SOUTHERN CALIFORNIA ACADEMY OF SCIENCES

BULLETIN

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Abstract.—One of the primary challenges to detecting anthropogenic environmental impacts is the high degree of spatial and temporal variability inherent in natural systems. Planned or routine events that result in disturbance to populations and communities provide an opportunity for scientists to apply well-replicated and statistically powerful sampling designs to assess subsequent biological effects. For example, a thick layer of sessile invertebrates is the prominent biotic feature of intertidal and shallow subtidal portions of offshore petroleum platforms in southern California. Given the central role of such invertebrates in providing food and shelter, their presence can reasonably be expected to influence associated fish community structure. At one platform on the San Pedro Shelf, invertebrate biomass was completely removed from support pilings and horizontal crossmembers to a depth of 20 m with high-pressure water during a standard "hydrocleaning" event in November 2007. Three nearby platforms remained undisturbed, providing a unique opportunity to test for disturbance-related changes in the local fish assemblage and the overall time course of community recovery. The potential impact of the abrupt and intense removal of the invertebrate layer was assessed with survey data collected periodically for one year prior- and one year post-hydrocleaning in a modified Before-After-Control-Impact (BACI) design. Asymmetrical multivariate analyses of variance revealed a significant effect of disturbance to fish, driven largely by reductions in the abundance of numerically dominant blacksmith (*Chromis punctipinnis*). Nevertheless, the system was surprisingly resilient, recovering to pre-disturbance conditions within ten months. Our results demonstrate that a well-replicated BACI sampling design can detect even subtle biological changes in response to disturbance, a key step towards developing a mechanistic understanding of community disassembly in the face of increasingly frequent and intense perturbations.

Introduction

Natural and anthropogenic perturbations are a major driver of current and anticipated changes in population dynamics, species interactions, and community structure from local to global scales (Paine et al. 1998; Chapin et al. 2000). Resulting changes in biodiversity have the potential to significantly alter important ecosystem properties such as productivity, nutrient cycling and resistance to disturbance or invasion (references in Hooper et al. 2005). As a consequence, understanding the potential ecological effects of such changes has been the focus of intense theoretical and empirical research effort in

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recent years. Environmental variability is currently increasing in many parts of the world and ecological communities are experiencing associated increases in the intensity, frequency and scale of disturbance events (Easterling et al. 2000). Predicting how natural communities will likely respond to higher levels of disturbance has therefore been recognized as a critical research priority (Benedetti-Cecchi 2003; Boyce et al. 2006).

One of the primary challenges to detecting natural and anthropogenic environmental impacts is the high degree of temporal and spatial variability inherent in natural populations and communities. Many current sampling designs are based on Green's (1979) Before-After-Control-Impact (BACI) design. Replicated samples are taken before and after a putative environmental disturbance at both a control and the impact site. Evidence of a disturbance would be found as a statistically significant interaction between the differences in sample means in the two locations before versus after the disturbance (reviewed by Underwood 1993; 1994). Although widely used, conclusions drawn from such analyses do not provide a strong test for the presence of an impact, given their lack of spatial replication (i.e., there is only a single control and impact location). A more logical approach is to compare a potentially impacted site to multiple control locations; the existence of an impact can then be tested with asymmetrical analyses of variance (Underwood 1993; 1994). A disturbance that causes more change at the impact location than at the control locations will be detected as a different pattern of statistical interaction among sites before versus after the event, rather than as a main effect. This approach is both logically sound and statistically powerful, however, difficulty in predicting where or when a disturbance might take place means that the amount of pre-disturbance sampling is quite limited in most cases. Planned or routine disturbance events associated with human activities can provide an important opportunity to investigate the effects of disturbance on natural populations and communities with well-replicated BACI sampling designs.

In southern California, the intertidal and shallow subtidal portions of offshore petroleum platforms are blanketed by a variety of sessile invertebrates that includes bryozoans, sponges, tunicates, barnacles, and bivalves, particularly mussels (*Mytilus* spp.) and rock scallops (Bram et al. 2005). Held together by a web of byssal threads produced primarily by the mussels, the invertebrate layer can accumulate to thicknesses of greater than 30 cm (Continental Shelf Associates, Inc. 2005). The presence of this thick layer adds structural complexity to the otherwise smooth steel surface by providing three-dimensional habitat; such increases in local rugosity particularly benefit smaller mobile invertebrates and reef-associated fishes (Suchanek 1979; Friedlander and Parrish 1998; Lingo and Szedlmayer 2006). Mussels are the dominant competitor for primary space on hard substratum and support a diverse community of small invertebrates within the bed that are prey for abundant microcarnivorous fish that represent a key intermediate link in coastal marine food webs (Seed and Suchanek 1992; Page et al. 2007). Mussels also provide strong benthic-pelagic coupling, moving large amounts of energy from the water column to the benthos and are themselves a key source of food for various fishes, seastars, whelks, and crabs (Paine 1966; Wootton 1994).

The sessile invertebrate layer encrusting the submerged support pilings and horizontal cross-members of petroleum platforms can rapidly become extremely dense and heavy due to elevated growth rates resulting from constant immersion (Page 1986). High offshore primary production (e.g., high phytoplankton concentration) typically enhances food supply to filter-feeders, leading to higher survival, growth rates and reproductive output (Menge et al. 1997). Mussels held on moorings offshore from intertidal sites grow
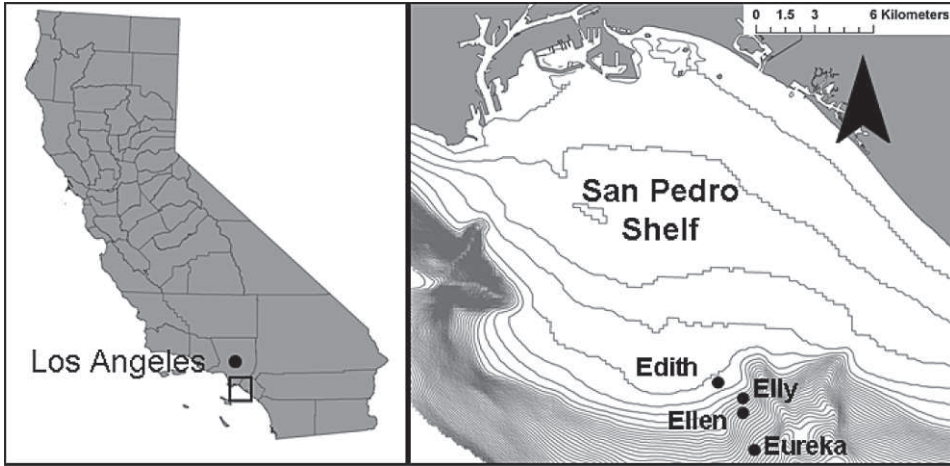
Fig. 1.   A bathymetry map of the San Pedro Shelf, southern California, USA, and the locations of the four offshore petroleum platforms surveyed in this study. Isobaths are in 10-m increments. Map created by C. Mireles (CSULB).

at much higher rates than those in the corresponding intertidal areas (Blanchette et al. 2007). On offshore petroleum platforms, the resulting high biomass levels create a safety concern for normal operations (G. Shackell, U.S. Minerals Management Service, pers. comm.), such that federal law requires the periodic removal of the invertebrate layer in order to maintain structural integrity of the platforms. The regular nature of this particular event presents a unique opportunity to investigate the potential effects of disturbance on a biological system.

The mid-water fish assemblages of petroleum platforms on the San Pedro Shelf are largely comprised of nearshore reef-associated species (Martin and Lowe 2010). As many of these species are typically dependent upon natural rocky reef habitats for shelter and prey, the dense invertebrate layer on these platforms presumably provides these resources in a location where they would otherwise not be found (Stephens et al. 2006). As a consequence, any changes in the abundance and distribution of *Mytilus* spp. on petroleum platforms will likely result in widespread and significant alterations to the species identity and relative abundances of platform-associated fish (e.g., Syms and Jones 2000). Here we use a spatially- and temporally-replicated BACI framework to document the effects of a hydrocleaning event on the associated mid-water fish community of a southern California petroleum platform, relative to multiple control locations. As there was only one hypothesized "impact" platform versus three "control" platforms, this is an asymmetrical design (Underwood 1993, 1994).

Methods

Fish abundance surveys

Bi-monthly mid-water fish surveys were conducted at four offshore petroleum platforms on the San Pedro Shelf between November 2006 and September 2008. All surveyed platforms (Edith, Ellen, Elly, and Eureka) were within a four-km^2 area in water depths ranging from 49 to 212 m (Fig. 1). Because of their close proximity to one another, surface water conditions (e.g., wave exposure, temperature, light, pH, and chlorophyll *a*) were similar among the four platforms (Martin 2009). In November 2007,

a routine hydrocleaning operation was conducted at platform Elly; this event removed most of the encrusting invertebrate layer to a depth of 20 m, converting species-rich spatially-heterogeneous biogenic habitat to species-poor spatially-homogeneous steel support beams. In contrast, the three other platforms remained undisturbed. All four platforms were surveyed seven times both before and after the hydrocleaning operation.

Methods used to survey fish assemblages at the SPS platforms were replicated from those used by Love et al. (2003). SCUBA divers identified, tallied, and estimated the length of all the fish encountered within a designated window along a volumetric belt transect (2 m $\times$ 2 m, except along the outside perimeter where the window was 6 m wide $\times$ 2 m high to potentially include platform-associated species in the nearby water column). One diver tallied and identified all fishes to the lowest possible taxonomic level and estimated fish total lengths into 5-cm intervals. A second diver followed while operating an underwater digital video camera. Video footage was used to calibrate fish identification and assess inter-observer variability. Surveys followed pre-determined transect patterns incorporating all major horizontal cross-members and vertical corner pilings at two depth levels: 7 m and 18 m (Love et al. 2003). The resulting species composition data were used to estimate ecological parameters typically of interest to managers, including fish density (number of fish 100 m^{-2}), biomass (kg 100 m^{-2}, calculated with established species-specific length-weight equations; Martin & Lowe 2010), and species richness.

Statistical analyses

Analyses to investigate the effects of hydrocleaning on platform-associated mid-water fish communities were based on a Before-After-Control-Impact (BACI) sampling design modified after Underwood (1993; 1994). Hypotheses about differences in fish assemblages were tested with asymmetrical distance-based permutational multivariate analysis of variance (PERMANOVA; PRIMER-E, Ltd., Plymouth, UK), a routine for testing the simultaneous response of multiple variables to one or more factors (Anderson 2001a; McArdle and Anderson 2001). This analysis tests for overall multivariate changes in community structure, which may include differences in composition, richness and/or abundances of individual species. A non-parametric procedure was used because, as with most studies of community structure, the multivariate data are not expected to meet the more stringent assumptions of traditional analyses (e.g., MANOVA). Furthermore, the power of MANOVA decreases rapidly as the number of variables (species) increases and there is no transformation available that will normalize a multivariate distribution with many zero counts (Scheiner 1993). The test statistic of PERMANOVA (*pseudo-F*) is a multivariate analogue of Fisher's *F* ratio and is calculated from a symmetric dissimilarity matrix; *P*-values are then obtained by permutation tests (Anderson 2001a, b). The primary advantage of PERMANOVA over standard rank-based non-parametric multivariate approaches (e.g., analysis of similarities, ANOSIM) is that the variation in response data can be explicitly partitioned according to complex experimental or sampling designs, including interactions among factors (Anderson et al. 2008). Asymmetrical permutational multivariate analyses of community responses to environmental impacts have already been successfully applied in other marine systems (e.g., Terlizzi et al. 2005). The assumption of homogeneity of dispersions was tested with the PERMDISP routine on data from the before period (Anderson et al. 2008).

Non-metric multidimensional scaling (nMDS; Field et al. 1982) was used to produce two-dimensional ordination plots displaying spatial and temporal variation in platform-

associated fish assemblages. All multivariate analyses were done on square root-transformed data using the Bray-Curtis similarity coefficient (Bray and Curtis 1957). This approach generally results in the more numerically dominant taxa having the largest contributions to similarity measures (Clarke 1993). The relative contribution of different fish species to observed variation in community structure was assessed with a "similarity percentages" routine (SIMPER; PRIMER-E, Ltd., Plymouth, UK) that calculates the percentage contribution of each species to the average Bray-Curtis dissimilarities between groups (Clarke 1993).

Hypotheses about overall fish density, biomass, species richness, and the densities of species with the highest relative contributions to community dissimilarity (as identified through SIMPER) were tested with univariate asymmetrical analyses of variance (Underwood 1993; 1994). Assumptions of additivity, homogeneity of variances, and normality were evaluated with interaction plots (before period) and residuals plots (Smith et al. 1993); where variances showed significant heterogeneity, the data were transformed using a $\ln(x + 1)$ function (Sokal and Rohlf 2011). Univariate analyses were done with SAS software, Version 9.3 (SAS Institute, Inc., Cary, NC).

Results

With respect to fish community structure, there was no evidence of differences in multivariate dispersions among platforms in the before period (PERMDISP, $F_{3, 24} = 2.16$, $P = 0.278$), suggesting that the samples are exchangeable under a true null hypothesis (Anderson et al. 2008). A significant interaction was not detected among control platforms on the San Pedro Shelf before the November 2007 hydrocleaning event and the period after the event (test of B × C; Table 1A), but a significant interaction was detected between platform Elly and the other platforms between periods (test of B × I; Table 1A).

These results show that the community structure did not vary significantly among the control platforms before and after the November 2007 hydrocleaning even; however, there was a significant interaction in the difference between Elly and the other platforms before hydrocleaning compared to after. Therefore, removing the invertebrate layer from an offshore petroleum platform with high pressure water had a statistically significant impact on the associated mid-water fish assemblage. This is also shown in the nMDS results where overlapping fish assemblages are present among all platforms prior to hydrocleaning (Fig. 2A), but clear differences among communities at platform Elly, compared to the others, are present after the event (Fig. 2B). While there was no evidence of a statistical interaction among the control and impact platforms before the hydrocleaning event, there was a significant interaction among locations after the disturbance. These results are consistent with the idea that the hydrocleaning event was a significant source of disturbance to the local fish assemblages at platform Elly. Total fish density (Fig. 3) and species composition (Fig. 2B) at platform Elly were back within the range of variability of the control platforms within ten months following the hydrocleaning event (September 2008).

As with fish community structure, there were consistent differences among platforms in overall fish densities after hydrocleaning. Although no significant interaction was detected among control platforms between periods (test of B × C; Table 1B), one was detected between platform Elly and the other platforms (test of B × I; Table 1B; Fig. 3). Even so, we found no evidence that overall fish biomass or species richness were significantly affected by hydrocleaning (tests of both B × C and B × I; Table 1C, D, respectively).

Table 1. Asymmetrical multivariate PERMANOVA (entire assemblage) (A) and univariate ANOVAs (species densities, biomass, and richness) (B–F) of mid-water fish associated with petroleum platforms on the San Pedro Shelf before and after a hydrocleaning event at platform Elly. Bolded P values are significant at the 0.05 level.

	df	(A) Entire assemblage			(B) Overall density		
		MS	pseudo-F	P	MS	F	P
Before vs After = B	1	1972.4	–	–	0.2	–	–
Times (B) = T(B)	12	2717.9	–	–	4.1	–	–
Locations = L	3	4680.7	–	–	4.7	–	–
Impact vs Controls = I	1	7436.0	–	–	14.1	–	–
Among Controls = C	2	3303.0	–	–	0.0	–	–
B × L	3	1367.9	–	–	3.3	–	–
B × I	1	2628.1	5.54	**0.024**	7.5	11.60	**0.002**
B × C	2	737.8	1.56	0.225	1.2	1.84	0.173
Residual	36	474.3	–	–	0.6	–	–

	df	(C) Overall biomass			(D) Species richness		
		MS	F	P	MS	F	P
Before vs After = B	1	618.6	–	–	3.0	–	–
Times (B) = T(B)	12	642.2	–	–	6.3	–	–
Locations = L	3	3736.9	–	–	13.8	–	–
Impact vs Controls = I	1	2727.4	–	–	37.1	–	–
Among Controls = C	2	4241.7	–	–	2.2	–	–
B × L	3	200.9	–	–	2.0	–	–
B × I	1	56.0	0.17	0.683	3.1	1.60	0.214
B × C	2	273.4	0.83	0.444	1.5	0.74	0.485
Residual	36	329.1	–	–	2.0	–	–

	df	(E) Blacksmith density			(F) Cabezon density		
		MS	F	P	MS	F	P
Before vs After = B	1	0.05	–	–	0.08	–	–
Times (B) = T(B)	12	4.69	–	–	0.02	–	–
Locations = L	3	8.63	–	–	0.04	–	–
Impact vs Controls = I	1	24.99	–	–	0.11	–	–
Among Controls = C	2	0.45	–	–	0.00	–	–
B × L	3	4.80	–	–	0.03	–	–
B × I	1	10.49	12.98	**0.001**	0.09	8.23	**0.007**
B × C	2	1.96	2.42	0.103	0.00	0.27	0.768
Residual	36	0.81	–	–	0.01	–	–

Notes: df = degrees of freedom, MS = mean square, pseudo-F = multivariate analogue of Fisher's F ratio calculated from a symmetric dissimilarity matrix (Anderson 2001a, b), F = F ratio, P = P value.

A SIMPER analysis revealed that the six species contributing the highest percentages to the overall dissimilarity between periods at platform Elly were blacksmith (*Chromis punctipinnis*; 43%), painted greenling (*Oxylebius pictus*; 5%), cabezon (*Scorpaenichthys marmoratus*; 4%), kelp rockfish (*Sebastes atrovirens*; 4%), garibaldi (*Hypsypops rubicundus*; 7%), and California sheephead (*Semicossyphus pulcher*; 3%). With the
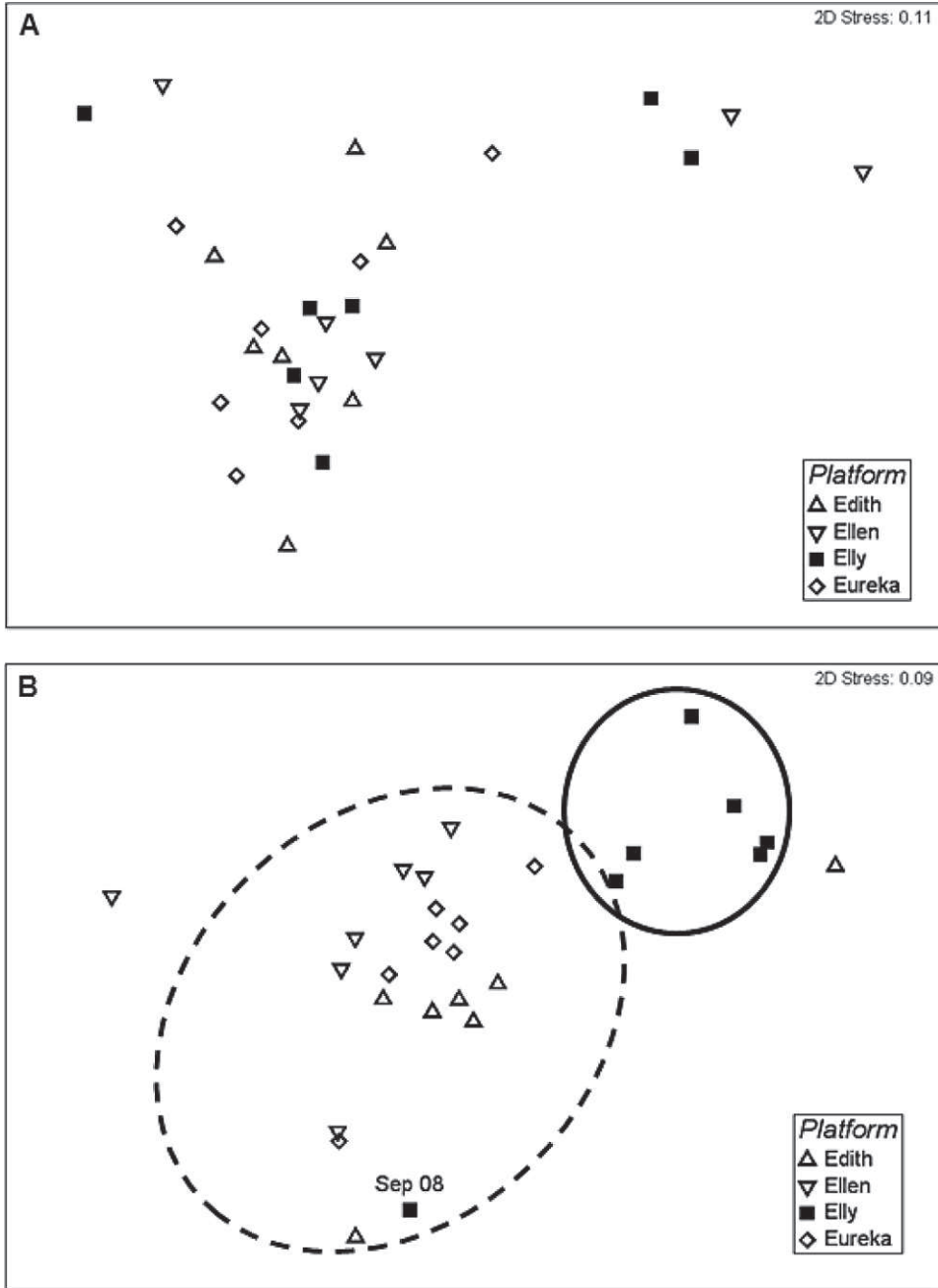
Fig. 2. Two-dimensional nMDS ordination plots comparing mid-water fish assemblages among offshore petroleum platforms on the San Pedro Shelf before (A) and after (B) a November 2007 hydrocleaning event at platform Elly. Circles drawn on graphs illustrate groups that are significantly different based on PERMANOVA results.
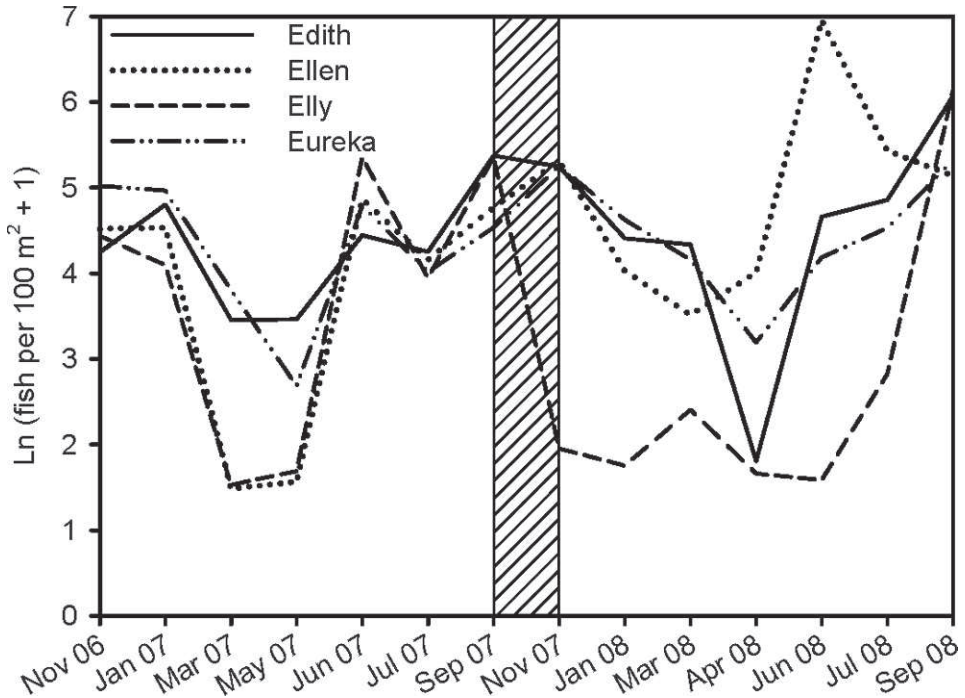
Fig. 3.   A time series plot of total fish densities ($\ln(x + 1)$) at offshore petroleum platforms on the San Pedro Shelf. The hatched bar represents the timing of the hydrocleaning event at platform Elly in November 2007. The observed decrease in fish density at that platform following the disturbance was statistically significant at the 0.05 level.

exception of cabezon whose density increased four-fold, all of the species listed above decreased in abundance after hydrocleaning. Nevertheless, the observed changes in density at platform Elly were only statistically significant for blacksmith (mean ± SE Before = 58.6 ± 26.28 vs. After = 13.9 ± 10.41, $P < 0.001$, Table 1E; Fig. 4) and cabezon (Before = 0.07 ± 0.023 vs. After = 0.36 ± 0.125, $P = 0.007$, Table 1F; Fig. 4). No significant changes were in detected in these species at the control platforms (Table 1E and 1F). There was some evidence of different temporal trends in cabezon density among platforms in the before period, suggesting that the results for that species should be interpreted with some caution (Smith et al. 1993). Several other species (e.g., anchovies (*Engraulis mordax*) and Pacific sardines (*Sardinops sagax*)) also contributed to observed dissimilarities, but were only seasonally abundant.

Discussion

The rapid and intense removal of encrusting sessile invertebrates dramatically altered the community structure and total density of fish associated with the support structure of platform Elly. Blacksmith in particular exhibited a significant decrease in density following the hydrocleaning operation, separate from observed seasonal variation due to recruitment and subsequent population decline (Fig. 4). Accounting for 92% of the total fish density (although only 19% of the total fish biomass; Martin and Lowe 2010), this temperate pomecentrid was one of the main drivers of the observed post-disturbance changes in fish community structure. Blacksmith typically seek small crevices in rocky
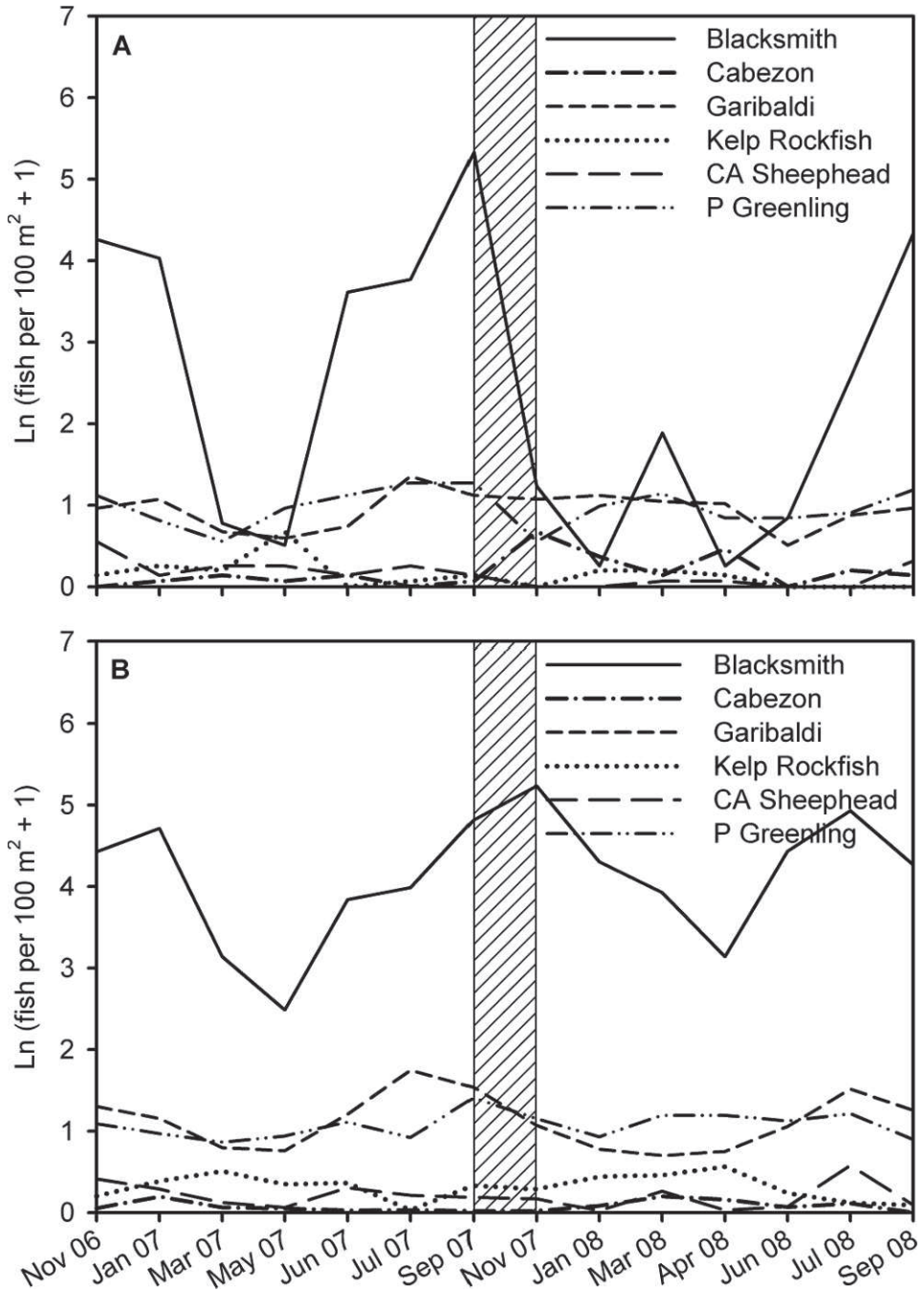
Fig. 4. Time series plot of the densities (ln(x + 1)) of the fish species consistently contributing the most to dissimilarity of samples collected before versus after the hydrocleaning event at platform Elly (timing represented by the hatched bar) (A) and mean densities at the three control platforms (B).

reefs for nocturnal shelter (Ebeling and Bray 1976) and the complex invertebrate layer on the platform would have provided similar microhabitat on an otherwise smooth steel surface. The near-total removal of this biogenic habitat presumably left a large proportion of the blacksmith population vulnerable to predation and high water flow speeds. Blacksmith are a rapidly colonizing planktivorous species, providing a consistent source of food for many piscivorous fishes, including rockfishes (*Sebastes* spp.) and kelp bass (*Paralabrax clathratus*) (Limbaugh 1964). Given their numerical dominance in the mid-water fish community, any significant decrease in blacksmith densities has the potential to negatively impact the entire fish assemblage via a reduction in prey resources. Similarly, by virtue of their high abundances, blacksmith may also contribute significant amounts of inorganic nitrogen to local primary producers via ammonium excretion (Bray et al. 1986).

The lack of an observed impact of hydrocleaning on the densities of larger fish species may have been due to their utilization of habitat below 20 m depth (Martin and Lowe 2010). Acoustic telemetry data on four species (California sheephead, cabezon, grass rockfish (*S. rastrelliger*), and kelp rockfish) at these same SPS platforms have revealed that they are capable of large vertical movements at both daily and seasonal scales (Mireles 2010). Species that feed on invertebrates (e.g., California sheephead; Cowen 1986) may have been foraging in the intact invertebrate layer deeper in the water column periodically while still utilizing the shallower disturbed region for other activities. Blacksmith, in contrast, are uncommon below 20 m (Limbaugh 1964; Martin and Lowe 2010), possibly due to a thermal preference for warmer waters, increased availability of their planktonic prey near the surface, and decreased predation risk from deeper-water predatory species such as rockfish. Only one fish species, cabezon, was observed to increase in density following the hydrocleaning event. However, this result was likely due to increased visibility due to the loss of its cryptic surroundings, rather than an actual increase in local abundances (Willis 2001).

The observed recovery of blacksmith densities (and as a consequence, overall fish community structure) within ten months of the hydrocleaning operation coincided with the rapid re-establishment of mussel beds on the disturbed structure (pers. obs.), suggesting that the shallow-water invertebrate layer associated with the SPS petroleum platforms is particularly important habitat for this species. The invertebrate assemblages on both offshore oil platforms and natural rocky reefs are an important source of prey to microcarnivorous fish like blacksmith (Page et al. 2007) and increases in substratum rugosity and provision of shelter have been shown to be positively related to the density and biomass of many other fish species (e.g., Friedlander and Parrish 1998). In addition to supplying food and shelter, the platform invertebrate layer may also contribute directly to increased reproductive success of local fish populations. Spawning aggregation sites of at least one temperate pomacentrid are characterized by higher substratum rugosity than non-spawning sites (Gladstone 2007) and two fish species, including the pomacentrid garibaldi, were observed protecting egg masses embedded in the invertebrate layer at the SPS platforms (Martin and Lowe 2010).

Hydrocleaning, a high-intensity but temporally discrete event, drastically altered the shallow subtidal invertebrate assemblage at platform Elly, and in turn, the structure of the associated fish community. Even so, the system appears to be resilient, recovering to pre-disturbance conditions within ten months. Presumably this is due in part to the rapid recruitment and growth of both sessile invertebrates and the numerically dominant blackfish on the platform. Our results provide some insight into the potential limitations

to resilience if disturbance events were to increase in frequency through time. Clearly, if disturbances such as the one produced by hydrocleaning were to happen more frequently than once per year, it is unlikely that the associated biological community would fully recover before the next event, presumably leading to a decrease in overall biodiversity (Connell 1978). It would also be interesting to know how the recovery trajectory of the local community might be altered if fish with life-histories markedly different from blacksmith were affected by a given disturbance (e.g., longer-lived or low-recruiting species), or how disturbance might alter other aspects of fish ecology such as diet or habitat utilization.

Although the desirability of temporally and spatially well-replicated sampling both before and after a disturbance event is widely accepted given the high degree of spatial and temporal variability inherent in natural systems (Underwood 1993; 1994), there are significant practical constraints to accomplishing this goal. In general, it is difficult (if not impossible) to know where or when a disturbance might take place or their potential magnitude and spatial extent, so the degree of pre-disturbance sampling tends to be quite limited. Hydrocleaning and other planned or routine disturbance events provide an important opportunity to investigate the effects of disturbance on natural populations and communities. Our results show that a well-replicated BACI sampling design can detect even subtle biological changes in response to disturbance. We also found that taking a multivariate approach to data analyses provided insights that would have been lost had we used only more traditional univariate statistics. For example, there was no evidence of an effect of hydrocleaning on species richness, although community composition overall was actually quite different for some time afterwards. While not explicitly addressed in our study, it is likely that functional diversity and associated ecosystem processes were also changed in response to the disturbance, given the observed changes in community composition (Micheli and Halpern 2005; Suding et al. 2008).

Widespread human impacts on the marine environment are significantly altering biodiversity from local to global scales (Jackson et al. 2001; Myers and Worm 2003; Pandolfi et al. 2003). Documenting such impacts is a key first step towards developing a mechanistic understanding of community disassembly in the face of increasingly frequent and intense perturbations (e.g., Easterling et al. 2000). Such knowledge will be critical to our ability to successfully protect and restore biological communities in the future.

References

Anderson, M.J. 2001a. A new method for non-parametric multivariate analysis of variance in ecology. Aust. Ecol., 26:32–46.

———. 2001b. Permutation tests for univariate or multivariate analysis of variance and regression. Can. J. Fish. Aquat. Sci., 58:626–639.

———, Gorley, R.N., and Clarke, K.R. 2008. PERMANOVA+ for PRIMER: guide to software and statistical methods. PRIMER-E: Plymouth, UK. 213 pp.

Benedetti-Cecchi, L. 2003. The importance of the variance around the mean effect size of ecological processes. Ecology, 84:2335–2346.

Blanchette, C., Helmuth, B., and Gaines, S. 2007. Spatial patterns of growth in the mussel, *Mytilus californianus*, across a major oceanographic and biogeographic boundary at Point Conception, California, USA. J. Exp. Mar. Biol. Ecol., 340:126–148.

Boyce, M.S., Haridas, C.V., and Lee, C.T. 2006. Demography in an increasingly variable world. Trends Ecol. Evol., 21:141–148.

Bram, J.B., Page, H.M., and Dugan, J.E. 2005. Spatial and temporal variability in early successional patterns of an invertebrate assemblage at an offshore oil platform. J. Exp. Mar. Bio. Ecol., 317: 223–237.

Bray, J.R. and Curtis, J.T. 1957. An ordination of the upland forest communities of southern Wisconsin. Ecol. Monogr., 27:325–349.

Bray, R.N., Purcell, L.J., and Miller, A.C. 1986. Ammonium excretion in a temperate-reef community by a planktivorous fish, *Chromis punctipinnis* (Pomacentridae), and potential uptake by young giant kelp, *Macrocystis pyrifera* (Laminariales). Mar. Biol., 90:327–334.

Chapin, F.S., Zavaleta, E.S., Eviner, V.T., Naylor, R.L., Vitousek, P.M., Reynolds, H.L., Hooper, D.U., Lavorel, S., Sala, O.E., Hobbie, S.E., Mack, M.C., and Diaz, S. 2000. Consequences of changing biodiversity. Nature, 405:234–242.

Clarke, K.R. 1993. Non-parametric analyses of changes in community structure. Aust. J. Ecol., 18: 117–143.

Connell, J.H. 1978. Diversity in tropical rain forests and coral reefs. Science, 199:1302–1310.

Continental Shelf Associates, Inc. 2005. Survey of invertebrate and algal communities on offshore oil and gas platforms in southern California: Final report. Prepared for the U.S. Department of the Interior, Minerals Management Service, Pacific OCS Region, Camarillo, CA. OCS Study MMS 2005-070. 232 pp.

Cowen, R.K. 1986. Site-specific difference in the feeding ecology of the California sheephead, *Semicossyphus pulcher* (Labridae). Env. Biol. Fish., 16:193–203.

Easterling, D.R., Meehl, G.A., Parmesan, C., Changnon, S.A., Karl, T.R., and Mearns, L.O. 2000. Climate extremes: observations, modeling, and impacts. Science, 289:2068–2074.

Ebeling, A.W. and Bray, R.N. 1976. Day versus night activities of reef fishes in a kelp forest off Santa Barbara, California. US Fish. Bull., 74:703–717.

Field, J.G., Clarke, K.R., and Warwick, R.M. 1982. A practical strategy for analysing multispecies distribution patterns. Mar. Ecol. Prog. Ser., 8:37–52.

Friedlander, A. and Parrish, J. 1998. Habitat characteristics affecting fish assemblages on a Hawaiian coral reef. J. Exp. Mar. Biol. Ecol., 224:1–30.

Gladstone, W. 2007. Selection of a spawning aggregation site by *Chromis hypsilepis* (Pisces: Pomacentridae): habitat structure, transport potential, and food availability. Mar. Ecol. Prog. Ser., 351:235–247.

Green, R.H. 1979. Sampling design and statistical methods for environmental biologists. Wiley Interscience, Chichester, England. 257 pp.

Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A.J., Vandermeer, J., and Wardle, D.A. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecol. Monogr., 75:3–35.

Jackson, J.B.C., Kirby, M.X., Berger, W.H., Bjorndal, K.A., Botsford, L.W., Bourque, B.J., Bradbury, R.H., Cooke, R., Erlandson, J., Estes, J.A., Hughes, T.P., Kidwell, S., Lange, C.B., Lenihan, H.S., Pandolfi, J.M., Peterson, C.H., Steneck, R.S., Tegner, M.J., and Warner, R.R. 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science, 293:629–638.

Limbaugh, C. 1964. Notes on the life history of two Californian Pomacentrids: garibaldis, *Hypsypops rubicunda* (Girard), and blacksmiths, *Chromis punctipinnis* (Cooper). Pac. Sci., 18:41–50.

Lingo, M.E. and Szedlmayer, S.T. 2006. The influence of habitat complexity on reef fish communities in the northeastern Gulf of Mexico. Environ. Biol. Fish, 76:71–80.

Love, M., Schroeder, D., and Nishimoto, M. 2003. The ecological role of oil and gas production platforms and natural outcrops on fishes in southern and central California: A synthesis of information. Prepared for the U.S. Department of the Interior, U.S. Geological Survey, Biological Resources Division, Seattle, WA. OCS Study MMS 2003–032. 78 pp.

Martin, C.J.B. 2009. Species composition and abundance of the fishes at offshore petroleum platforms on the San Pedro Shelf, Southern California. M.S. thesis. California State University, Long Beach. 105 pp.

——— and Lowe, C.G. 2010. Assemblage structure of fish at offshore petroleum platforms on the San Pedro Shelf of Southern California. Mar. Coast. Fish. Dynam. Manag. Ecosyst. Sci., 2:180–194.

McArdle, B.H. and Anderson, M.J. 2001. Fitting multivariate models to community data: a comment on distance-based redundancy analysis. Ecology, 82:290–297.

Menge, B., Daley, B.A., Wheeler, P.A., and Strub, P.T. 1997. Rocky intertidal oceanography: an association between community structure and nearshore phytoplankton concentration. Limnol. Oceanogr., 42:57–66.

Micheli, F. and Halpern, B.S. 2005. Low functional redundancy in coastal marine assemblages. Ecol. Lett., 8:391–400.

Mireles, C. 2010. Site fidelity and depth utilization of nearshore reef fish on offshore San Pedro Shelf petroleum platforms. M.S thesis. California State University, Long Beach. 101 pp.

Myers, R.A. and Worm, B. 2003. Rapid worldwide depletion of predatory fish communities. Nature, 423: 280–283.

Page, H.M. 1986. Differences in population structure and growth rate of the stalked barnacle *Pollicipes polymerus* between a rocky headland and an offshore oil platform. Mar. Ecol. Prog. Ser., 29: 157–164.

———, Dugan, J.E., Schroeder, D.M., Nishimoto, M.M., Love, M.S., and Hoesterey, J.C. 2007. Trophic links and condition of a temperate reef fish: comparisons among offshore oil platforms and natural reef habitats. Mar. Ecol. Prog. Ser., 344:245–256.

Paine, R.T. 1966. Food web complexity and species diversity. Am. Nat., 100:65–75.

———, Tegner, M.J., and Johnson, E.A. 1998. Compounded perturbations yield ecological surprises. Ecosystems, 1:535–545.

Pandolfi, J.M., Bradbury, R.H., Sala, E., Hughes, T.P., Bjorndal, K.A., Cooke, R.G., McArdle, D., McClenachan, L., Newman, M.J.H., Paredes, G., Warner, R.R., and Jackson, J.B.C. 2003. Global trajectories of the long-term decline of coral reef ecosystems. Science, 301:955–959.

Scheiner, S.M. 1998. MANOVA: multiple response variables and multispecies interactions. Pp. 94–112 in Design and analysis of ecological experiments. (S.M. Scheiner and J. Gurevitch, eds.) Chapman and Hall, New York. 445 pp.

Seed, R. and Suchanek, T. 1992. Population and community ecology of *Mytilus*. Pp. 87–169 in: The mussel Mytilus: ecology, physiology, genetics and culture. (E. Gosling, ed.) Elsevier, Amsterdam. 590 pp.

Smith, E.P., Orvos, D.R., and Cairns, J. Jr. 1993. Impact assessment using the Before-After-Control-Impact (BACI) model: concerns and comments. Can. J. Fish. Aquat. Sci., 50:627–637.

Sokal, R.R. and Rohlf, F.J. 2011. Biometry, 4th ed. W.H. Freeman and Co, New York. 937 pp.

Stephens, J.S. Jr., Larson, R., and Pondella, D.J. II. 2006. Rocky Reefs and Kelp Beds. Pp. 227–252 in The Ecology of Marine Fishes: California and Adjacent Waters. (L.G. Allen, D.J. Pondella II, and M. Horn, eds.) University of California Press, Los Angeles. 670 pp.

Suchanek, T.H. 1979. The *Mytilus californianus* community: studies on the composition, structure, organization and dynamics of a mussel bed. Ph.D. thesis, University of Washington, Seattle. 286 pp.

Suding, K.N., Lavorel, S., Chapin, F.S., Cornelissen, H., Diaz, S., Garnier, E., Goldberg, D., Hooper, D.U., Jackson, S.T., and Navas, M.L. 2008. Scaling environmental change through the community-level: a trait-based response-and-effect framework for plants. Glob. Change Biol., 14:1125–1140.

Syms, C. and Jones, G.P. 2000. Disturbance, habitat structure, and the dynamics of a coral-reef fish community. Ecology, 81:2714–2729.

Terlizzi, A., Benedetti-Cecchi, L., Bevilacqua, S., Fraschetti, S., Guidetti, P., and Anderson, M.J. 2005. Multivariate and univariate asymmetrical analyses in environmental impact assessment: a case study of Mediterranean subtidal sessile assemblages. Mar. Ecol. Prog. Ser., 289:27–42.

Underwood, A.J. 1993. The mechanics of spatially replicated sampling programmes to detect environmental impacts in a variable world. Aust. J. Ecol., 18:99–116.

———. 1994. On beyond BACI: Sampling designs that might reliably detect environmental disturbances. Ecol. App., 4:3–15.

Willis, T.J. 2001. Visual census methods underestimate density and diversity of cryptic reef fishes. J. Fish Biol., 59:1408–1411.

Wootton, J.T. 1994. Predicting direct and indirect effects: an integrated approach using experiments and path analysis. Ecology, 75:151–165.