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RESEARCH ARTICLE

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Role of food subsidies and habitat structure in influencing benthic communities of shell mounds at sites of existing and former offshore oil platforms

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Abstract Mussels (*Mytilus californianus, M. galloprovincialis*) and other organisms sloughed from offshore oil platforms provide a food subsidy to benthic consumers and alter underlying soft bottom habitat by creating hard substrate. The removal of overlying platforms eliminates this food subsidy, but large shell mounds remain. The distribution, abundance, and population characteristics of mobile macroinvertebrates differed among shell mounds beneath existing offshore oil platforms, shell mounds at the former sites of offshore oil platforms, and soft bottom. Predatory and omnivorous echinoderm and mollusk species were more abundant and generally larger on shell mounds under platforms than on shell mounds without platforms. Omnivorous and deposit feeding echinoderms were the most abundant macroinvertebrate taxa sampled on mound-only sites. The brown rock crab (*Cancer antennarius*), known to have a strong preference for hard substrate, was significantly more abundant on shell mounds, with or without platforms, than adjacent soft bottom sites. Results suggest that the effects of platform removal differed among benthic species according to trophic level, degree of mobility, and substrate preference. Although the shell mound habitat persists after removal of platform structures, species abundance and the composition of the associated benthic community is altered by removal of the platform structure.

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Introduction

Two important controls on the structure of benthic communities are the physical characteristics of the habitat and food availability. Artificial structures, such as constructed reefs and offshore platforms, can directly influence the species composition, distribution, and abundance of local invertebrate and fish fauna through the provision of hard substrate habitat and topographic relief (Wolfson et al. 1979; Davis et al. 1982; Bohnsack 1989; Herrnkind et al. 1997). The aggregation of mobile invertebrates and fishes on and around artificial structures, which are typically located on soft bottom, is well documented and usually attributed to the attraction and/or possible production of reef-associated species at or on the structures. At the same time, these structures often provide food chain support for higher level consumers and may indirectly subsidize the adjoining soft bottom benthic community through the production and export of organic matter (Wolfson et al. 1979; Page et al. 1999). Food availability has been shown to exert a strong influence on the species composition, densities, and growth rates of consumers in many marine habitats (Bustamante et al. 1995; Polis et al. 1996; Dahlhoff and Menge 1996; Link and Almeida 2002; Dugan et al. 2003). Such bottom-up controls are considered an important organizing force in marine ecosystems (e.g., Menge 1992; Bustamante and Branch 1996).

Offshore oil and gas platforms are among the largest artificial structures in the marine environment. Off the coast of southern and central California, oil platforms provide hard substrate for the attachment of sessile and semi-mobile organisms that are not typical of the soft bottom habitat over which platforms are installed (Wolfson et al. 1979; Page and Hubbard 1987; Page et al. 1999). The principal components of this assemblage at depths of <15 m are mussels (*Mytilus californianus*, *M. galloprovincialis*), with encrusting bivalves (e.g., *Chama arcana*, *Crassodoma giganteus*), barnacles (e.g., *Megabalanus californicus*), and anemones (e.g.,

Metridium senile) predominating deeper (Page et al. 1999). Waves/swell, storm events and platform cleaning dislodge clumps of the mussel community, which fall to the seafloor (Fig. 1a). Page et al. (1999) estimated that from 47 to 1,031 kg wet weight mussel community week^{-1} fell from vertical conductor pipes, a fraction of the platform structure, to the seafloor beneath Platform Holly (offshore of Goleta, California). Wolfson et al. (1979) estimated faunal litterfall from Platform Eva (offshore of Huntington Beach, California) to be from 678 to 1,169 kg wet weight mussels week^{-1}.

This "faunal litterfall" alters the benthos in two distinct ways. First, allochthonous organic matter falling to the seafloor provides a food subsidy to benthic consumers (Fig. 1a). Second, the input of mussel shells alters the physical characteristics of the seafloor by creating hard substrate habitat and altering bottom topography (Fig. 1b). The resulting shell mound habitat differs dramatically from the surrounding soft bottom, rising up to 8.5 m above the surrounding seafloor and measuring up to 70 m across (de Wit 2001). The phenomenon of shell mound formation has been documented at most offshore oil platforms off the coast of California (MEC 2003).

During platform decommissioning, obsolete structures are removed, or if they are destined to serve as artificial reefs, they may be cropped or toppled in place or towed and submerged in a different location (reviewed in Love et al. 2003). If the platform structure is removed, the deposition of faunal litterfall ceases, but the hard substrate habitat provided by the shell mound remains.

We used the "natural" experimental opportunity provided by the removal of platform structures to explore the effects of substrate characteristics and food subsidies on the distribution and abundance of mobile epibenthic invertebrates. We predicted that the removal of platforms (and loss of food subsidy and potential recruitment habitat) would dramatically alter the shell mound community through changes in species composition and trophic structure, and reductions in the densities and sizes of shell mound associated species. To investigate this prediction, we compared the abundance and population structures of mobile macroinvertebrates on shell mounds beneath existing platform sites, shell mounds from which the overlying platform structure was removed 4–5 years prior to data collection, and soft bottom sites. We used a combination of transect sampling using SCUBA at shallow sites, trapping at shallow and deep sites, and historical photographs of mound habitat. Results suggest that platforms alter benthic communities both through food subsidies and habitat modification. Although the shell mound habitat persists after removal of platform structures, the associated benthic community is profoundly altered by removal of the platform structure.

Materials and methods

Study sites

This study was conducted in the Santa Barbara Channel at three shell mounds beneath existing offshore oil

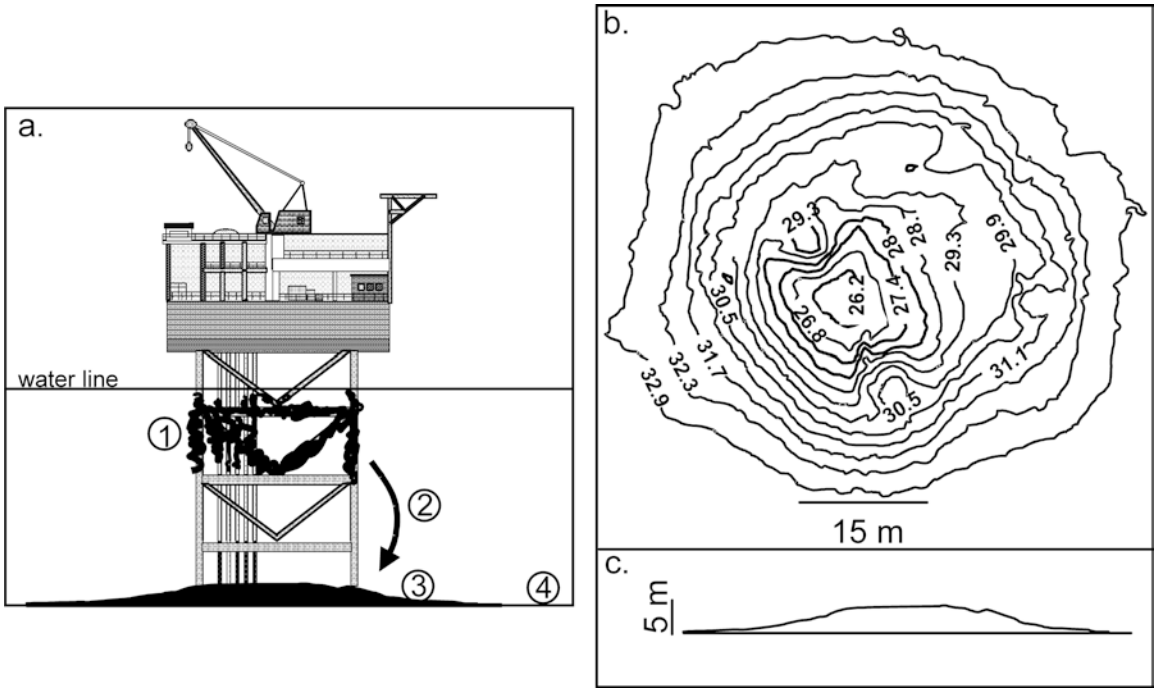

Fig. 1a–c Diagrammatic illustrations of the fall of mussels and other organisms from the structure of offshore oil platforms to the seafloor and the formation and topography of shell mounds. **a** Platform with shell mound showing *1* encrusting invertebrates *2* detaching from platform structure and falling to the seafloor, where soft tissue is consumed by benthic invertebrates, leaving *3* a mound of empty shells surrounded by *4* soft bottom. **b** Topography of shell mound Hilda, which is typical of shell mounds in this study. Depth contours are in meters. **c** Cross section of the shell mound beneath Platform Gina, also typical of shell mounds in this study

platforms (Gina, Houchin, and Hogan), four shell mounds without overlying platforms (the former sites of Platforms Hazel, Hilda, Hope, and Heidi), and five soft-bottom sites (Table 1, Fig. 2). All shell mounds except Gina are located offshore of Summerland, California. Shell mounds Hazel and Hilda are located in water depths of ~30 m. Platforms Houchin and Hogan and shell mounds Hope and Heidi are arranged in a line oriented northeast-southwest along a depth gradient of ~40–50 m. Platform Gina is located in a water depth of 29 m offshore of Oxnard, California, 33 km southeast of Platform Hogan and is the only extant platform in the Santa Barbara Channel in which the shell mound is easily accessible using conventional SCUBA (Table 1). Soft-bottom sites were established within 1 km of each of the four shell mound-only sites and Platform Gina (Fig. 2).

The shell mounds are composed of clay and drill cuttings covered by a 0.3 to 2.1-m thick layer of empty shells (de Wit 2001). The shell mounds vary from 45 to 84 m in diameter and extend from 4 to 8.5 m above the seafloor (Table 1, Fig. 1b). The platform structure at the sites of former Platforms Hazel, Hilda, Heidi, and Hope was removed ~5 years prior to our study. A thin layer of sediment covers these mounds (de Wit 2001).

Distribution and abundance of mobile macroinvertebrates on shell mounds

We used three approaches to explore the effect of the presence of the platform on the distribution and abundance of mobile benthic invertebrate species. First, at the shallow sites (depth < 35 m), which included shell mound-only (Hazel, Hilda), shell mound under platform (Gina), and soft bottom habitats (SB-Gina), we sampled invertebrates within band transects using SCUBA (Table 2). Second, at the shallow and deep sites, which included shell mound only (Hazel, Hilda, Heidi, Hope), shell mound under platform (Houchin, Hogan), and soft bottom sites (SB-1, 2, 3, 4), we sampled commercially important crabs (primarily *Cancer* spp.) as well as other mobile macroinvertebrate species using baited commercial traps (Fathoms Plus) (Table 2). Finally, we recorded species present and estimated densities of macroinvertebrates in historical photographs taken at shell mound Hilda prior to platform removal. These approaches are elaborated on below.

Transect sampling

We sampled invertebrates in 1×20-m band transects at mound-only sites, Hazel ($n = 4$) and Hilda ($n = 3$), and in 1×10-m transects at Platform Gina ($n = 3$). Transect length was shorter at Gina because of the much higher density of organisms at this site. To expedite sampling at depths of 30–33 m in poor visibility (< 2 m), transects were situated in a radial design with equal angular spacing from a central reference point (i.e., base of marker buoy chain). Divers collected all mobile benthic macroinvertebrates encountered along the transects. Invertebrates were returned to the boat for identification and measurement to the nearest millimeter. Sea stars were measured from the center of the disk to the tip of the longest arm, sea cucumbers were measured on the longitudinal axis while contracted, and gastropods were measured along the longest axis of the shell.

To compensate for over sampling at the center due to the radial transect design, organism densities in the band transects were weighted according to proximity to the center. Band transects were divided into four segments of equal length. Organism densities in each segment were multiplied by weighting factors assuming an imaginary wedge-shaped transect with the same area as the band transect. Weighting factors, determined by dividing the areas of each segment of a hypothetical wedge-shaped transect by the area of the corresponding segment in the band transect, ranged from 0.25 to 1.75.

Table 1 Details of study sites, including habitat type and name, depth class, depth, distance from shore, coordinates, year of platform installation and removal. Data from de Wit (2001) and MEC (2003)

Habitat	Depth class	Depth (m)	Distance from shore (km)	Coordinates	Year installed	Year removed	Shell mound height (m)	Shell mound dimensions (m)
Mound-only								
Hazel	Shallow	31	3.4	34°22′N, 119°34′W	1958	1996	8.5	66×72
Hilda	Shallow	34	3	34°23′N, 119°35′W	1960	1996	6.7	66×72
Heidi	Deep	40	4.8	34°20′N, 119°32′W	1966	1996	7.3	60×75
Hope	Deep	42	5.2	34°20′N, 119°31′W	1965	1996	6.7	51×60
Mound under platform								
Gina	Shallow	29	6.9	34°07′N, 119°16′W	1980	-	3.9	45×63
Hogan	Deep	47	6.9	34°20′N, 119°32′W	1967	-	7.8	78×78
Houchin	Deep	50	7.6	34°20′N, 119°33′W	1968	-	6.3	84×84
Soft bottom								
SB-Gina	Shallow	30	6.9	34°07′N, 119°16′W	-	-	-	-
SB-1	Shallow	30	~3	34°22′N, 119°33′W	-	-	-	-
SB-2	Shallow	30	~3	34°23′N, 119°35′W	-	-	-	-
SB-3	Deep	41	~5	34°20′N, 119°31′W	-	-	-	-
SB-4	Deep	41	~6	34°20′N, 119°32′W	-	-	-	-

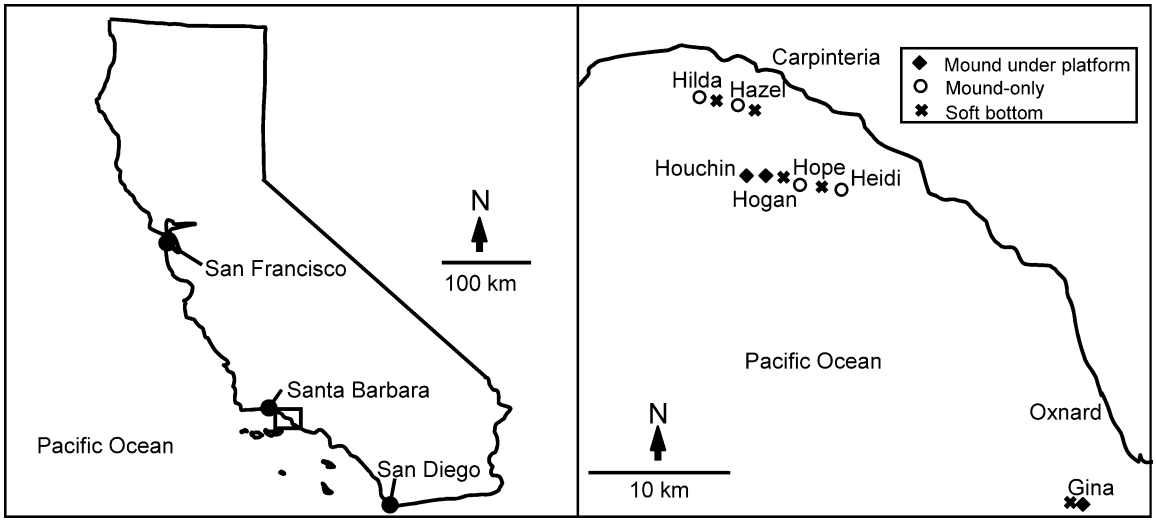

Fig. 2 The study region and the locations of the oil platform, shell mound-only, and soft bottom study sites in the Santa Barbara Channel

Table 2 Summary timetable for the field sampling of shell mound sites by transect and trap. Transect sampling was conducted only at the shallow sites

Category	Transect sampling		Trap sampling	
	2000	2001	2000	2001
Mound-only				
Hazel		X	X	X
Hilda		X	X	X
Heidi			X	X
Hope			X	X
Mound under platform				
Gina		X		
Hogan				X
Houchin				X
Soft bottom				
SB-Gina		X		
SB-1			X	
SB-2			X	
SB-3				X
SB-4				X

In addition, we compared the body weight of the chestnut cowry (*Cypraea spadicea*) among the shallow shell mounds (Hazel, Hilda, and Platform Gina) since body weight may reflect nutritional condition (e.g., Gabbott 1976, 1983; Shriver et al. 2002). The soft tissues of individuals of a range of shell-lengths were excised and oven dried at 60°C to a constant weight. Dry body weight was regressed against shell length for each site.

Trap sampling

We sampled commercially important crabs and other macroinvertebrates using traps. Sampling was conducted from September through December because crabs were found in highest abundance at this time of year in a previous study (Page et al. 1999). In 2000, we sampled the shallow and deep shell mound-only (Hazel, Hilda, Hope, Heidi) and soft-bottom (SB-1, SB-2) sites 4 times from November through December. In 2001, we again sampled the shell mound-only sites (Hazel, Hilda, Hope, Heidi), but also the deep mound under platform (Hogan, Houchin) and soft-bottom sites (SB-3, SB-4) 4 times from September through November. The shallow mound under platform site at Gina was not sampled because of logistical difficulties. Consistent trap placement at mound-only and soft bottom stations was achieved using GPS (Furuno FBX-2).

Traps were baited with a total of 1.4 kg of coarsely chopped mackerel (*Scomber japonicus*) enclosed in rigid plastic mesh (8 mm) containers. Traps ($n = 2$ per site) were retrieved after a 24-h soak time. Captured crabs were identified to species and counted. Trapping results are expressed as catch per unit effort (CPUE), which is the mean number of crabs per trap per site captured after 24 h, and compared over time in a repeated measures design (Zar 1999).

Historical photographs

There were no sampling data available on shell mound communities prior to the removal of Platforms Hazel, Hilda, Heidi, and Hope in 1996. However, color photographs, taken in 1976 to document fauna associated with the shell mound at Platform Hilda, were used to record species present and to estimate historical densities of mobile benthic invertebrate species on the shell mound beneath this platform prior to platform removal. This information was useful for comparisons with data from the existing shallow platform site (Gina) and published data. Only photographs taken perpendicular to the bottom and covering an area of ~70 cm^2 were used in the analyses ($n = 5$).

Statistical analyses

All statistical analyses were carried out using JMP 4.04 and SPSS 11.5. The effect of site on density and mean

size of mobile benthic invertebrates sampled by band transect was evaluated using one-way ANOVA. The effect of site on the relationship between body weight and shell length of *Cypraea spadicea* was explored using a *t*-test of homogeneity of slopes. The effect of habitat type on the abundance of crabs, as CPUE, was evaluated using repeated measures ANOVA; this statistic was appropriate since our study involved repeated sampling of the same study sites. Crab abundance data were log transformed [$x' = \log_{10}(x+1)$] prior to analysis to correct for heteroscedasticity (Zar 1999).

Table 3 Results of one-way ANOVA on transect data evaluating the effect of site on the densities of mobile benthic mollusks and echinoderms

Species	*F*	*P*	*df*
Cypraea spadicea	3.20	0.10	2, 7
Kelletia kelletii	1.64	0.26	2, 7
Parastichopus californicus	6.18	< 0.05	2, 7
P. parvimensis	0.55	0.60	2, 7
Asterina miniata	20.43	< 0.001	2, 7
Pisaster giganteus	32.85	< 0.001	2, 7

Results

Distribution and abundance of macroinvertebrates: transect sampling at shallow sites

Densities of mobile macroinvertebrate species varied by trophic level and taxa among shell mound sites (Table 3, Fig. 3). Density of predatory echinoderms was highest on the mound under Platform Gina. The predatory sea stars, *Pisaster giganteus* (0.89 ± 0.17 m^{-2}, $\bar{x} \pm 1x \pm 1$ SE) and *P. ochraceus* (0.05 ± 0.03 m^{-2}), were found only on the shell mound under Platform Gina. One individual of a congener, *P. brevispinus*, was found at Hilda (0.03 ± 0.03 m^{-2}). Density of the predatory-omnivorous sea star, *Asterina miniata*, was an order of magnitude higher on the shell mound under Platform Gina (2.54 ± 0.53 m^{-2}) than at the shell mound-only sites (Hazel, 0.34 ± 0.14 m^{-2}; Hilda, 0.12 ± 0.02 m^{-2}, $P = 0.0012$, $F = 20.43$, $df = 2, 7$, one-way ANOVA: Table 3, Fig. 3).

Densities of the predatory cowry, *Cypraea spadicea*, were 5–15 times higher on the shell mound under Platform Gina (0.45 ± 0.21 m^{-2}) than at mound-only sites (Hazel, 0.08 ± 0.08 m^{-2}; Hilda, 0.03 ± 0.03 m^{-2}, $P = 0.1$: Table 3, Fig. 3). The density of *C. spadicea* under

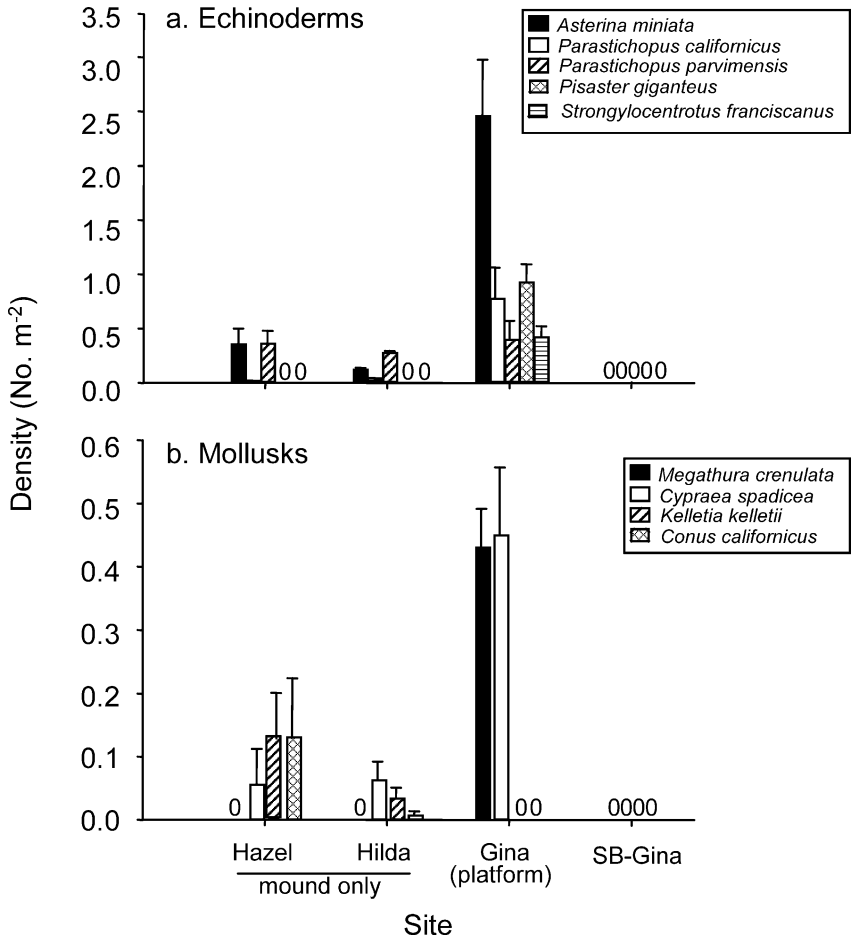

Fig. 3 Densities of selected **a** echinoderms and **b** mollusks on shallow mound-only (Hazel and Hilda), shallow mound under an existing platform (Gina), and soft bottom sites (SB-Gina). Mean values ± 1 SE, $n = 3$–4 transects per site. Note difference in y-axis scale among panels

Platform Gina was significantly higher than on shell mound-only Hazel and Hilda when data for the latter two sites were pooled ($P < 0.05$, $t = 2.66$, $df = 8$, Student's t-test). The gastropods, *Conus californicus*, a predator, and *Kelletia kelletii*, a carnivorous scavenger, occurred at low densities (< 0.2 m^2) at the shell mound-only sites and were not found on the mound under Platform Gina; the omnivorous gastropod, *Megathura crenulata*, and sea urchin, *Strongylocentrotus fransicanus*, were found only on the mound under Platform Gina (Fig. 3).

In contrast, the density of the deposit-feeding sea cucumber, *Parastichopus parvimensis*, did not differ significantly among platform and mound-only sites (Table 3, Fig. 3). However, density of a congener, *P. californicus*, was significantly higher under Platform Gina (0.74 ± 0.03 m^{-2}) compared to mound-only Hazel (0.05 ± 0.05 m^{-2}) and Hilda (0.02 ± 0.02 m^{-2}, $P < 0.05$, $F = 6.18$, $df = 2, 7$, one-way ANOVA: Table 3, Fig. 3).

There was no overlap in species composition between the macroinvertebrate community at the mound under Platform Gina and the adjacent soft bottom. Species composition on the soft bottom was typical of sandy and muddy bottom and included the echinoderms *Luidia foliolata* (0.02 m^{-2}) and *Lytechinus anamesus* (1.2 m^{-2}), and the mollusks *Cancellaria cooperi* (0.02 m^{-2}), *Megasurcula carpenteriana* (0.05 m^{-2}), *M. stearsiana* (0.02 m^{-2}), and *Polinices lewisii* (0.02 m^{-2}).

Population structures of benthic macroinvertebrates

We compared the population structures of the more abundant species (*Asterina miniata*, *Parastichopus parvimensis*, *Cypraea spadicea*) among sites (Fig. 4). The population structure of *Asterina miniata* differed among sites (Fig. 4a). Mean arm radius of this sea star was significantly larger on the mound under Platform Gina (87.3 ± 1.3 mm) than at shell mound-only Hazel (48.1 ± 2.1 mm) and Hilda (50.4 ± 1.2 mm; $P < 0.0001$, $F = 301.29$, $df = 2, 284$, one-way ANOVA, $P < 0.05$, Tukey post hoc test: Fig. 4a). Mean length (contracted) of the deposit feeder, *Parastichopus parvimensis,* also varied significantly among sites (Gina, 110.4 ± 6.9 mm; Hazel, 128.4 ± 4.9 mm; Hilda, 92.7 ± 3.8 mm; $P < 0.0001$, $F = 16.96$, $df = 2, 176$, one-way ANOVA: Fig. 4b). Mean length of *P. parvimensis* was significantly greater at Hazel than at Hilda ($P < 0.05$, Tukey post hoc test), but neither mean was significantly different from the mean length of individuals on the mound under Gina ($P > 0.05$, Tukey post hoc test).

There was no difference in mean lengths of the predatory cowry, *Cypraea spadicea*, among sites (Fig. 4c); however, there was a significant difference in the relationship between dry body weight and shell length ($P < 0.001$, $t = -3.918$, $df = 19$, t-test of homogeneity of slopes: Fig. 5). Cowries were heavier for a given shell length on the mound under Platform Gina compared with mound-only sites Hazel and Hilda.

Distribution and abundance of crabs: trap sampling

Four species of brachyuran decapods, the cancrid crabs, *Cancer antennarius*, *C. anthonyi*, *C. productus*, and the majid crab, *Loxorhynchis grandis*, were caught in traps. Only four individuals of *C. productus* were caught in traps during this study (in 2000) and were not included in the analyses. The mean CPUE of all crab species did not vary over time within each sampling season ($P > 0.05$, repeated measures ANOVA: Table 4).

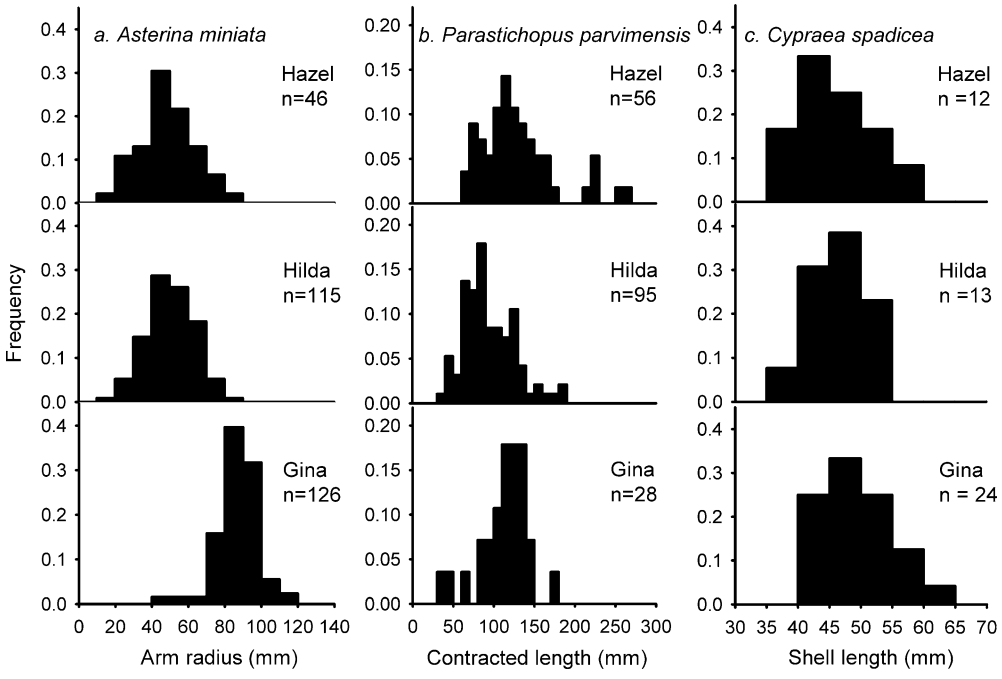

Fig. 4 Size frequency distributions of **a** *Asterina miniata*, **b** *Parastichopus parvimensis*, and **c** *Cypraea spadicea* on the shallow shell mounds. Note difference in axis scales and units among panels

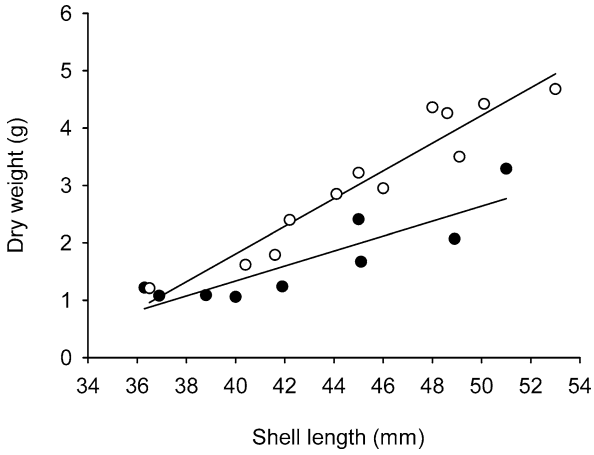

Fig. 5 Regressions of body dry weight versus shell length for *Cypraea spadicea* sampled from shell mounds at former platform sites Hazel and Hilda (●, y = 0.13x−3.88, $r^2 = 0.77$, $n = 9$) and from the shell mound beneath platform Gina (○, y = 0.24x–7.84, $r^2 = 0.91$, $n = 12$)

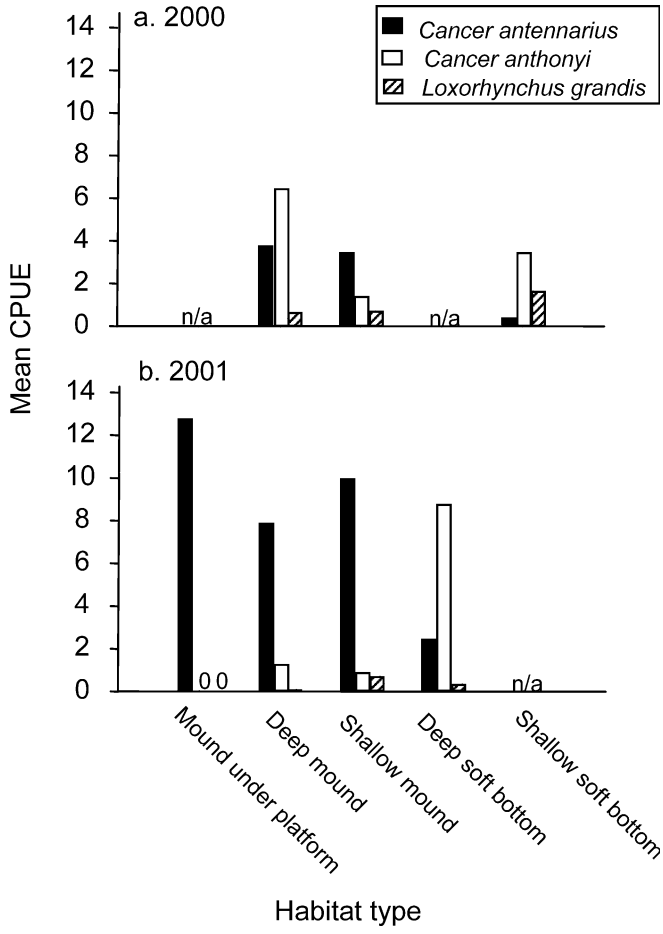

Fig. 6 Mean CPUE of the crabs, *Cancer antennarius*, *C. anthonyi*, and *Loxorhynchus grandis* in traps deployed in **a** 2000 and **b** 2001. $n = 2$ sites per habitat type (four sampling dates per year)

The CPUE of *Cancer antennarius* varied among habitat type in both 2000 and 2001 ($P < 0.05$, repeated measures ANOVA: Table 4). In 2000, the mean CPUE of *C. antennarius* on the shallow (3.4 ± 0.8 crabs trap^{-1}) and deep (3.8 ± 0.7 crabs trap^{-1}) shell mounds was significantly greater than at the shallow soft bottom sites SB-1 and SB-2 (0.4 ± 0.3 crabs trap^{-1}; $P < 0.05$, post hoc paired *t*-test with Bonferroni correction: Fig. 6a). In 2001, patterns of abundance of *C. antennarius* were similar to the previous year, but overall CPUE was higher, ranging from 2.4 to 10.2 crabs trap^{-1} (Fig. 6b). Mean CPUE at the shell mounds was again significantly higher than at the soft bottom sites ($P < 0.05$, post hoc paired *t*-test with Bonferroni correction).

In contrast, the CPUE of *Cancer anthonyi* was more variable among habitats. In 2000, there was a trend of higher CPUE on deep shell mound-only (6.4 ± 1.7 crabs trap^{-1}) compared with shallow soft bottom (3.4 ± 0.9 crabs trap^{-1}) and shallow mound-only sites (1.4 ± 0.5 crabs trap^{-1}: Fig. 6a). However, differences in mean values were not significant due to high variability in CPUE among sampling dates. In 2001, we observed a trend of higher CPUE on soft bottom (8.9 ± 2.7 crabs trap^{-1}), compared with mounds under platforms (0 crabs trap^{-1}), and deep (1.1 ± 0.5 crabs trap^{-1}) and shallow (0.9 ± 0.3 crabs trap^{-1}) shell mound-only sites (Fig. 6b). Again, these differences in abundance were not significant due to high variability in CPUE among sampling dates.

The CPUE of the majid crab, *Loxorhynchus grandis*, was generally much lower than for *Cancer* spp. and no patterns were evident among habitats. In 2000, mean CPUE ranged from 0.6 ± 0.2 crabs trap^{-1} at deep shell mound-only to 1.6 ± 0.4 crabs trap^{-1} at shallow soft bottom sites (Fig. 6a). In 2001, CPUE of *L. grandis* was significantly greater on shallow shell mound-only (0.7 ± 0.1 crabs trap^{-1}) and deep soft bottom (0.4 ± 0.2 crabs trap^{-1}) than deep shell mound-only (0.06 ± 0.06

Table 4 Results of repeated measures ANOVA evaluating the effect of habitat type and time on the abundance (CPUE) of two *Cancer* spp. and of *Loxorhynchus grandis* in 2000 and 2001. Data $\log_{10}(x + 1)$ transformed prior to analysis

		Habitat type			Time			Habitat × time		
		F	*P*	*df*	*F*	*P*	*df*	*F*	*P*	*df*
2000	*C. antennarius*	13.06	< 0.05	2,3	0.43	0.78	3,1	2.42	0.32	6,2
	C. anthonyi	1.74	0.32	2,3	2.32	0.44	3,1	2.89	0.28	6,2
	L. grandis	1.00	0.46	2,3	8.81	0.24	3,1	5.52	0.16	6,2
2001	*C. antennarius*	26.00	< 0.01	3,4	5.57	0.16	3,2	0.44	0.86	9,5
	C. anthonyi	4.29	0.10	3,4	0.24	0.86	3,2	0.67	0.72	9,5
	L. grandis	7.33	0.42	3,4	1.83	0.37	3,2	1.39	0.37	9,5

crabs trap^{-1}) and mounds beneath platform sites (0 crabs trap^{-1}; Table 4, $P < 0.05$, post hoc *t*-test with Bonferroni correction).

In addition to *Cancer* spp. and *Loxorhynchus grandis*, several other species of mobile invertebrates were present in traps during sampling in 2000 and 2001 (Fig. 7). The most abundant were the sea stars, *Asterina miniata*, which were caught in traps at shallow and deep depths on shell mounds, but not on soft bottom, and *Pisaster giganteus*, which were present in traps only at mounds under platforms. Individuals of the whelk, *Kelletia kelletii*, were most abundant in traps at shallow mound-only sites (Fig. 7).

Comparison of current and historical estimates of macroinvertebrate abundance at shallow shell mound sites

The species composition and ranges of densities of macroinvertebrates on the mound under Platform Hilda prior to platform removal were comparable to those found by us on the mound under Platform Gina (Table 5). Species present in photographs and sampled in this study included the sea stars, *Pisaster brevispinus*, *P. giganteus*, *P. ochraceus*, and *Asterina miniata*, sea urchin, *Strongylocentrotus franciscanus*, sea cucumbers, *Parastichopus parvimensis* and *P. californicus*, and rock crab, *Cancer antennarius*. Species in the photographs at Hilda prior to platform removal that were not found on the mound under Platform Gina included the predatory sea stars, *Dermasterias imbricata* and *Pycnopodia helianthoides*.

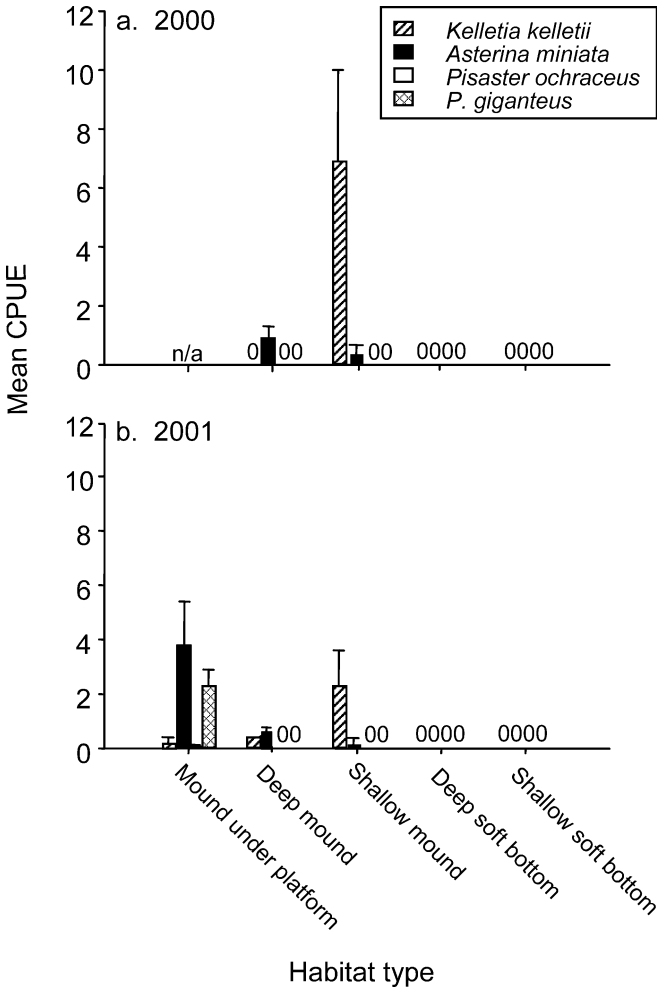

Fig. 7 Mean CPUE of invertebrates other than crabs in traps deployed in **a** 2000 and **b** 2001. $n = 2$ sites per habitat type (four sampling dates per year)

Discussion

Structure of shell mound communities

Our results suggest that the structure of shell mound communities is strongly influenced by the presence of the platform structure and the food provided by the clumps of mussels and associated organisms that continually slough from the platform to the seafloor. Predatory and omnivorous sea stars (*Pisaster* spp., *Asterina miniata*), in particular, were much less abundant and smaller at the shell mound-only sites. Mussels, the major component of this faunal litterfall (Wolfson et al. 1979; Page et al. 1999), are the primary prey of *Pisaster* spp. in rocky intertidal and subtidal habitats, where these sea stars are the dominant predators (Landenberger 1969; Paine 1974).

Pisaster spp. prey upon fallen mussels on the shell mounds under platforms (Simpson 1977; Wolfson et al. 1979; R.E. Bomkamp, personal observation). The low density (Fig. 3a) and small size (one individual of 10-cm arm radius) of *Pisaster* spp. at the mound-only sites suggests that these predators were food limited. In addition, individuals of *Pisaster* were present in historic photographs of the mound-only sites prior to platform removal (Table 5). These sea stars (particularly *P. giganteus* and *P. ochraceus*; Morris et al. 1980) have a strong preference for hard substrate habitat and are rarely found on soft bottom. Given that sea stars would have to cross an expanse of >3 km of soft bottom to reach inshore hard bottom habitat, we hypothesize that nearly complete mortality of sea stars may have occurred on the shallow mounds-only sites following platform removal in 1996.

Individuals of the omnivorous sea star, *Asterina miniata*, were also more abundant and larger at the mounds under platform sites than at mound-only sites (Figs. 3a, 4a). On the mound under Platform Gina, these sea stars were observed feeding on barnacles fallen from the platform and aggregated around fallen mussel clumps, but at mound-only sites they were never observed with large food items (H.M. Page, personal observation). *A. miniata* prefer hard substrate habitat (Morris et al. 1980) and appear unlikely to cross the wide expanse of soft bottom to neighboring shell

Table 5 Species and densities of benthic macroinvertebrates estimated from photographs taken in 1976 on the shell mound under Platform Hilda; $n = 5$ photographs

Species	Common name	Mean ± 1 SE (no. m^{-2})	Range (no. m^{-2})
Cancer antennarius	Crab	0.5 ± 0.3	0–1.1
Asterina miniata	Sea star	4.5 ± 0.8	2.7–7.1
Dermasterias imbricata	Sea star	0.1 ± 0.1	0–0.5
Pisaster giganteus	Sea star	0.1 ± 0.1	0–0.5
Pisaster ochraceus	Sea star	0.2 ± 0.1	0–0.5
Pisaster brevispinus	Sea star	0.6 ± 0.3	0–1.6
Pycnopodia helianthoides	Sea star	0.3 ± 0.2	0–1.1
Strongylocentrotus franciscanus	Sea urchin	0.1 ± 0.1	0–0.5
Parastichopus californicus	Sea cucumber	0.9 ± 0.4	0–2.2
Parastichopus parvimensis	Sea cucumber	4.3 ± 1.7	1–10.4

mounds or inshore to natural reefs. Our observation of the significantly lower density and smaller body size of *A. miniata* at mound-only compared to mound under platform sites suggests that the individual size and population density of these sea stars respond to the presence of greater food availability under existing platforms.

The predatory gastropod, *Cypraea spadicea*, was present in significantly higher densities on the mound under platform than mound-only sites (Fig. 3b), also suggesting a response to the overlying platform structure. Although there was no difference in the size structure of *C. spadicea* populations among sites, tissue dry weight standardized for shell length was significantly greater for individuals from mounds under platform than mound-only sites (Fig. 5), suggesting better condition (e.g., more glycogen reserves, Gabbott, 1976, 1983) and/or gonadal development of these individuals in the presence of faunal litterfall provided by platform structures.

The large gastropod mollusk, *Megathura crenulata*, was absent from the shallow mound-only sites. It is not known whether the presence of the platform structure influences the distribution and abundance of *M. crenulata* because there is no evidence for the presence of this species at mound-only sites prior to platform removal in the historical photographs we analyzed. However, on the mound under Platform Gina, individuals of this species were often associated with aggregations of sea stars feeding on freshly deposited litterfall (H.M. Page, personal observation).

Two species of gastropods, the carnivorous predators/scavengers, *Conus californicus* and *Kelletia kelletii*, were found in low densities (~0.01 to 0.1 individuals m^{-2}) during transect sampling only at the mound-only sites. The diet of *C. californicus* and *K kelletii* is diverse (Kohn 1966, Rosenthal 1971), so the absence of these predatory species in samples from the shell mound under Platform Gina is puzzling. *K. kelletii* has been reported to be a major component of the prey of *P. giganteus* (Rosenthal 1971). Thus, one possible explanation for the absence of these gastropods on the mound under Gina is predation pressure by the abundant *Pisaster*. However, this possibility remains to be tested.

In contrast to the pattern for predatory echinoderms, the relative abundance (as CPUE) of commercially important crabs, *Cancer antennarius* and *C. anthonyi*, did not differ among shell mound sites (Fig. 6). These crabs are predators and carnivorous scavengers (Morris et al. 1980) and likely consume components of faunal litterfall when available, but have greater mobility than other invertebrate taxa of shell mounds, and can forage over a larger area both on and off the mounds. For example, Page et al. (1999) reported that local fishermen captured a specimen of *C. anthonyi*, tagged at Platform Holly, 8 km from the platform.

Populations of two macroinvertebrate detritivores on shell mounds, *Parastichopus parvimensis* and *P. californicus*, appeared to be little affected by the removal of the platform structure. These sea cucumbers are non-selective deposit feeders, ingesting organic matter and infaunal organisms within soft sediments (Yingst 1974; Rogers-Bennett and Ono 2001). There were no differences in the density of *P. parvimensis* among mound-only and mound under platform sites (Fig. 3a). Differences in population structure of this sea cucumber among sites (Fig. 4b) were likely due to factors other than the food provided by the platform as the mean body length of animals from the mound under platform site was intermediate between those of the shell mound-only sites. The significantly higher density of *P. californicus* on the mound under Gina than on mound-only sites is also probably not related to the food provided by the platform since *P. californicus* employs the same feeding mode as *P. parvimensis*.

Effects of the allochthonous food subsidy and platform structure on mobile epibenthos

We hypothesize that the food provided by the dislodged organisms (clumps of mussels and associated organisms) that fall from platform structures to the shell mounds exerts bottom up control upon populations of predatory and omnivorous sea stars. Bottom up effects may influence overall community structure by shifting the relative abundance of organisms at different trophic levels, and/or by altering the densities of particular strongly interacting species such as *Pisaster* spp. (e.g., Menge 1992; Bustamante et al. 1995; Sanford and Menge 2001). Other studies have reported unusually high densities of predatory echinoderms beneath oil

platforms (Wolfson et al. 1979) and also suggested that food subsidies from platforms increase the density of some species immediately beneath and adjacent to the structure (Bascom et al. 1976; Wolfson et al. 1979; Davis et al. 1982; Page et al. 1999).

The platform structure could also affect the abundance and size structure of benthic organisms through the provision of recruitment habitat. For example, individuals of the crab, *Cancer antennarius* were hypothesized to move (or fall) from Platform Holly to the shell mound beneath the structure based on observations of juvenile crabs on the structure and the higher abundance of adult crabs on the shell mound than the structure (Page et al. 1999). However, some species sampled in this study on shell mounds (*Asterina miniata*, *Cypraea spadicea*, *Parastichopus* spp.) have not been sampled or observed on the structure of seven existing platforms (including Gina) in the Santa Barbara Channel (Page et al., unpublished data), suggesting that these species recruit preferentially to the hard benthos provided by the shell mound.

Effects of benthic substrate composition

There was no overlap in species composition of mobile macroinvertebrates between benthic communities on the shell mound under Platform Gina and the adjacent soft bottom locations. Similarly, qualitative descriptions of the soft bottom near shell mound-only locations prior to platform removal mention the presence of sea pens, tube worms and anemones, all soft bottom species (Simpson 1977; de Wit 2001). Thus, our results also suggest that the presence or absence of hard substrate was an important factor in determining the distribution of shell mound associated taxa. The distribution of the two most abundant crab species in our study corresponded with known substrate preferences. *Cancer antennarius,* which prefer hard substrata (Winn 1985), occurred in significantly higher abundance at shell mound than soft bottom sites (Fig. 6).

In contrast, *Cancer anthonyi*, which prefer sandy or muddy habitat or the interface between hard and soft substrata (Carroll and Winn 1989), showed a trend of higher abundance at the soft bottom sites (Fig. 6). Despite the potential for suitable habitat on the edge of the shell mound, *C. anthonyi* was not captured at mound under platform sites. This pattern of distribution of *C. anthonyi* differs from that reported in Page et al. (1999) where female *C. anthonyi* were found in high abundance on the shell mound under Platform Holly (~35 km west of these study sites) at the same time of year as in this study. However, depth may be important in accounting for this difference, as the bottom at Holly is ~66 m, compared with the deepest site (50 m) in the present study (Platform Houchin). Both Reilly (1987) and Page et al. (1999) suggested that *C. anthonyi* migrates seasonally between depths. In summary, our results suggest that highly mobile species, such as crabs, may respond more to the habitat structure provided by the shell mounds, and are less dependent on the food provided by the faunal litterfall.

Temporal changes following platform removal

The present study provided a unique opportunity to compare similar benthic habitats in the presence and absence of a platform structure. The relative effect of the platform on the benthic community appeared to vary among mound species in relation to trophic level, degree of mobility, and substrate preference. At the time of the current study, 5–6 years after platform removal, the mound-only sites appear to have lost most predatory and omnivorous sea stars, based on photographs of the shell mound under Platform Hilda and sampling data from Platform Gina. Those sea stars remaining on the shell-mound only sites were smaller than those on the mound under Platform Gina. Mobile crabs (e.g., *Cancer antennarius*) and the sea cucumber, *Parastichopus parvimensis*, which prefer hard substrate, were seemingly less affected, but given the estimated sedimentation rate at mound-only sites (Hazel and Hilda, 0.9–1.4 mm year^{-1}; Heidi and Hope, 1.5–2.0 mm year^{-1}; de Wit 2001), these sites may no longer provide suitable habitat in a few years. Thus, while the presence of the platform structure may enhance secondary productivity in the benthic community, this effect may disappear rapidly (<5 years in this case) after the platform is removed. Although not an experimental manipulation, the "natural experiment" of platform removal investigated here strongly suggests that the "artificial reef" communities under offshore oil platforms may not be resilient to platform removal.

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