

Effects of an offshore oil platform on the distribution and abundance of commercially important crab species

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ABSTRACT: The distribution, abundance, and population characteristics of large, highly mobile crab species (*Cancer antennarius*, *C. anthonyi*, *C. productus*, *Loxorhynchus grandis*) differed in relation to an offshore oil platform in the Santa Barbara Channel, California, USA. Only *C. antennarius* individuals recruited onto the platform, primarily into the attached community of *Mytilus galloprovincialis* and *M. californianus* at depths of <12 to 15 m. The higher CPUE (catch per unit effort) of *C. antennarius* beneath the platform, compared with nearby soft bottom stations, suggested that this species remained primarily in the vicinity of the platform. Although *C. anthonyi* did not recruit at the platform, adult female *C. anthonyi* were attracted to the platform from surrounding habitat. The higher CPUE of female *C. anthonyi* beneath the platform, compared with soft bottom stations, suggested that habitat selection is related to reproduction in this species. *C. productus* and *Loxorhynchus grandis* were present in low numbers at all benthic stations. The distribution and abundance of these crab species fit into 3 of 4 hypothesized scenarios that described different combinations of recruitment, distribution and abundance of mobile species around oil platforms: (1) 'recruitment/emigration', a platform provides recruitment habitat and individuals that recruit to the platform emigrate at some point to the surrounding environment, (2) 'recruitment/resident', a platform provides recruitment habitat, but individuals remain in the vicinity of the structure (*C. antennarius*), (3) 'attraction', individuals that recruited elsewhere are attracted to and aggregate at a platform (*C. anthonyi*), and (4) 'visitor', individuals that recruited elsewhere occur temporarily at the platform without aggregation (*C. productus*, *L. grandis*). Our results, in the context of these scenarios, illustrate the need to consider the responses of individual species to artificial structures.

KEY WORDS: Oil platform · Crabs · Cancridae · Majidae · Mussels · *Mytilus*

INTRODUCTION

Artificial structures can dramatically alter the species composition, distribution, and abundance of local invertebrate and fish fauna. Typically located on soft mud or sand bottom, artificial structures provide hard attachment sites for sessile invertebrates and may attract and aggregate mobile invertebrates and fishes (e.g. Wolfson et al. 1979, Davis et al. 1982, Bohnsack 1989, Love et al. 1994, Herrnkind et al. 1997). Observations of aggregations of fishes around artificial reefs

and oil platforms, in particular, have fueled the 'production versus attraction' controversy. Do these structures enhance the recruitment, growth, and/or survival of individuals or do they simply attract and concentrate individuals from surrounding habitats (e.g. Reggio 1989, Bohnsack et al. 1997, Carr & Hixon 1997, Herrnkind et al. 1997, Lindberg 1997)?

Offshore oil and gas platforms are among the largest artificial structures in the marine environment. It has been proposed in the 'rigs to reef' concept that obsolete oil and gas structures can serve as artificial reefs (Reggio 1987, 1989). Obsolete structures are cropped or toppled in place or towed and submerged in a dif-

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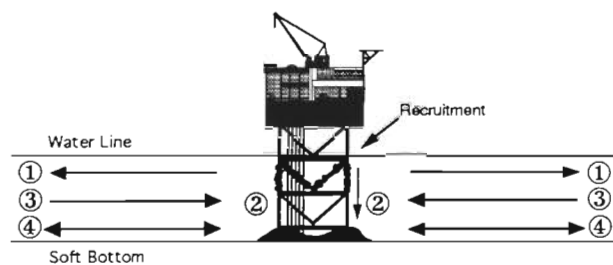


Fig. 1. Diagram illustrating 4 possible distribution and abundance scenarios for large, mobile crab species relative to an offshore oil platform. (1) 'Recruitment/emigration'-recruitment to platform; emigration from platform, (2) 'recruitment/resident'-recruitment to platform; resident population, (3) 'attraction'-attraction of individuals that recruited elsewhere, (4) 'visitor'-individuals that recruited elsewhere occur temporarily at the platform without aggregation

ferent location, providing hard substrata in a typically soft bottom environment. However, the 'rigs to reef' concept is controversial in some regions. While recreational fishermen may support the concept because of the apparent aggregation of fishes around these structures, commercial trawl fishermen often prefer platform removal due to the potential of fouling gear and loss of access to fishable areas (Picken & McIntyre 1989, MMS/State Lands Commission 1994). Part of the controversy exists because of a lack of information on the mechanisms by which active oil platforms, de facto artificial reefs, affect the distribution and abundance of recreational and commercially important species.

Three species of commercially important cancrivora crabs (*Cancer antennarius*, *C. anthonyi*, *C. productus*), and the majid crab *Loxorhynchus grandis* are fished in the vicinity of platforms offshore of southern California, USA. Platforms may affect the distribution and abundance of these large, mobile crustaceans through the alteration of physical habitat and local infaunal and epifaunal benthic communities. The platform structure (support members, conductor pipes) and attached invertebrate community may provide potential habitat and food for crabs. The attached invertebrate community is often many centimeters thick on platforms along the central and south coast of California; many of the species (e.g. *Mytilus californianus*, *M. galloprovincialis*, *Pollicipes polymerus*) are also components of rocky and pier piling intertidal and subtidal communities (Bascom et al. 1976, Stimpson 1977, Wolfson et al. 1979, Page 1986, Page & Hubbard 1987).

Food availability and habitat heterogeneity beneath a platform may also attract crabs. Clumps of mussel community, dislodged from the platform structure, fall to the bottom as 'faunal litterfall'. Over time, faunal litterfall creates a 'shell mound' extending in height several meters off the original bottom (reviewed in MBC

1987). The shell mound provides hard attachment sites, microhabitats, and food for an assemblage of invertebrate species typically not present on soft bottom. For example, Wolfson et al. (1979) reported unusually high densities of echinoderms (e.g. *Pisaster* spp., *Patiria miniata*) beneath Platform Eva, 3 km offshore of Huntington Beach, southern California (33° 40' N, 118° 93' W), feeding on mussels dislodged from the structure.

Based on our preliminary observations and on ideas developed for the potential effects of artificial reefs on fish populations (reviews by Bohnsack & Sutherland 1985, Bohnsack 1989, Pickering & Whitmarsh 1997), we hypothesized that the distribution and abundance of highly mobile, commercially important crab species may fit into 1 of 4 scenarios (Fig. 1). In the 'recruitment/emigration' scenario, a platform provides recruitment habitat and individuals that recruit to the platform emigrate at some point to the surrounding environment, contributing to the regional production of a species. There may be no way of knowing whether the recruitment of these individuals would have occurred elsewhere, but this scenario is closest to the production of new biomass hypothesis reviewed in Bohnsack (1989). In the 'recruitment/resident' scenario, the platform also provides recruitment habitat, but individuals remain in the vicinity of the structure, forming a resident population. In the 'attraction' scenario, individuals that recruited elsewhere are attracted to and aggregate at the platform. The attraction scenario could also lead to increased regional production through, for example, the increased growth rate and/or survival of individuals while at the structure. This pattern may occur seasonally or throughout the year. Finally, in the 'visitor' scenario, individuals that recruited elsewhere occur temporarily at the platform without aggregation; these individuals may also be present seasonally or throughout the year.

The objectives of our study, emphasizing commercially important crab species, were to: (1) test whether crabs occurred in higher densities beneath a platform compared to adjacent soft bottom, (2) characterize spatial and temporal patterns of crab recruitment to a platform, including the importance of the platform invertebrate community as a potential habitat and source of food for crabs, and (3) evaluate our data in the context of the 4 hypothesized scenarios described above which reflect different combinations of recruitment, and of distribution and abundance of mobile species around oil platforms.

MATERIALS AND METHODS

Study site. This study was conducted ~3 km offshore of Goleta, California (34° 25' N, 119° 52' W), in the

Santa Barbara Channel at and in the vicinity of the oil and natural gas platform 'Holly' (Mobil, Venoco; Fig. 2). The platform is 19 × 36 m at the water line. Bottom depth at the platform is ~66 m.

Support members and conductor pipes are covered intertidally and subtidally by a community of sessile and semi-mobile invertebrates. On Platform Holly, mussels contributed most to community biomass to a depth of ~12 m while barnacles (e.g. *Megabalanus californicus*, *Balanus aquila*), encrusting bivalves (e.g. *Chama arcana*, *Crassadoma gigantea*), and anemones (*Metridium senile*), were more abundant deeper. *Mytilus galloprovincialis* comprised nearly 100% of the mussels at depths shallower than ~6 m while large clumps of *Mytilus californianus* were present between 9 m and 12 m. Thirty conductor pipes arranged in 3 rows of 10 pipes 1 m apart provided replicate surfaces for measurements of invertebrate community thickness and the sampling of crabs on the structure.

Invertebrate community and faunal litterfall. To characterize the invertebrate community as potential crab habitat, we determined community thickness on randomly selected conductor pipes (1.64 m diameter without attached invertebrates, $n = 4$) monthly at 4 depths (6, 12, 18, and 24 m) from August 1995 to August 1996. Measurements of circumference were converted to estimates of radius ($r = C/2\pi$). Invertebrate community thickness was calculated as the difference between the radius of a conductor pipe with and without the attached invertebrates.

To estimate rates of faunal litterfall from conductor pipes to the benthos, traps ($n = 3$) were suspended between pairs of pipes at a depth of 18 m and retrieved monthly from October 1995 to September 1996. The traps consisted of 38 cm internal diameter (area = 0.113 m²) plastic circular hoops with attached 1.4 mm mesh bags. Since faunal litterfall consisted primarily of mussels and associated epifauna by weight (e.g. attached barnacles, anemones), the contents of the bags were sorted by mussel species (*Mytilus californianus* or *M. galloprovincialis*). Wet biomass of each mussel species and associated epifauna was determined using a spring scale after draining the sample of excess water. Displacement volume was measured for some samples by water displacement in a calibrated bucket.

Video recordings taken from a manned submersible (Delta) on October 29, 1996 provided qualitative information on bottom topography. The video recordings were taken along the north, south, east, and west outer margins of the structure.

Effect of platform structure on benthic distribution and abundance of crabs. Baited traps (Fathom Plus™) were used to evaluate the effect of location (immediately beneath the platform vs soft bottom) and time of

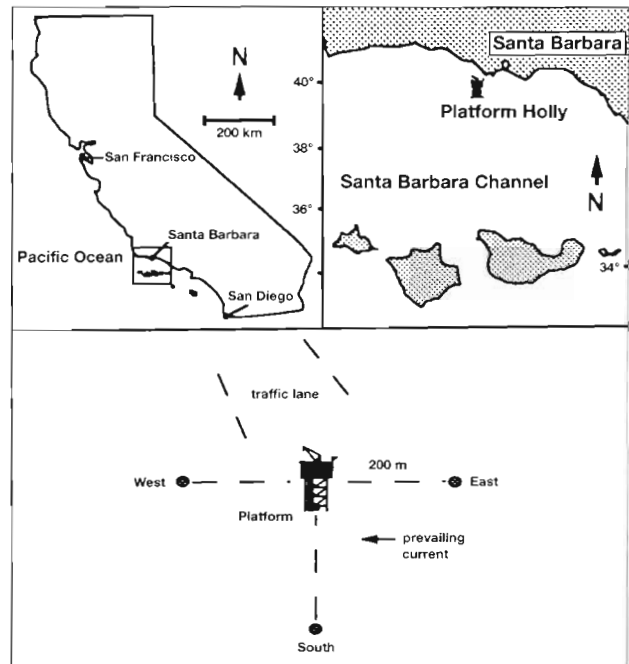


Fig. 2. Map showing the location of the oil and natural gas platform study site in the Santa Barbara Channel (Platform Holly) and the arrangement of sampling stations around the platform

year on the abundance of adult crabs. The traps were baited with a total of 1.4 kg of coarsely chopped mackerel *Scomber japonicus* enclosed in 2 plastic mesh containers (mesh size = ~5 mm). Traps were deployed monthly beneath the platform from July 1995 to August 1997 ($n = 4$ traps) and retrieved after a 22 to 24 h immersion time. Because of prevailing east to west currents, traps were deployed along the west side of the platform to prevent entanglement in the structure. Traps were deployed on soft bottom every 2 mo ~200 m east, south, and west of the platform from October 1995 to May 1997 ($n = 3$ traps at each location; Fig. 2). Depth of the bottom at these stations ranged from ~60 to 64 m. The crewboat transportation corridor along the north side of the platform precluded deployment of traps at this location.

Crabs in the traps were identified to species and sex, measured, and the presence of eggs recorded. For cancerid crabs, carapace width (CW) was measured as the distance to the nearest 1 mm between the outermost anterolateral teeth. For majid crabs, carapace length (CL) was measured to the nearest 1 mm from the notch in the rostrum to the posterior end of the carapace. Trapping results are expressed as catch per unit effort (CPUE).

Video recordings taken from the submersible also provided semi-quantitative information on the abun-

dance of adult cancrid and majid crabs on the bottom. Crabs in the video within an ~2 m wide swath along each of the 4 sides of the structure were counted and identified to genus or species where possible.

To assess potential movement of crabs between the platform and surrounding benthic habitats, all cancrid crabs >95 mm CW were tagged ~1 cm from the right margin of the epimeral suture with individually labeled yellow T-bar anchor tags (Floy FD-94) and released at the site of capture.

The platform structure as habitat. Recruitment of crabs: To measure spatial and temporal variation in the recruitment of crabs to the platform, we deployed recruitment cages (12 × 30 cm cylinders of 12 mm mesh vevax) filled with 5 kg of mussel community typically found at a depth of 12 m (*Mytilus californianus*, *M. galloprovincialis* and associated organisms) from March 1996 to September 1997. Prior to deployment, the mussel community was carefully searched and all crabs removed. The recruitment cages were attached to conductor pipes at depths of 12, 18, and 24 m, and deployed on the bottom (66 m) (n = 3 to 4 at each depth). Cages were retrieved bimonthly and the mussel community removed and searched. Crabs within the cages were identified to species and sex (where possible) and measured.

Distribution and abundance of crabs: To further examine temporal variation in the recruitment and size structure of crabs on the platform, crabs were sampled on at least 4 conductor pipes at 3 depths (12, 18, and 24 m) using SCUBA every other month from October 1995 to November 1996 and monthly from December 1996 to July 1997. Conductor pipe sites were selected randomly at each depth. On the conductor pipes, a 0.82 × 2.46 m (2 m²) area was searched by 2 divers and crabs removed by hand.

Crabs concealed within the mussel community at a depth of 12 m were sampled by removing 5 to 10 kg of mussels at each station into 1.4 mm mesh bags. The wet weight of *Mytilus californianus* and *M. galloprovincialis* and associated fauna was determined in the laboratory as above. Crabs in the samples were identified to species and sex (where possible) and measured. Crab density was standardized to 5 kg wet wt of mussel community, or to area (m²) using data on the volume of the mussel sample (m³) divided by the thickness of the attached community (m).

Crabs were also sampled on horizontal and diagonal support members between depths of 9 m and 18 m in February 1995, December and May 1996 and August 1997. Support members were carefully searched by divers and crabs removed by hand.

To compare the relative abundance of larger crabs (>80 mm CW) on the platform with the bottom, 3 Fathom Plus traps were deployed on horizontal mem-

bers among the conductor pipes at a depth of 9 m on 7 dates from November 1995 to June 1997.

Statistical analyses. All statistical analyses were done using Systat 5.2 (Wilkinson et al. 1992). The effects of independent variables (depth, location, and/or time) on the dependent variables (i.e. thickness of the invertebrate community, faunal litterfall rates, and crab density) were evaluated using repeated measures analysis of variance (ANOVA). This statistic was appropriate since our study involved repeated sampling at 1 platform. Post hoc univariate *F*-tests were used to identify significant differences in mean values among locations, depths, and times. Tests for differences in the relative abundance of crab species between depths of 9 and 66 m were made using a paired *t*-test by sampling date. Comparisons of individual mean size between locations were made for each crab species with unpaired *t*-tests. Data were log transformed [$x' = \log_{10}(x + 1)$] prior to analysis to correct for heteroscedasticity (Zar 1984). A chi-square test was used to test for significant deviations from a predicted proportion of 0.50 male individuals for each species.

RESULTS

Platform invertebrate community and faunal litterfall to the benthos

The invertebrate community on platform conductor pipes varied in thickness with depth and time (depth × time, $p < 0.05$, $F = 1.85$, $df = 24, 56$, 2-way ANOVA). Thickness was greatest over time at a depth of 12 m (except on July 27, 1996, $p < 0.05$, post hoc *F*-tests) and least at depths of 18 and 24 m (Fig. 3a). The increase in mean thickness over time at 6 m from 6.3 ± 1.2 in August 1995 to 15.3 ± 0.4 cm in August 1996 reflects the recolonization of conductor pipes by mussels (primarily *Mytilus galloprovincialis*) following a maintenance cleaning at this depth during summer 1995.

Rates of faunal litterfall to the benthos varied significantly over time ($p < 0.05$, $F = 2.32$, $df = 9, 27$, 1-way ANOVA), ranging from 0.08 ± 0.03 to 2.60 ± 0.81 kg wet wt trap⁻¹ wk⁻¹ ($\bar{x} \pm 1$ SE; Fig. 3b). Rates of faunal litterfall were significantly higher October to March and August to September compared with April to June ($p < 0.05$, $F = 18.83$, $df = 1, 3$, post hoc *F*-test). Overall, dislodged clumps of *Mytilus galloprovincialis* formed $92.8 \pm 3.3\%$ (n = 28) of this material. The wet weight and displacement volume of mussel clumps were highly correlated and described by the following relationship: $v = 0.74 (\pm 0.02, \pm 1 \text{ SE})w - 0.04 (\pm 0.12)$, $r = 0.99$, $p < 0.001$, $df = 28$, where v = volume ($\times 10^3$ cm³) and w = wet weight (kg).

Video recordings from the submersible showed that the topography of mud soft bottom beneath the plat-

form is covered by a mound of mussel shells and other debris with an estimated height of 3 to 4 m. The mound was highest towards the west and north side of the platform. Mud substratum was visible on the east side of the platform.

Effect of platform structure on benthic distribution and abundance of crabs

Three species of *Cancer* (*C. antennarius*, *C. anthonyi*, *C. productus*) and the majid crab *Loxorhynchus grandis* were caught in traps deployed on the bottom. There were no significant differences among soft bottom stations in CPUE with location or time ($p > 0.1$, 2-way ANOVA) and these data were pooled for each species in subsequent analyses ($n = 9$ stations). There was a strong effect of location (platform vs soft bottom) on CPUE for *C. antennarius* and *C. anthonyi* ($p < 0.001$, 2-way ANOVA: Table 1). The mean CPUE of *C. antennarius* was significantly higher beneath the platform than at the soft bottom stations on each sampling date ($p < 0.05$, post hoc *F*-tests: Fig. 4a). The mean CPUE of *C. anthonyi* was also significantly higher at the platform compared with the soft bottom stations ($p < 0.05$, post hoc *F*-tests: Fig. 4b) except in November 1996 and January 1997. No effect of location on CPUE was found for *C. productus* and *L. grandis* (Table 1, Fig. 4c,d).

Video recordings showed a patchy distribution of crabs on the mussel mound. The density of cancid crabs ranged from 0.5 crab 10 m^{-2} (east, west, and south transects) to 2 crabs 10 m^{-2} along the north transect. Densities of *Loxorhynchus grandis* ranged from 0.2 crab 10 m^{-2} along the east and south transects to 2 crabs 10 m^{-2} along the west and north transects.

A strong effect of time on CPUE was found for *Cancer anthonyi* and *Loxorhynchus grandis* (Table 1, Fig. 4). For *C. anthonyi*, mean CPUE values during the winter and spring (January to May, ≥ 3.0 crabs trap^{-1}) were significantly higher than during summer and fall (June to November, ≤ 2.0 crabs trap^{-1} ; $p < 0.001$, $F = 24.94$, $df = 1, 9$, post hoc *F*-test). For *L. grandis*, mean CPUE values were significantly higher in the fall and early winter months than other times of the year (Octo-

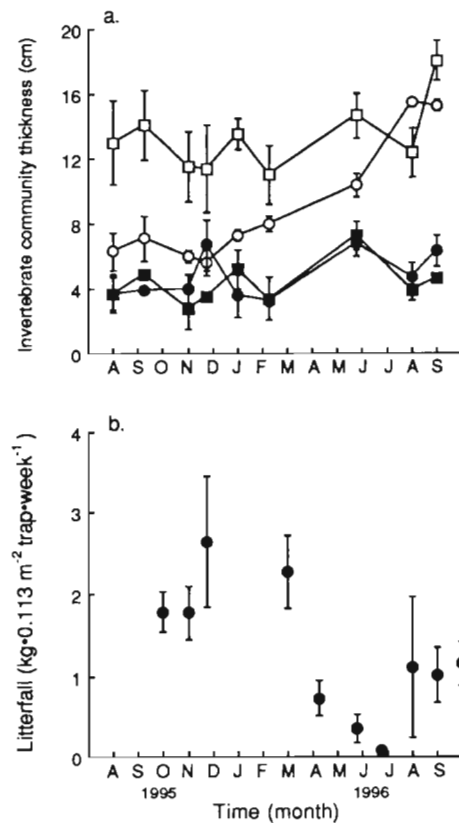


Fig. 3. (a) Thickness of the invertebrate community at depths of 6 m (○), 12 m (□), 18 m (●), and 24 m (■). $n = 4$ to 6 conductor pipes, and (b) faunal litterfall over time measured at a depth of 18 m, $n = 3$ faunal litterfall traps, $\bar{x} \pm 1$ SE

ber 1995 and November 1996 vs the other 7 mo, $p < 0.05$, $F = 5.31$, $df = 1, 9$, post hoc *F*-test).

There was no correlation ($p > 0.1$) between the monthly mean CPUE of *Cancer antennarius*, *C. anthonyi*, *C. productus*, or *Loxorhynchus grandis* beneath the platform and monthly faunal litterfall rates measured at the conductor pipes.

A total of 780 cancid crabs were tagged in this study (368 *Cancer antennarius*, 347 *C. anthonyi*, and 65 *C. productus*). Recapture rates were low for all species at the platform (*C. antennarius*: 1.4%, *C. anthonyi*: 0.9%, *C. productus*: 3.1%). No tagged individuals were

Table 1. Results of repeated measures 2-way ANOVA evaluating the effect of location and time (platform vs soft bottom) on the abundance (CPUE) of *Cancer* spp. and of *Loxorhynchus grandis*. Data $\log_{10}(x+1)$ transformed prior to analysis

| Species | Location | | | Time | | | Location × Time | | |
|-----------------------|----------|--------|-----|------|-------|------|-----------------|--------|------|
| | F | p | df | F | p | df | F | p | df |
| <i>C. antennarius</i> | 98.33 | <0.001 | 1,9 | 1.89 | 0.07 | 8,72 | 3.09 | <0.01 | 8,72 |
| <i>C. anthonyi</i> | 27.13 | <0.001 | 1,9 | 2.87 | <0.01 | 8,72 | 4.54 | <0.001 | 8,72 |
| <i>C. productus</i> | 0.76 | >0.1 | 1,9 | 1.99 | 0.06 | 8,72 | 1.62 | >0.1 | 8,72 |
| <i>L. grandis</i> | 0.12 | >0.1 | 1,9 | 3.69 | 0.001 | 8,72 | 0.91 | >0.1 | 8,72 |

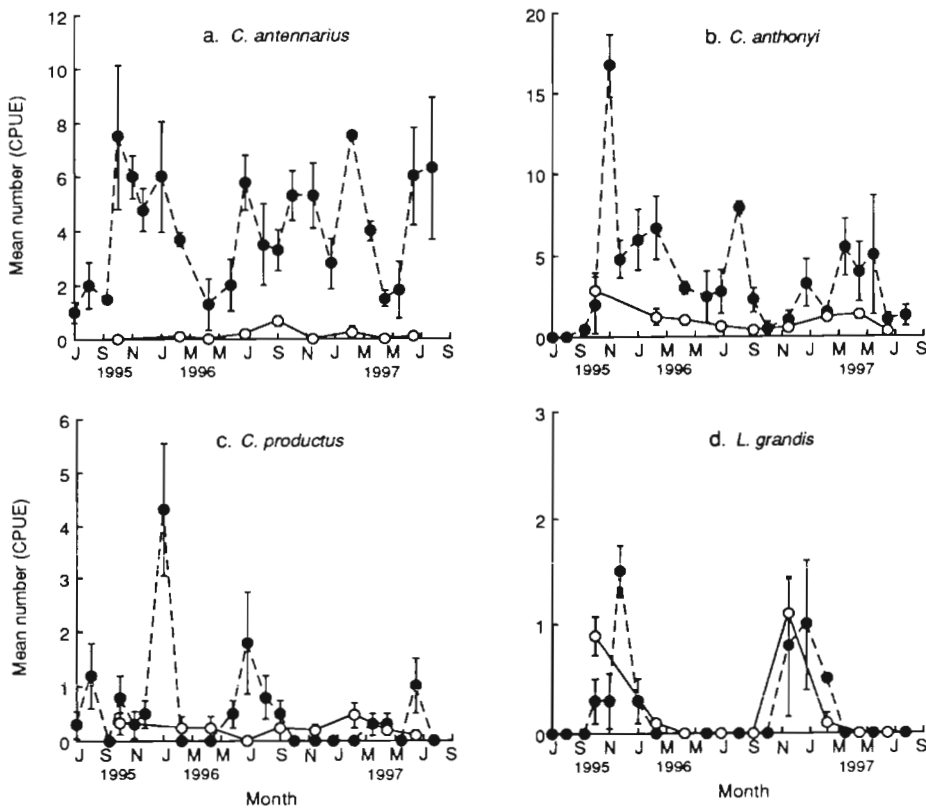


Fig. 4. Spatial and temporal patterns in the abundance (expressed as CPUE) of (a) *Cancer antennarius*, (b) *C. anthonyi*, (c) *C. productus*, and (d) *Loxorhynchus grandis* beneath Platform Holly and on adjacent soft bottom. Locations: Platform Holly (●), grouped soft bottom stations (○). n = 3 to 4 traps at Holly, n = 9 traps at soft bottom stations, $\bar{x} \pm 1$ SE. Note differences among figures in scale of y-axis

recaptured at the soft bottom stations. However, by November 1997, 10 tagged *C. anthonyi* were caught in traps set by local fishermen at distances of up to 8 km

from the platform and up to 1.5 yr after initial tagging. No tagged individuals of the other species were reported by fishermen.

Table 2. Population characteristics of *Cancer* spp. and *Loxorhynchus grandis*. x_m : mean size of male crabs; x_f : mean size of female crabs, carapace width for *Cancer* spp., carapace length for *L. grandis*, mean values, mm \pm 1SE, sample sizes in parentheses, $n_m/(n_m + n_f)$: proportion of male crabs in the samples; significance levels for chi-square test against a theoretical proportion of 0.50 male crabs. *p < 0.05, ***p < 0.001

| Species | Location | |
|-----------------------------|--------------------|-------------------|
| | Platform | Soft bottom |
| <i>Cancer antennarius</i> | | |
| x_m | 102 \pm 15 (110) | 111 \pm 14 (16) |
| x_f | 103 \pm 14 (216) | 104 \pm 8 (7) |
| $n_m/(n_m + n_f)$ | 0.34*** | 0.70 |
| <i>Cancer anthonyi</i> | | |
| x_m | 143 \pm 20 (33) | 136 \pm 18 (63) |
| x_f | 115 \pm 15 (220) | 121 \pm 12 (20) |
| $n_m/(n_m + n_f)$ | 0.13*** | 0.76* |
| <i>Cancer productus</i> | | |
| x_m | 161 \pm 26 (5) | 175 \pm 18 (8) |
| x_f | 151 \pm 18 (45) | 150 \pm 21 (11) |
| $n_m/(n_m + n_f)$ | 0.10*** | 0.42 |
| <i>Loxorhynchus grandis</i> | | |
| x_m | 176 \pm 16 (16) | 169 \pm 16 (17) |
| x_f | 150 (2) | 172 \pm 22 (3) |
| $n_m/(n_m + n_f)$ | 0.89 | 0.85 |

Population characteristics of crabs: benthos

All *Cancer* spp. individuals captured in traps on the bottom exceeded the minimum size of maturity (*C. antennarius*: 73 mm CW, Carroll 1982; *C. anthonyi*: 89 mm CW, Anderson & Ford 1976; *C. productus*: 70 mm CW, Orensanz & Gallucci 1988) and can be considered adults. The mean size of *C. antennarius* and *C. productus* captured in traps did not differ with sex or between platform and soft bottom locations (Table 2). The mean size of male *C. anthonyi* was significantly larger than that of female individuals at both platform ($p < 0.001$, $t = 10.10$, $df = 254$, Student's t -test) and soft bottom locations ($p < 0.01$, $t = 2.78$, $df = 63$). Female *C. anthonyi* were larger at soft bottom stations than beneath the platform ($p = 0.05$, $t = 1.97$, $df = 240$).

At the platform, the proportion of male crabs (number of male crabs/total number of trapped crabs) of *Cancer antennarius* (0.34), *C. anthonyi* (0.13) and of *C. productus* (0.10) differed significantly from 0.50 (Table 2). In contrast, at the soft bottom stations, the proportion of male crabs was not significantly different from 0.50 for *C. antennarius* and *C. productus* and

biased towards male crabs for *C. anthonyi* (0.76: Table 2). Although not significantly different from 0.5, a trend of more male than female *Loxorhynchus grandis* were trapped at both platform (0.89) and soft bottom (0.85) locations.

Very few *Cancer antennarius* (≥ 80 mm CL) were ovigerous. Overall, only 1.8% ($n = 169$) and 8.3% ($n = 12$) of female *C. antennarius* were ovigerous beneath the platform and on the structure, respectively. Data for *C. anthonyi* were grouped by quarter (winter = December–February, spring = March–May, summer = June–August, fall = September–November) to increase statistical power for analysis. The percent of female *C. anthonyi* that were ovigerous ranged from 0% in summer and fall to 28 and 37%, respectively in winter 1996, and spring 1997. Percentage of ovigerous female crabs was positively correlated ($p < 0.05$, $r = 0.83$, $df = 6$) with the CPUE of females beneath the platform, if the outlying mean value of 15.3 crabs trap⁻¹ in November 1995 was excluded from the analysis.

The platform structure as habitat

Recruitment of crabs

Of the 4 crab species on the benthos, only *Cancer antennarius* recruited onto the platform structure (Fig. 5). Recruitment was clearly seasonal; crabs ≤ 10 mm CW were most abundant during late spring and summer. In the recruitment cages, there were no differences in the densities of crabs ≤ 10 mm CW among depths of 12, 18, and 24 m ($p > 0.05$, 1-way ANOVA) and the data were grouped. Densities of *C. antennarius* ≤ 10 mm CW were generally < 0.5 crabs 5 kg mussels⁻¹, but reached 11.0 ± 5.0 and 7.1 ± 2.8 crabs 5 kg mussels⁻¹ in June 1996 and May 1997, respectively. In the mussel community samples, densities of *C. antennarius* ≤ 10 mm CW were also generally < 0.5 crabs 5 kg mussels⁻¹, except in June 1996 and June 1997 when values of 3.0 ± 2.2 and 2.7 ± 1.8 crabs 5 kg mussels⁻¹ were recorded.

Small *Cancer antennarius* were also found in recruitment cages deployed on the bottom. Mean number of crabs ≤ 10 mm CW ranged from lows of 0 to 1.7 ± 0.9 crabs 5 kg mussels⁻¹ in August 1996 through January 1997 ($n = 3$ or 4 cages), to a high of 11.5 ($n = 2$ cages) in late March 1997.

Distribution, abundance, and population structure of crabs

Of the 4 crab species, only *Cancer antennarius* were observed in visual surveys on the platform. *C. antennarius* ≤ 10 mm CW were hidden within the mussel

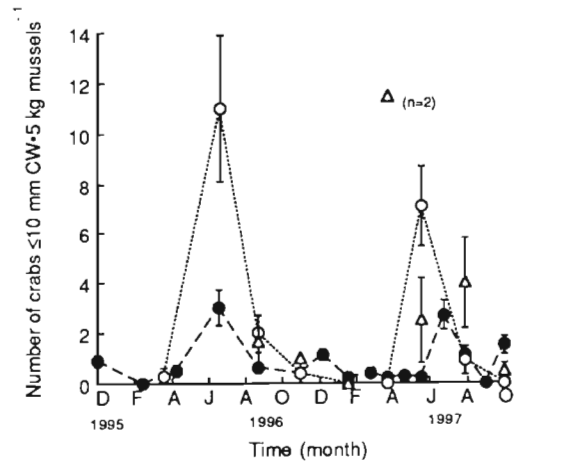


Fig. 5. Mean number of *Cancer antennarius* ≤ 10 mm CW in mussel community samples from a depth of 12 m (●) and from recruitment cages deployed at depths of 12, 18, and 24 m (○) and 64 m (Δ). $n = 3$ to 6 samples or cages, $\bar{x} \pm 1$ SE

community and rarely observed in those surveys. The density of crabs observed in the open and collected during visual surveys ranged from 0 to 4 crabs m⁻². There was no effect of time or depth (12, 18 and 24 m) on crab density which, for grouped data, averaged 0.8 ± 0.1 crab m⁻² ($\bar{x} \pm 1$ SE, $n = 153$ quadrats).

However, if data from mussel community samples and visual surveys are combined, the density of crabs was dramatically higher at 12 m than at 18 or 24 m during late spring and early summer due to crab recruitment. For example, the density of *Cancer antennarius* ranged from low mean values of 1 crab m⁻² on February 18, 1996 and 9 crabs m⁻² on January 18, 1997 to high values of 134 crabs m⁻² on May 25, 1996, and 183 crabs m⁻² on June 21, 1997.

Trapping data suggested that adult *Cancer antennarius* were less abundant on the structure than on the bottom. Mean CPUE values of adult *C. antennarius* ranged from 0 to 0.7 ± 0.5 crabs trap⁻¹ at a depth of 6 m compared with from 2.0 ± 1.9 to 6.0 ± 1.6 crabs trap⁻¹ on the bottom ($p < 0.001$, $t = 7.76$, $df = 20$, paired t -test: Fig. 6).

Approximately 90% of *Cancer antennarius* in the mussel community samples from 12 m ($n = 137$) were ≤ 20 mm CW (Fig. 7). Although a distinct period of recruitment into mussel clumps was evident, there were no temporal changes in the size distribution of *C. antennarius* > 20 mm CW sampled on the structure that might reflect individual growth within this cohort, and the data were grouped across time (Fig. 7). Most *C. antennarius* individuals on the structure ranged between ~ 30 and 70 mm CW. The proportion of male crabs collected during visual surveys (0.56, $n = 615$) was not significantly different from 0.50 ($p > 0.1$, chi-square test).

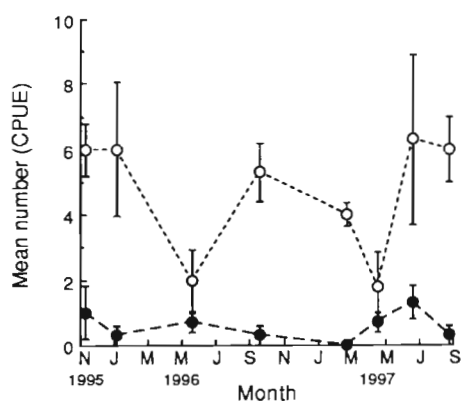


Fig. 6. Comparison of the relative abundance (as CPUE) of *Cancer antennarius* (>80 mm) trapped among the conductor pipes on the structure (6 m, ●) and on the bottom (66 m, ○). $n = 3$ to 4 traps at each location, $\bar{x} \pm 1$ SE

DISCUSSION

Two of the 4 crab species, *Cancer antennarius* and *C. anthonyi*, occurred in higher densities at the platform compared to the surrounding soft bottom. The platform structure, associated invertebrate community, and the altered benthos beneath the platform may contribute to this pattern by providing crabs with (1) food, (2) recruitment habitat, (3) preferred habitat of adults, and/or (4) increased shelter from predation. These 4 mechanisms, potentially responsible for the effect of the platform on the distribution and abundance of these crab species, are discussed below.

Both *Cancer* species could be attracted to the platform by food provided by the mussel community found from the surface to depths of <12 to 15 m and, through faunal litterfall, on the bottom. Physical disturbance is an important process that structures mussel communities in the Santa Barbara Channel (Harger 1972a,b). At Platform Holly, disturbance from storm events and platform maintenance facilitated the recruitment and growth of *Mytilus galloprovincialis* and this species was the principal biomass component of faunal litterfall. This species also has relatively weak byssal threads and is more easily dislodged by wave action than is *M. californianus* (Harger 1972a,b). Faunal litterfall has greatly modified the benthic habitat beneath the platform, creating a high relief mound qualitatively similar to that reported at other platforms offshore of California (Wolfson et al. 1979).

Faunal litterfall is continuous though temporally variable. Using mean values ranging from 121 to 2644 g 0.113 m^{-2} (Fig. 2b), we estimate that the mussel community attached to the 30 conductor pipes contributed from 47 to 1031 kg mussels wk^{-1} to the bottom. Since the area of the conductor pipes represents only a frac-

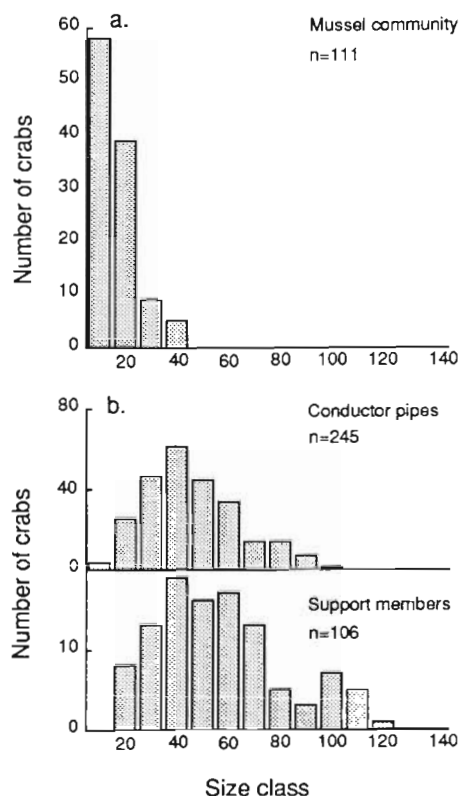


Fig. 7. Size frequency distribution of *Cancer antennarius* (a) within the mussel community at a depth of 12 m on the platform and (b) collected during visual surveys of conductor pipes and support members. Note that data collection methods differed for (a) and (b)

tion of the total submerged surface area of the platform, rates of faunal litterfall from the entire structure would be considerably higher. If food is abundant, the growth rate of crabs should be rapid. Growth rates of *Cancer antennarius* on the structure were considerably higher (2- to 3-fold, D. Dugan unpubl. data) than rates reported for this species in the rocky subtidal (Carroll 1982), supporting this conclusion.

The platform provides recruitment habitat only for *Cancer antennarius*. Recruitment contributed to elevated densities of small individuals of this species during the late winter and spring months. The timing of peak recruitment (late spring and early summer) is similar to that reported for this species elsewhere in southern California (Winn 1985). The presence of the smallest juvenile *C. antennarius* within mussel clumps is consistent with reports that this species recruits preferentially onto hard substrata (Winn 1985). This species is also reported to recruit preferentially in shallow water and late stage rock crab larvae (*Cancer* spp.) have been noted near the surface (Shanks 1986). There was no effect of depth (12, 18, 24, 66 m) on the density

of *C. antennarius* ≤ 10 mm CW in recruitment cages. However, crabs could have recruited in shallow water, dropped to the bottom indirectly in association with faunal litterfall, and moved into the cages.

Recruitment cannot explain the higher densities of *Cancer anthonyi* at the platform compared to soft bottom. *C. anthonyi* megalopae may have a preference for soft substrata (Winn 1985) and we hypothesize that individuals of this species recruit onto sand or mud bottom in shallow water and move into deeper water as they grow larger. Such an ontogenic shift in habitat use exists for other *Cancer* species. For example, young-of-the-year *C. magister* occur in high densities in intertidal beds of eelgrass and patches of bivalve shell fragments and move into deeper water as they grow (Armstrong & Gunderson 1985, Stevens & Armstrong 1985).

Habitat use is reported to differ between adult *Cancer antennarius* and *C. anthonyi* and a preference for hard substrata and/or structurally complex habitats may also explain, in part, the dramatically higher densities of adult *C. antennarius* at the platform compared to surrounding soft bottom. Winn (1985) reported that *C. antennarius* adults have a behavioral preference for hard substrata that includes rocky shores, subtidal reefs, and the interface between hard and soft bottom habitats. In contrast, *C. anthonyi* adults are reported to occur primarily on silty sand to mud substrata. This species also occurs at the interface between rocky and soft bottom habitats (Carroll & Winn 1989) and was an important component on and around experimental artificial reefs in Santa Monica Bay (Turner et al. 1969). The recapture of *C. anthonyi*, tagged at the platform, at a distance of several kilometers by fishermen, supports the view that this species moves between the platform and surrounding soft bottom habitat.

Two lines of evidence suggest a link between elevated densities of adult *Cancer anthonyi* at the platform and the reproductive cycle of this species. First, the sex ratio of *C. anthonyi* beneath the platform was highly skewed towards female crabs (87% female), compared to the sex ratio of this species from the surrounding soft bottom (24% female). Second, peak abundance of this crab beneath the platform coincided with the peak in the percentage of ovigerous females (excluding the outlying data from November 1995).

Sex-specific differences in movement and habitat use also have been reported for other species of *Cancer*. Ovigerous *C. irroratus* are found in water <30 m deep although the distribution of this species extends from 9 to 274 m (Musick & McEachran 1972). *C. magister* is present in estuaries and along the open coast, but ovigerous females are found primarily along open coasts (Armstrong & Gunderson 1985). Ovigerous *C. magister* are also reported to burrow deeply into sedi-

ments possibly as protection against predation (O'Clair & Freese 1985). Similarly, seasonal changes in the preferred habitat of female *C. anthonyi* may enhance the survival of these individuals especially when ovigerous. The greater abundance of *C. anthonyi* beneath the platform during the winter and early spring compared with summer and fall months suggests that female crabs move seasonally between the platform and surrounding areas.

Spatial refuges from predation could be provided by the attached invertebrate community and mussel mound. Nevertheless, small *Cancer antennarius* (<35 mm CW) are susceptible to predation by fishes (e.g. *Scorpaenichthys marmoratus*), conspecifics, and other invertebrates (e.g. *Octopus* spp.) and we hypothesize that predation on juvenile crabs strongly influences the density and size distribution of crabs on the structure. This view is supported by 3 lines of evidence. First, our observations of an abrupt decline in crab density at sizes of >20 mm CW. Second, recruitment cohorts failed to affect the size distribution of crabs on the structure over time through individual growth; a pattern that reflects the decline in density of newly recruited crabs. Finally, densities of crabs ≤ 10 mm CW were dramatically higher in recruitment cages, protected from large predators, than in uncaged mussels. In contrast, large crabs (>100 mm) are less vulnerable to predation by fish and invertebrates (Carroll & Winn 1989) and from humans since commercial and sport fishing activity is prohibited in the vicinity of the structure.

The distribution and abundance of 2 crab species, *Cancer productus* and *Loxorhynchus grandis*, were not influenced by the platform. Individuals of these species were caught much less frequently than were *C. antennarius* and *C. anthonyi*. Not much is known about the distribution and abundance of these crabs. In general, *C. productus* is more abundant in northern California while *C. antennarius* and *C. anthonyi* are more abundant in southern and central California (Carroll & Winn 1989, Parker 1992). *C. productus* may prefer hard substrata (Parker 1992), but this species did not recruit or aggregate at the platform. Overall, 90% of the *C. productus* individuals trapped beneath the platform were females, compared with 58% of the crabs on soft bottom, suggesting that the behavioral patterns of female crabs of this species are similar to those of *C. anthonyi*.

Loxorhynchus grandis individuals were present at the platform and soft bottom stations only during the late fall and early winter. Most individuals (85 to 89%) were male. This species undergoes seasonal movements and male *L. grandis* are reported to move offshore (to depths of 50 to 60 m) in fall and winter and onshore in early spring (Culver & Kuris 1992). Female

crabs may also undertake offshore movements, but to shallower depths. Both sexes migrate onshore in early spring and piles of adult female crabs surrounded by male crabs are observed at depths of 7 to 10 m in spring and summer. In general, larger crab species are highly mobile, capable of moving distances of several kilometers during seasonal migrations (e.g. review by Rebach 1983, Rodin 1989, Stone & O'Clair 1989). In addition, seasonal differences in the distribution of male and female crabs are common. For example, female *Paralithodes camtschatica* are less mobile and have a narrower depth distribution than male crabs, occurring in water <50 m deep during the summer and moving to deeper sites in the winter (Rodin 1989).

In conclusion, we hypothesized that the distribution and abundance of commercially important crab species around oil platforms may fit into 1 of 4 scenarios (Fig. 1). However, none of the crab species clearly fit the recruitment/emigration scenario. Although *Cancer antennarius* recruits to the platform, emigration of this species from the platform appears limited. There was no evidence of large-scale movement of this crab from the platform into the surrounding soft bottom habitat and a behavioral preference for hard substrate may preclude such movement. This *Cancer* species most closely fits the recruitment/resident scenario. In contrast, *C. anthonyi* most closely fits the attraction scenario with movement between the platform and surrounding habitat. The presence of primarily female *C. anthonyi* around the platform during the winter and spring months may involve seasonal changes in habitat use related to reproduction, behavior that has not been invoked previously to explain the attraction of mobile species to artificial structures. Finally, the distribution and abundance of *C. productus* and *Loxorhynchus grandis* most closely fit the visitor scenario. *C. productus* is present in low densities throughout the year while *L. grandis* is present seasonally. Our results, in the context of these scenarios, reflect interspecific differences in patterns of abundance, recruitment, and behavior, and illustrate the need to consider the responses of individual species to artificial structures such as oil platforms.

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