA. Organic enrichment of benthic marine communities has been documented extensively under nearshore fish farms — primarily from fish feces and feed pellets — but relatively few studies have examined the effects of deeper, offshore operations. In this study, we investigate the effects of a 6 mo non-operational fallow period on benthic invertebrate communities surrounding a commercial offshore fish farm. Polychaete species diversity and community structure were analyzed at distant reference sites and farm-adjacent affected sites before, during and after the fallow period. The relative abundances of 3 polychaete indicator species for organic enrichment were also analyzed. During the fallow period, community structure at affected sites became more similar to communities at distant reference sites. Additionally, the sudden disappearance of enrichment indicator species at previously affected sites during the fallow period further suggests the beginnings of a recovery. However, species diversity did not increase significantly during the fallow period, indicating that the affected communities had not been fully restored to pre-culture or distant reference conditions. This study demonstrates the potential environmental benefits of scheduled fallow periods or crop rotations in offshore aquaculture.

KEY WORDS: Aquaculture · Fallow · Recovery · Organic enrichment · Offshore · Indicator species · Polychaete · Hawai'i

INTRODUCTION

Open-ocean or offshore cage operations are a relatively new technology in commercial fish aquaculture. They were developed with the intent to reduce the environmental effects that arise from shallow nearshore operations such as organic enrichment from fish fecal wastes and excess fish feed (Naylor 2006a). Organic enrichment can lead to decreased benthic diversity, enhanced microbial growth and anoxic or reducing conditions in sediments (Wu 1995, Hall-Spencer et al. 2006, Pergent-Martini et al. 2006). Moving fish culture operations to deeper offshore sites can potentially allow prevailing currents and the surrounding water mass to dilute and disperse fish waste products and excess feed, thus potentially reducing their environmental effects (Fernandes et al. 2001, Henderson et al. 2001). However, very few studies have investigated the effectiveness of this 'dilution solution' (Naylor 2006a) for farms operating at commercial-scale production rates (but see Lee et al. 2006). Open-ocean aquaculture has attracted recent controversy in the USA after legislation was proposed to permit farming operations to expand into federal waters 5.6 to 370 km offshore. The National Offshore Aquaculture Act of 2005 (S. 1195, http://aquaculture.noaa.gov/us/2005.html) drew strong criticism for omitting proper legal safeguards against any environmental impacts (Goudey et al. 2006, Naylor 2006a,b), and calls were made for further research on the effects of open-ocean farming (Marine Aquaculture Task Force 2007).

The environmental effects of nearshore commercial fish culture have been well documented (Wu 1995, Goldburg et al. 2001, Kalantzi & Karakassis 2006, Pergent-Martini et al. 2006), and there is a growing body of literature on the potential recovery of affected

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[*]Email: david.t.lin@ucla.edu

benthic communities after organic enrichment is halted or temporarily paused (Table 1). To our knowledge, there have been no previous studies of benthic recovery around offshore, open-ocean fish farms. It is possible that the environmental effects of organic enrichment can be mitigated by planned cessations in farming operations or rotational 'fallow periods' among multiple farming sites, net-pens or fish cages. Fallow periods may also benefit the aquaculturists. Mandatory fallow periods have been instituted in Maine and Norway to 'break the life cycle' of fish parasites and diseases plaguing some nearshore salmon farms (Holm et al. 2003, Marine Aquaculture Task Force 2007). Similar practices of fallow crop rotation have been commonplace in terrestrial agriculture for centuries in an effort to thwart pests, increase farm productivity and move towards environmental sustainability (Bailey 1908).

One of the first studies of the benthic environmental effects of open-ocean aquaculture was conducted off southern O'ahu in Mamala Bay, Hawai'i (Bybee & Bailey-Brock 2003, Lee et al. 2006). The investigators documented reduced benthic invertebrate diversity, low oxygen levels in surface sediments and increased abundances of organic enrichment indicator species in locations closest to the commercial fish farm (Lee et al. 2006). These findings are consistent with those made at shallower nearshore locations with similar intensive fish culture (Tsutsumi 1987, 1995, Henderson & Ross 1995, Yokoyama 2002) and closely follow the Pearson & Rosenberg (1978) model of benthic community response to organic enrichment. The Hawai'i study was the first in a tropical setting featuring open-ocean cage fish culture (Lee et al. 2006).

This previously monitored Hawai'i fish farm (Lee et al. 2006) provided a unique opportunity to study a temporary cessation in offshore aquaculture operations when fish fry production was interrupted and the cages were left fallow for 6 mo. Such a long fallow period without stocked fish and a complete cessation of feeding in a tropical coastal environment is rare and unknown in the literature. When in operation, Pacific threadfin *Polydactylus sexfilis*, or moi, is grown successfully in submerged mesh cages anchored over a sand bottom at depths between 31 and 39 m. Commercially produced pellet feed is added daily directly into the cages, providing optimum nutrition for growth. This feeding routine proved successful and thousands of kilograms of fish have been marketed each month since 2001. This study examines changes in the benthic community residing in the sediments under and around the fish farm when the cages were not operational. During this time, no fish or feed pellets were added to the cages (R. Cates pers. comm.).

Table 1. Summary of previous studies conducted on fish culture fallow periods or operational cessations. nr = not reported

Cultured species	Location	Substrate[a]	Depth (m)	Current flow (cm s^{-1})	Fallow time (mo)	Biological recovery response after fallow period	Source
Seabream	Minorca, Spain	Seagrass	5.5	nr	36	'[Seagrass] decline is still occurring'	Delgado et al. (1999)
Seabream and sea bass	W Greece	Silt	19	nr	23	'Not fully recovered' under farm; partial recovery at site 10 m away	Karakassis et al. (1999)
Salmon	British Columbia, Canada	Sandy silt	47.7–56.0	3.4	6	'Biological remediation was complete' compared with reference sites	Brooks et al. (2003)
Salmon	British Columbia, Canada	Silty sand	34.1–39.0	5.9	48	Biological remediation not complete compared with reference sites	Brooks et al. (2004)
Salmon	SE Tasmania, Australia	Silt–clay	20–22	3.4–4.3	36	'Remained impacted' compared with reference sites	Macleod et al. (2004)
Salmon	W Scotland	Silt	19	3.8	15	'Still highly impacted […] with opportunistic species dominant'	Pereira et al. (2004)
Salmon	SE Tasmania						Macleod et al. (2006, 2007)
	Creeses Mistake	Sand	20	2–4[b]	3	Partial recovery, remained different compared with reference sites	
	Stringers Cove	Silt–clay	40	2–4[b]	3	Partial recovery, faster recovery than exposed site	
Bluefin tuna	SE Spain	Sand	32	6.0	6	Partial recovery, 'stressed community' under farm	Vita & Marin (2007)
Pacific threadfin	O'ahu, HI, USA	Sand	31–39	30–50	6	Partial recovery, remained different compared with reference sites	This study

[a] After Shepard (1954)
[b] C. Macleod (pers. comm.)

It was expected that the previously affected benthic community under the fish cages would become more similar to reference sites and/or begin to recover to pre-disturbance conditions. We hypothesized an increase in polychaete species diversity under the fish cages during the fallow period relative to reference sites as predicted by the Pearson & Rosenberg (1978) model. The extent of this diversity increase would be one measure of the degree of recovery of the affected community at this location. It was also expected that polychaete community structure (species composition) would become more similar across reference and affected sites during the fallow period. Lastly, the disappearance of specific disturbance indicator species from affected sites was expected, suggesting the beginning of a recovery.

The present study is the first to examine the ecological effects of a non-operational fallow period on affected benthic communities surrounding a commercial offshore fish farm. The offshore nature of this study makes it particularly pertinent to ongoing discussions regarding open-ocean aquaculture environmental regulations in the USA. We provide evidence suggesting a partial recovery of previously degraded infaunal polychaete communities during the fallow period, as well as their sudden decline after farming operations resumed. Additionally, we discuss various factors influencing the degree and rate of ecological recovery from benthic aquacultural impacts.

MATERIALS AND METHODS

Study sites. This study was conducted around a privately owned and operated fish farm raising Pacific threadfin. Four submerged open-ocean aquaculture cages are anchored at a designated leased site over a sand bottom approximately 2.3 km offshore of ‘Ewa Beach, O‘ahu, Hawai‘i. These biconical structures are submerged about 10 m above the bottom in water column depths of 31 to 39 m. Each cage encloses ca. 3000 m^3 and can hold 130 000 fish. All cages were not equally stocked; sometimes 2 age classes of fish were raised concurrently in a cage. Since commercial operations began in November 2001, the fish farm has expanded from a single experimental cage to its current status with 4 cages and has harvested on average 52 000 to 55 000 kg yr^{-1} (R. Cates pers. comm.).

The fish farm was allowed to run fallow for slightly over 6 mo beginning on 20 August 2006 after completing a harvest. During the fallow period, no feed pellets or fingerling fish were added to the cages. Farming operations resumed on 8 March 2007 when approximately 100 000 fingerling fish were added to one cage. Feeding resumed at 40 to 50 kg d^{-1} and increased to approximately 100 kg d^{-1} within 1 mo (R. Cates pers. comm.).

Six sampling sites were identified at the aquaculture cages and at varying distances from them (Fig. 1). Two affected sites under and near the cages (U and W) and 2 distant reference sites (FW and E) were identified previously (Lee et al. 2006). The sampling site under the first original fish cage was designated Site U. Site W was located 80 m to the west and down current. Two far-field reference sites were used 390 m to the west (Site FW) and 360 m to the east (Site E). Additionally, 2 intermediate sites were added for this study: near west (Site NW) between Sites W and FW, and near east (Site NE) between Sites U and E. All sampling sites were at approximately the same depth between 39 and 41 m except for Site NE at 45 m. All sites are influenced by current patterns predominantly moving westward between 30 and 50 cm s^{-1} (Roberts 1995).

Sampling methods: benthic invertebrates. Collection of benthic samples by SCUBA divers was identical to the methods used in the previous study (Lee et al. 2006) and was conducted by the same personnel. Benthic samples were collected using hand tube corers (11 cm diameter, 5 cm deep) over 19 sampling periods from November 2001 to May 2007. In particular, 2 collections were made during the fallow period in mid-September 2006 and early December 2006. Sampling after the end of the fallow period was done in late May 2007, 3 wk after fish were re-stocked. Three replicates were collected from each station, except for September 2006, December 2006 and May 2007 samplings, when 5 replicates were collected. Samples were fixed in 15%

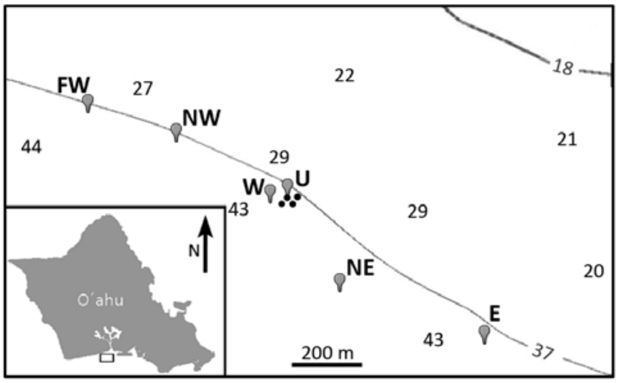

Fig. 1. Study area on the southern coast of O‘ahu, Hawai‘i (inset). Site U is located under the first fish culture cage, Site W is 80 m to the west, Site NW is 250 m distant, Site FW is 390 m distant, Site NE is 170 m distant and Site E is 360 m away. Depth soundings reported in meters (rounded to the nearest meter). Grey drop-marks indicate approximate sample site locations and black circles indicate fish cage sites. Sites FW, NE and E were considered control or reference sites in this study. Map modified from NOAA nautical chart #19362

formalin with rose bengal solution and later elutriated over a 0.5 mm mesh sieve to remove the infauna according to procedures detailed by Sanders (1958). Specimens preserved in 70% ethanol were sorted and identified to the lowest possible taxonomic level with the aid of dissecting and compound microscopes.

Sampling methods: environmental variables. Oxidation and reduction potential (ORP) measurements were made in the field with a handheld Oakton ORPTestr 10 meter by placing the probe on the water-covered sediment when the sample containers were brought aboard the boat by the SCUBA divers. After ORP measurements were completed, formalin was added to the containers to fix the benthos.

Sediment grain sizes were assessed by means of a wet sieve gravimetric method (McCarthy 1996). All grain size fractions were oven-dried at 80°C for at least 12 h before weighing. Characterization of the substrate — based on 8 consecutive samplings of sediment during a 3 yr period — showed consistent grain size proportions at each of the original 4 sampling sites, Sites U, W, FW and E (Lee et al. 2006). As the composition of grain sizes had not changed by the 8th sampling from a predominantly medium to fine sand profile at all stations, granulometry was discontinued. Further grain size analyses were considered unnecessary because the 2 additional samplings sites were located between the existing sites.

Data analysis. Shannon diversity (H' log-transformed data) was calculated for polychaete infauna in each replicate sediment core for all sampling dates. Spatial and temporal variation in H' was analyzed by ANOVA, using sampling date and location as factors for one reference and one treatment site (Sites E and U, respectively). Pre-planned ANOVA contrasts were used to test our *a priori* hypothesis of an increase in Shannon diversity under the fish culture cages during the fallow period. Data transformations were not needed to meet the assumptions of the analysis. ANOVA was also used to compare diversity between reference and treatment sites during the fallow period.

Changes in community structure were analyzed using a Bray-Curtis similarity matrix. Bray-Curtis coefficients were calculated based on the similarity of polychaete community species composition between samples. Samples with many species in common at similar abundances had high Bray-Curtis similarity coefficients. Construction of the Bray-Curtis similarity matrix was based on polychaete abundance data pooled across replicate sediment cores (n = 3 or 5) at each site and for each sampling date, divided by the number of replicates and then 4th-root transformed.

The Bray-Curtis similarity matrix was used for a 2-factor analysis of similarities (ANOSIM; Clarke & Warwick 2001) crossed between sampling dates and sites. This procedure tested for significant differences in overall polychaete community structure between sampling dates using averaged site values and between sites using averaged sampling date values. A 1-factor ANOSIM and subsequent planned comparisons were used to test for significant differences in community structure among treatment groups (operational versus fallow versus reference). Each ANOSIM procedure was run through 999 permutations. Results from the Bray-Curtis similarity matrix were visualized in a non-metric multidimensional scaling (nMDS) plot.

Statistical analyses were performed with R-2.6.0 (R Development Core Team 2007), SPSS 16 (SPSS 2007) and PRIMER 6 (PRIMER-E 2006).

RESULTS

Oxidation–reduction potential

Negative ORP values were reported at all sampling sites prior to the fallow period. Lowest possible average values of –50 mV were recorded at Sites U, NE, W and FW. Site E had positive values at the 4 samplings prior to the fallow period with one exception while all other stations had 2 or more samplings with negative readings. During the fallow period, the 2 samplings (September 2006 and December 2006) had positive values within a range of +20 to +95 mV. Post-fallow period ORP values (May 2007) were not available for analysis.

Infaunal data

Three polychaete species were identified from the literature as positive indicators of organic enrichment to the benthos: *Capitella capitata* (Grassle & Grassle 1974, Tsutsumi 1987), *Neanthes arenaceodentata* and *Ophryotrocha adherens* (Bailey-Brock et al. 2002, Lee et al. 2006). Cumulative abundances for these 3 indicator species at each site are shown in Fig. 2, beginning from our first sampling in November 2001 to the fallow period. Abundance is given as a mean percentage of the total number of individuals at each site averaged across replicates (n = 3 or 5). Five replicates were used from all samplings after December 2005. The relative abundance of the indicator species increased after commercial aquaculture operations began in November 2001 at near-cage Sites U and W, and later at intermediate Site NE as previously reported (Lee et al. 2006). Indicator species appear to have become rare or absent under and near the fish cages during the fallow period. A sharp decline in the abundance of the 3 polychaete indicator species was

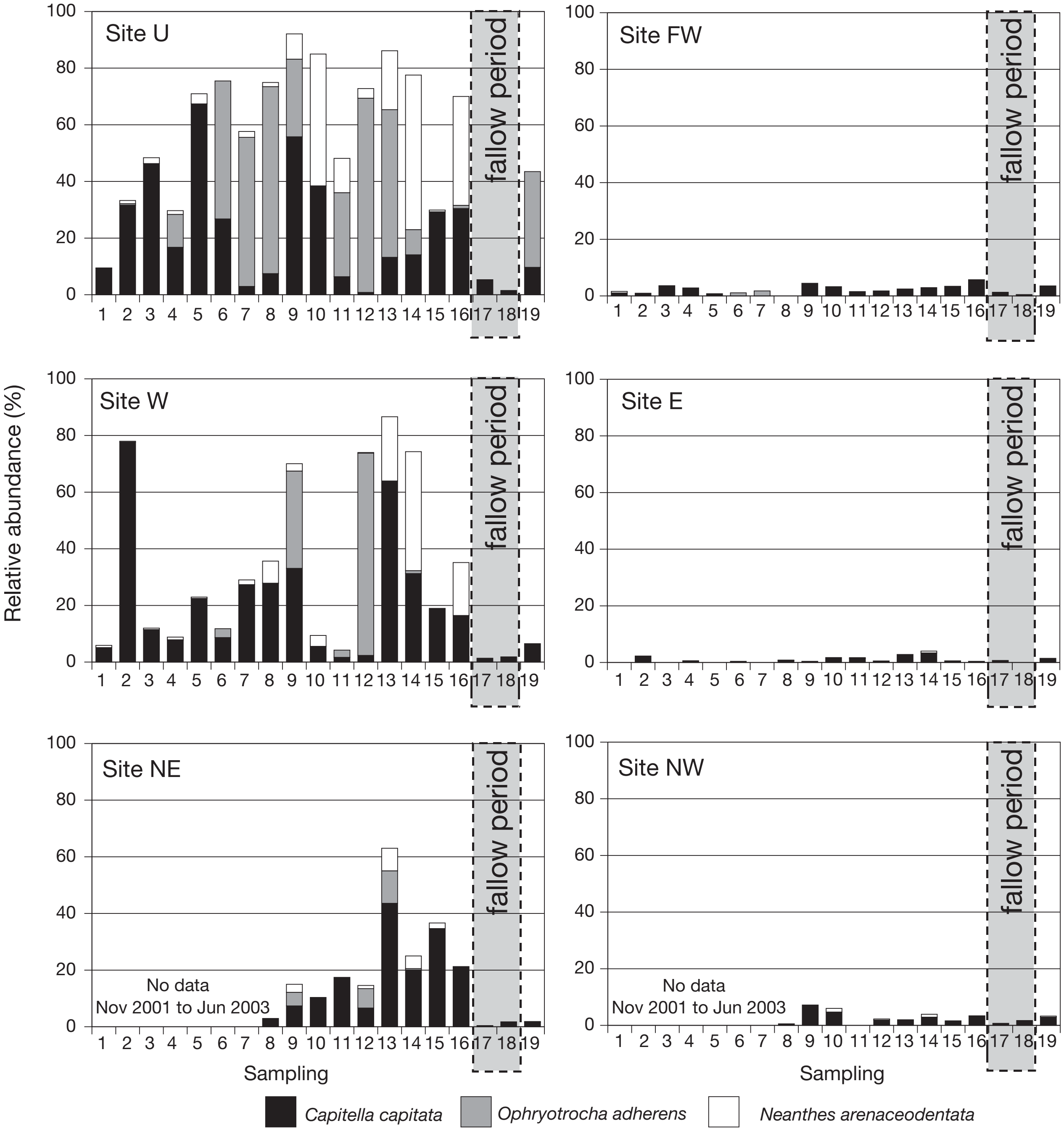

Fig. 2. Relative abundances of the known organic enrichment indicator species as a percentage of total polychaete abundances at each sampling site. Numbers represent sample dates, 1: Nov 2001; 2: Jan 2002; 3: Apr 2002; 4: Jul 2002; 5: Dec 2002; 6: Feb 2003; 7: Jun 2003; 8: Oct 2003; 9: Feb 2004; 10: May 2004; 11: Sep 2004; 12: Nov 2004; 13: Jan 2005; 14: May 2005; 15: Aug 2005; 16: Dec 2005; 17: Sep 2006; 18: Dec 2006; 19: May 2007

noted at Sites U, W and NE beginning in September 2006 and continuing until the end of the fallow period. During this period, there was a complete absence of the indicator species *Neanthes arenaceodentata* and *Ophryotrocha adherens* from all sampling sites (Fig. 2).

After the end of the fallow period in May 2007, indicator species were found under the fish cages at Site U (Fig. 2). *Ophryotrocha adherens* was the most abundant polychaete at Site U, accounting for 34% of all polychaetes, but was virtually absent from the other sites.

Species diversity

The difference in Shannon diversity between reference and treatment sites (E and U, respectively) changed significantly with time over all sampling dates (Site × Sampling: $F_{5,36} = 3.36$, $p < 0.05$; Fig. 3). However, a pre-planned contrast on this Site × Sampling interaction between the sites during the fallow period (sampling dates September 2006 and December 2006) and all other sampling periods was not significant ($F_{1,36} = 1.18$, $p = 0.286$). During the latest fallow period sampling in December 2006, Shannon diversity was significantly lower at treatment Site U compared with reference Site E ($F_{1,8} = 11.06$, $p < 0.05$).

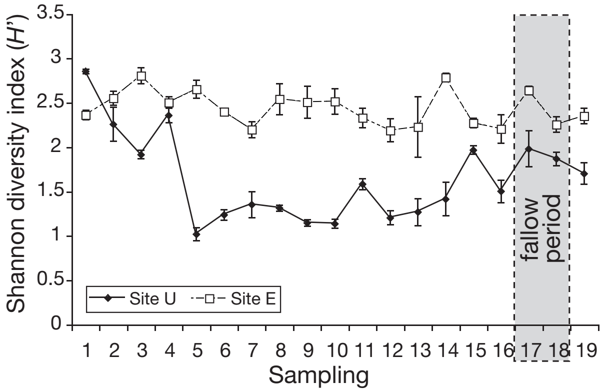

Fig. 3. Shannon diversity index values for polychaete communities at Sites U and E. Error bars represent 1 SE. Sampling dates represented by numbers as in Fig. 2

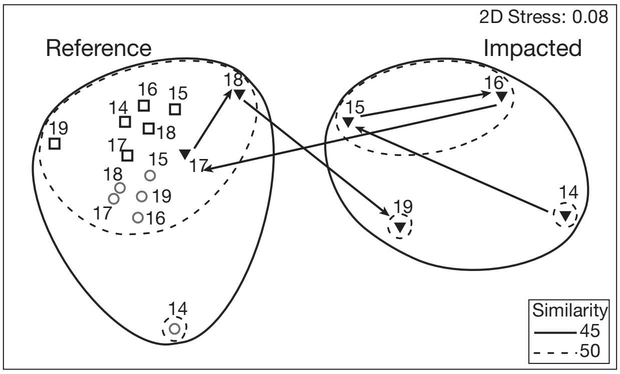

Fig. 4. The non-metric multidimensional scaling (nMDS) plot illustrates Bray-Curtis similarities in community structure on a 2-dimensional plot. Sites: ○: E; ▼: U; □: FW. Distances between points on the plot indicate relative similarity between infaunal communities of those 2 points. Arrows between points have been added to indicate the temporal sequence of change in community structure at Site U. Circles indicate similarity levels as shown on figure. Sampling dates represented by numbers as in Fig. 2

Community structure

The 2-factor crossed ANOSIM determined significant differences in community structure between sites averaged across all dates (global rho = 0.807, $p < 0.001$) as well as between sampling dates averaged across all sites (global rho = 0.632, $p < 0.001$). The 1-factor ANOSIM by treatment groups (fallow versus operational versus reference) with planned comparisons indicated that community structure at treatment Site U during the fallow sampling dates was significantly different from the community structure found there during farm operational periods (rho = 0.535, $p < 0.001$).

DISCUSSION

The ecological effects of a fish farm fallow period on soft-sediment benthic communities were investigated in terms of polychaete species diversity, community structure and the abundance of known organic enrichment indicator species. The difference in polychaete species diversity between reference and affected sites was not significantly lower during the fallow period in comparison with normal operational sampling periods. Additionally, species diversity at the end of the 6 mo fallow period remained significantly lower below the fish farm at the affected site relative to a distant reference site (Fig. 3). The fallow period did not appear to have any major effect on polychaete species diversity in the previously affected benthic community.

Overall community structure — in terms of species composition and abundance — was also analyzed by site location and sampling period. The nMDS plot (Fig. 4) illustrates relatively little change in community structure (little species turnover) at reference sites over the course of this study. The relative lack of change in community structure at these locations (Sites E and FW) indicates an absence of any major seasonal trends or natural succession patterns — a stark contrast to the affected community (Site U). The graphic information in Fig. 4 also reveals major changes in community structure at affected Site U during the fallow period (sampling periods 17 and 18 in Fig. 4; September 2006 and December 2006, respectively). ANOSIM results indicate significant differences in community structure between the operational and fallow period samplings at impacted Site U.

The occurrence of certain organic enrichment indicator species was also used to assess the effects of the fallow period on the benthos. While species diversity did not change dramatically in response to the fallow period, the sudden and unprecedented decline of previously common enrichment indicator species was noted (Fig. 2; sampling periods 17 and 18). Intensive commercial fish culture activity at the cage site beginning in 2001 led to an eventual dominance of the infaunal polychaetes *Capitella capitata*, *Ophryotrocha adherens* and *Neanthes arenaceodentata* (Lee et al. 2006). However, the relative abundance of these 3 enrichment indicator species decreased rapidly underneath the fish cages (Site U) from 70% of all polychaetes in December 2005 to 5.3% in September 2006, just 1 mo after the fallow period began. Adjacent near-cage Sites NE and W displayed similar trends with indicator species approaching 0% during the fallow period. An earlier sharp decline in the relative abundance of the 3 indicator species at affected Site W was observed in May 2004 and September 2004 (Fig. 2). However, this occurrence can largely be explained by a sudden increase in the relative abundance of the polychaete *Myriochele oculata* in May 2004 and September 2004 (68 and 13% of all polychaetes, respectively) and *Armandia intermedia* in September 2004 (59% of all polychaetes). These 2 species have also been identified as possible enrichment indicators, although their utility has been far less documented than that for *C. capitata*, *N. arenaceodentata* and *O. adherens* (Bailey-Brock et al. 2002). *M. oculata* and *A. intermedia* accounted for a relatively small proportion of the polychaete community during the fallow period. Thus, the dramatic decline of indicator species abundance observed at the near-cage sites during the fallow period was the first decline observed in the 7 yr since our benthic sampling began in November 2001.

Our analyses of overall polychaete community structure and indicator species abundance suggest that the previously affected benthic community under the fish farm began to recover during a 6 mo non-operational fallow period. However, significant differences in community structure and species diversity between reference and near-cage sites at the end of the fallow period indicate that these communities have not been fully restored to pre-culture or reference conditions. Additionally, polychaete species diversity did not significantly increase at the affected site during the fallow period, relative to a reference site. It is possible that species diversity is a more sensitive indicator of whole-community health, and the community may require more time to reassemble following such a lengthy 'press' disturbance.

It is also important to note that both community structure (Fig. 4) and the abundance of indicator species (Fig. 2) changed greatly at the end of the fallow period when fish farming operations resumed in early March 2007. This combined evidence suggests a rapid return to earlier affected conditions.

Previous studies on the effects of fallow periods or complete farming cessations on the benthic community have almost exclusively occurred in shallow, temperate and nearshore waters (Table 1). Some studies have reported complete 'biological remediation' within a mere 6 mo of fallowing onset (Brooks et al. 2003) while others saw no full recovery or even continuing declines 3 to 4 yr after farming ended (Delgado et al. 1999, Brooks et al. 2004, Macleod et al. 2004). Differences in hydrodynamic properties such as current velocity and tidal flushing can greatly influence the degree and rate of these fallow period or post-farming recoveries (Brooks et al. 2003). Our study presents a unique case with an offshore aquaculture operation in relatively fast currents (30 to 50 cm s^{-1}; Roberts 1995). Although we documented only a partial recovery of affected benthic communities after a 6 mo fallowing, a lesser degree of recovery might have been observed had the fish cages been shallower or situated in calmer waters. Thus, the hydrodynamic properties around the open-ocean fish farm possibly aided in the partial recovery. Extending the fallowing time might have assisted in an eventual restoration to pre-culture conditions, although further study is needed to determine a proper fallow period length. Our study demonstrates the potential value of scheduled fallow periods or crop rotations in offshore aquaculture to mitigate benthic environmental impacts. Additionally, such fallow periods could potentially improve culture conditions and minimize fish disease risks to increase farm productivity.

Open-ocean or offshore aquaculture has attracted recent controversy in the USA due to government efforts to promote new operations in federal waters (Goudey et al. 2006, Naylor 2006b). There have been several calls for environmental safeguards to be added to the proposed legislation (Naylor 2006a,b, Marine Aquaculture Task Force 2007), and we hope that our findings can contribute to the development of such safeguards in an effort to promote sustainable aquaculture.

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