



Trophic Links and Condition of a Temperate Reef Fish: Comparisons among Offshore Oil Platforms and Natural Reef Habitats

Final Technical Summary

Final Study Report



**U.S. Department of the Interior
Minerals Management Service
Pacific OCS Region**

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FINAL TECHNICAL SUMMARY

STUDY TITLE: Ecological Performance and Trophic Links: Comparisons among Offshore Oil Platforms and Natural Reefs for a Selected Fish and Their Prey

REPORT TITLE: Trophic Links and Condition of a Temperate Reef Fish: Comparisons among Offshore Oil Platforms and Natural Reef Habitats

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KEY WORDS: food web, exotic species, oil platform, *Caprella mutica*, *Erichthonius brasiliensis*, condition factor, *Oxylebius pictus*, artificial reef

BACKGROUND:

Habitat-related variation in the type and availability of invertebrate prey and its implication for higher trophic levels is of particular interest when comparing offshore oil platforms with the natural reef environment. In general, the invertebrate and fish assemblages associated with coastal oil platforms contain species present in natural reef habitats inshore of these structures; however, attributes of the assemblage, including differences in the relative abundance and

density of the constituent species, may differ dramatically from natural habitats. Additionally, exotic species have been found to occur at a higher abundance at platforms than natural reefs.

Microcarnivorous fishes are ubiquitous members of shallow reef assemblages and are important trophic intermediates between invertebrate prey and higher level piscivorous fishes. Although the quantity and quality of prey available to microcarnivorous fishes likely varies among reefs, few studies have explored habitat-related patterns in prey type and density and the implications of these patterns for indices of fish individual performance.

OBJECTIVES: This study explored habitat-related variability in prey resources and the consequences of this variability to the diet and individual performance of resident microcarnivorous reef fishes. We compared the composition and abundance of small benthic invertebrates, and fish condition, among two offshore oil platforms and two natural rocky reefs in the Santa Barbara Channel. We used the ubiquitous microcarnivorous fish, the painted greenling (*Oxylebius pictus*), as a model fish species.

DESCRIPTION: This study was conducted in the Santa Barbara Channel at two offshore oil and natural gas platforms (Holly, Houchin) and two inshore natural rocky reef outcrops (Naples, Mohawk). To compare the species composition, density, and standing crop of potential invertebrate prey of painted greenling among platforms and reefs, we sampled small invertebrates in the foraging areas of this fish approximately monthly from April 2003 to September 2004. To compare the diet of painted greenling among platforms and natural reefs, we sampled fish from all sites in September 2003 and in April 2004. Painted greenling individuals were collected using hand nets in the same area that invertebrates were sampled. The stomach from each fish was removed and the contents sorted by taxonomic group and enumerated under a dissecting microscope. We explored selectivity in predation of painted greenling fish on caprellid and gammarid amphipod prey at platform and natural reef sites. To compare the "individual performance" of painted greenling among platforms and natural reefs, an index of fish "condition" was calculated. We also explored the use of otolith analysis to compare the daily growth rate of painted greenling among sites, but the otoliths proved unsuitable for these measurements. To enable a calculation of per capita prey availability, we used SCUBA to visually estimate the density of painted greenling at each platform and reef on three dates each during August-September 2003 and April-March 2004.

SIGNIFICANT CONCLUSIONS: Previous studies show that the composition and abundance of larger epibenthic invertebrate species associated with offshore platforms differs from that of natural reefs. In the present study, these habitat-related differences in assemblage composition were extended to include the small invertebrates that are potential prey of microcarnivorous fishes. A greater proportion of potential non-amphipod prey were available on the natural reefs than the platforms; however, amphipod crustaceans comprised an important component (>40% by individual) of all assemblages. At finer taxonomic resolution, pronounced habitat-related differences existed in the composition of the amphipod assemblage with exotic species comprising >50% of the amphipod individuals at the platform sites; these species were rare or absent on the two natural reefs.

Prey abundance also varied among sites, but relationships to habitat type (platform vs. natural reef) were less clear than for assemblage composition. Densities of potential prey were highest at an offshore platform (Holly) and lowest at a natural reef (Mohawk) with overlap in prey densities between the second platform (Houchin) and the other natural reef (Naples). The high density of *Caprella mutica* contributed to the overall high prey density at Platform Holly compared with the other sites.

The diet of painted greenling was comparable among our sites in that it consisted almost entirely of amphipod crustaceans (89-98% by number). Condition of painted greenling was correlated with absolute and per capita biomass of amphipod prey. Much of the small invertebrate biomass at the platforms consisted of the exotic *Caprella mutica*, and this amphipod comprised a high proportion of fish diet at these sites.

An important concern regarding the impacts of exotic species on ecosystems is their potential effects on food web structure and higher trophic levels. Our results appear most similar to those described for exotic amphipod invasions of lotic ecosystems where the amphipod invader(s) proliferates in the novel habitat, achieving high densities. Fish harvest the exotic species, which then comprises a high proportion of fish diet and may provide a food subsidy in invaded areas. This food subsidy provides positive effects on fish individual performance. Greater prey availability could also influence other life history and fitness attributes of painted greenling not measured in this study.

STUDY RESULTS: Amphipod crustaceans comprised the highest proportion of the small invertebrate assemblage at all sites. There were significant differences in the assemblages of small invertebrates among sites. Variation in proportions of gammarid and caprellid amphipods were the two most important contributors to the dissimilarity in all pairwise comparisons between sites. Differences were more apparent among sites when the amphipod assemblages were compared at a finer scale of taxonomic resolution. Amphipod assemblages at the platforms differed markedly from natural reefs and were characterized by a high proportion (>50%) of exotic species. Amphipod assemblages from the two platforms were more similar to each other than to the two natural reefs. The exotic caprellid amphipod, *C. mutica*, and the exotic gammarid, *Erichthonius brasiliensis*, contributed most to the dissimilarity of amphipod assemblages between platforms and natural reefs.

Densities of gammarid amphipods were approximately 100x higher at Platform Holly compared with Mohawk Reef, but similar between Platform Houchin and Naples Reef. Densities of caprellid amphipods were also often 10 to 100x higher and less variable over time at Platform Holly compared with the other sites. Densities of *C. mutica* on the two platforms were much higher, several hundred individuals per 400 cm², than densities of native caprellid species either on the platforms or natural reefs.

Diet of painted greenling was similar across platform and natural reef sites with amphipod crustaceans comprising from 89 to 98% by number of the stomach contents. There were significant differences in several pairwise comparisons between sites in the relative proportion of prey types in fish stomachs in September and April. However, a consistent pattern related to habitat (platform vs. natural reef) was not evident.

From 29 to 38% of the caprellid amphipods in the stomachs of fish were identifiable to species. The exotic *Caprella mutica* comprised from 31 to 52% of these identified individuals at Platforms Holly and Houchin. As expected, *C. mutica* was not found in the stomachs of painted greenling from the natural reefs.

In September, painted greenling of a given size weighed significantly more at length at Platform Holly compared with fish from Platform Houchin and Naples and Mohawk Reefs. In April, painted greenling weighed more at length at the two platforms and Naples Reef compared to Mohawk Reef. Fulton's condition factor (K) reflected the significant differences in body length and weight relationships observed among sites. In September, values of K were higher at Platform Holly compared with the other sites. In April, values of K were lower at Mohawk Reef compared with the other sites.

There was a significant positive relationship between K and amphipod biomass for both the September and April samples. We calculated amphipod prey availability per capita by dividing the biomass values of amphipods by the density of painted greenling at each site for each sampling period. There were also significant positive relationships between K and per capita amphipod biomass for both September and April.

STUDY PRODUCTS:

Presentations: Page, H. M., J.E. Dugan, M. Love, D. M. Schroeder, and M. Nishimoto. Trophic links and ecological performance: comparisons among offshore oil platforms and natural reefs for a resident fish and its prey. 8th International Conference on Artificial Reefs and Artificial Habitats, Biloxi, Mississippi.

Publications: Page HM, Dugan JE, Schroeder DM, Nishimoto MM, Love MS, Hoesterey JC (*in press*) Trophic links and condition of a temperate reef fish: comparisons among offshore oil platform and natural reef habitats. *Marine Ecology Progress Series*

FINAL STUDY REPORT

INTRODUCTION

Bottom up processes exert a major influence on the life history and fitness attributes of reef organisms. One mechanism by which this can occur is through the effects of habitat on the quality and quantity of food resources available to reef consumers (Munday 2001, Berumen et al. 2005, Ruttenberg et al. 2005). Such effects have been documented in tropical settings for fish and include variation in the physiological condition, growth, and/or reproduction of coral reef fishes associated with food availability (Jones 1986, Forrester 1990, Clifton 1995, Berumen et al. 2005). Fewer examples are available from temperate settings, but the growth of planktivorous and microcarnivorous reef fishes on rocky reefs has been linked to spatial variation in the quantity and/or quality of invertebrate prey (Holbrook & Schmitt 1992, Anderson & Sabado 1995). Food availability in general is considered an important factor that influences the species composition, densities, and growth of organisms in coastal marine ecosystems (Menge 2000, Coma et al. 2000).

Microcarnivorous fishes are ubiquitous members of shallow reef assemblages and are important trophic intermediates between invertebrate prey and higher level piscivorous fishes. Although the quantity and quality of prey available to microcarnivorous fishes likely varies among reefs, few studies have explored habitat-related patterns in prey type and density and the implications of these patterns for indices of fish individual performance (but see Holbrook & Schmitt 1992). Habitat-related variation in the type and availability of invertebrate prey and its implication for higher trophic levels is of particular interest when comparing artificial structures with the natural reef environment. Among the largest artificial structures are offshore oil and gas production platforms. World-wide, there are nearly 7000 of these structures (Hamzah 2003); twenty-seven oil and gas platforms are located on the Pacific offshore continental shelf (POCS) of central and southern California (Schroeder and Love 2004).

In general, the invertebrate and fish assemblages associated with coastal oil platforms contain species present in natural reef habitats inshore of these structures; however, attributes of the assemblage, including differences in the relative abundance and density of the constituent species, may differ dramatically from natural habitats (Wolfson et al. 1979, Love et al. 2003). Additionally, exotic species have been found to occur at a higher abundance at platforms than natural reefs (Page et al. 2006). While exotic invertebrate species can provide a food subsidy for vertebrate predators (Custer & Custer 1996, Kelleher et al. 1998, Kelly & Dick 2005), their presence can also have negative effects on food web structure and the condition and survival of higher level consumers (Spencer et al. 1991, Alpine et al. 1992, Stetter et al. 2005).

The aim of the present study was to explore habitat-related variability in prey resources and the consequences of this variability to the diet and individual performance of resident microcarnivorous reef fishes. To address this goal, we compared the composition and abundance of small benthic invertebrates, and fish condition, among two offshore oil platforms and two natural rocky reefs in the Santa Barbara Channel. Specifically, we tested three null hypotheses: 1) the composition and density of potential invertebrate prey available to benthic

microcarnivorous fishes does not differ among platform and reef habitats, 2) the diet of a resident fish does not differ among platforms and reefs, and 3) fish condition, an index of individual performance, was not associated with the abundance and composition of available prey resources.

We examined the latter two null hypotheses using a ubiquitous microcarnivorous fish, the painted greenling (*Oxylebius pictus*), as a model species. Painted greenling is one of the few fish species found on every surveyed oil platform and natural reef in the Santa Barbara Channel region (Love et al. 2003). They are demersal, solitary, and nonmigratory with small home ranges or territories as post-settlement fish (<10m², DeMartini 1976) and were predicted to feed exclusively on small benthic invertebrates resident on the platform or reef (Hobson and Chess 2001).

MATERIALS AND METHODS

Study sites

This study was conducted in the Santa Barbara Channel at two offshore oil and natural gas platforms and two inshore natural rocky reef outcrops (Figure 1). We sampled Platform Holly (Venoco, Inc.) located ~3 km offshore of Goleta, California (34°22'N, 119°52'W) in a water depth of 66 m and Platform Houchin (Pacific Operators Offshore, Inc., DCOR, LLC) located 7 km offshore of Carpinteria, California (34°20'N, 119°33'W) in a water depth of 49 m. The size (Holly, 36 x 48 m; Houchin, 38 x 38 m at the bottom) and general configuration of these platforms is similar with the subtidal portion consisting of vertical, oblique, and horizontal steel cross members together with conductor pipes through which the wells are drilled. Naples Reef (34°25'N, 119°57'W) is located 1.6 km offshore in a water depth of 7.6 to 10.7 m, 5 km northwest of Platform Holly. Mohawk Reef (34°23' N, 119°43'W) is located 0.2 km offshore in 7.3 m of water, 16 km northwest of Platform Houchin.

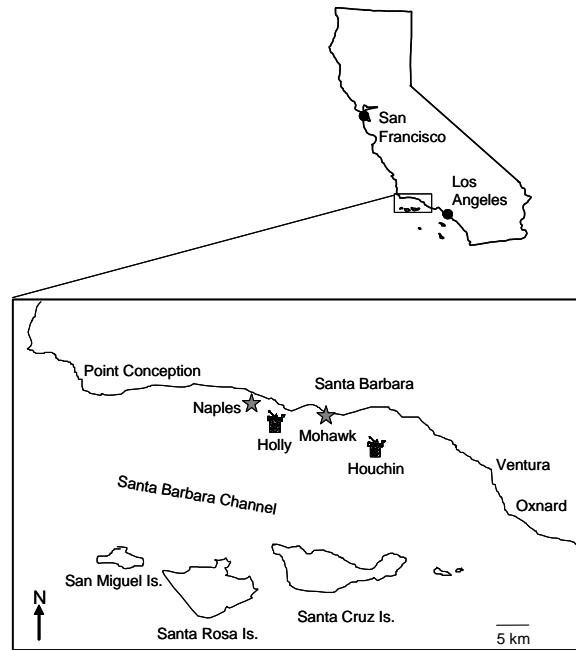


Figure 1. Location of the study sites: offshore oil and gas platforms Holly and Houchin (🏗️) and natural rocky reefs Naples and Mohawk (★).

The biotic structure of the platform habitat differs from that of natural reefs. The support members and conductor pipes of Platforms Holly and Houchin are covered intertidally and subtidally by an assemblage of sessile and semi-mobile invertebrates that can reach several centimeters in thickness (Page et al. 1999). Prominent space-holders at shallow depths (to 12 m) include mussels (*Mytilus californianus*, *M. galloprovincialis*), barnacles (e.g. *Megabalanus californicus*, *Balanus trigonus*) and anemones (*Corynactis californica*, *Metridium senile*). Macroalgae are sparse and, when present, generally occur around the periphery of the structure in shallow depths.

In contrast, the rock substratum of the natural reefs is covered with filamentous and bladey brown and red macroalgae, coralline algae, giant kelp (*Macrocystis pyrifera*), encrusting and branching bryozoans, and hydroids. A variety of larger macroinvertebrates typical of other rocky reefs in the Santa Barbara Channel inhabit the study reefs, including the sea urchin, *Strongylocentrotus purpuratus*, anemone, *Corynactis californica*, gastropods, *Conus californicus* and *Lithopoma undosa*, and barnacle, *Megabalanus californicus*.

Composition and abundance of small benthic invertebrates

To compare the species composition, density, and standing crop of potential invertebrate prey of painted greenling among platforms and reefs, we sampled small invertebrates in the foraging areas of this fish approximately monthly from April 2003 to September 2004. Divers scraped the substrate and used an air lift vacuum to collect invertebrates within 20 x 20 cm quadrats at depths of 9-10 m at each site. Four quadrats were situated randomly along three fixed 20 m transect lines at each site.

On return to the laboratory, small invertebrates were separated from other items, which commonly included turf-forming algae and, from the platforms, mussels and other large macroinvertebrates, by vigorous washing over a 0.5 mm mesh screen. Following this preliminary processing, small invertebrates were fixed in 10% buffered formalin and stored in 70% ethanol pending identification and enumeration under a dissecting microscope (e.g. Holbrook and Schmitt, 1992). Invertebrates were identified to different levels of taxonomic resolution based on the abundance and diversity of the different taxa and the taxonomic expertise available using Smith & Carlton (1975) and Blake et al. (1997). In samples taken in December 2003 and April, June, and September 2004, caprellid amphipods were generally identified to species and gammarid amphipods to the lowest level practically possible, which varied from the species to family. Standing crop of small invertebrates in terms of ash free dry weight (AFDW) was also determined in selected samples. The small invertebrates were combined into major taxonomic groups, dried at 60°C for 48 hours to determine dry weight then combusted at 450°C for 4 hours to determine AFDW.

Diet, condition, and density of painted greenling

To compare the diet of painted greenling among platforms and natural reefs, we sampled fish from all sites in September 2003 and in April 2004. Painted greenling individuals (n=10-20 per site) were collected using hand nets in the same area that invertebrates were sampled. Immediately following collection, stomach contents were preserved through injection with 10% buffered formalin. On return to the laboratory, we recorded standard length and blotted wet weight for each fish. The stomach from each fish was removed and the contents stored in 70% ethanol. Stomach contents were sorted by taxonomic group and enumerated under a dissecting microscope. For invertebrates that were disarticulated in the stomachs, only the heads were counted. When possible, caprellid amphipods were identified to species. Results are reported for fish that measured 80 to 110 mm SL, which are ~2 years old (DeMartini & Anderson 1980). We used Chesson's index (Chesson 1983) to explore selectivity in predation of painted greenling fish on caprellid and gammarid amphipod prey at platform and natural reef sites: $\alpha_i = (r_i/p_i)/\sum(r_i/p_i)$, where α_i is the Chesson's selectivity index, r_i is the relative abundance of prey (i) in the diet of painted greenling, p_i is the relative abundance of the prey in the habitat, $\sum\alpha_i = 1$, and m is the number of prey types. The index was evaluated as follows: $\alpha_i = m^{-1}$ indicates that a prey type is being consumed at the same proportion as it is found in the environment, $\alpha_i > m^{-1}$ indicates selection for a particular prey type, and $\alpha_i < m^{-1}$ indicates avoidance of a particular prey type.

To compare the "individual performance" of painted greenling among platforms and natural reefs, an index of fish "condition" was calculated (Williams 2000). Here, we use the term condition to describe the well being or robustness of individual fish with the implication that heavier fish for a given length are in better physiological condition (e.g. have higher tissue energy reserves) (Le Cren 1951, Bolger & Connolly 1989). Standard length and body weight data were used to calculate Fulton's Condition Factor (K) = $10^n * W/L^3$ for fish from each site where W =wet weight (g), L =length (mm), and n =exponent employed to bring K close to one. We also explored the use of otolith analysis to compare the daily growth rate of painted greenling among sites, but the otoliths proved unsuitable for these measurements.

To enable a calculation of per capita prey availability, we used SCUBA to visually estimate the density of painted greenling at each platform and reef on three dates each during August-September 2003 and April-March 2004. Sampling was conducted along 8 transects (30 x 2 x 2 m, 920m³) at Naples and Mohawk Reefs and within a 528 m³ area at Platform Holly and a 672 m³ area at Platform Houchin. In each platform survey, scuba divers swam a pattern which incorporated all four corner legs as well as major horizontal crossbeams and portions inside the platform jacket. Sampling was conducted at ~10 m at all sites except Mohawk Reef, which was sampled at a depth of ~8 m.

Data analysis

We used multivariate analyses to explore the null hypothesis of no difference in the assemblage of small invertebrates among platforms and natural reefs. We grouped data by sites over time and used non-metric multidimensional scaling (nMDS) to examine assemblage patterns (Primer v5, Primer-E Ltd 2001). This analysis used Bray-Curtis dissimilarity indices computed using untransformed taxonomic composition and density data. We tested for differences in assemblage structure among sites using analysis of similarity (ANOSIM). ANOSIM is non-parametric permutation test based on Bray-Curtis dissimilarity matrices that is useful for comparing benthic assemblages because no assumptions are required of the data (Clarke & Warwick 1994). We identified those taxa contributing most to significant differences between assemblages using Similarity of Percentages (SIMPER).

For taxa identified as important prey of painted greenling, we tested for differences in density among sites and over time using Analysis of Variance (ANOVA). Density data were log (x+1) transformed prior to analysis to satisfy assumption of homogeneity of variances.

We tested for differences in the composition of prey in fish stomachs among sites using ANOSIM. Proportional data were arcsine transformed prior to analysis (Zar 2003). We tested for differences in length-weight relationships of painted greenling among sites using Analysis of Covariance (ANCOVA). Parametric analyses were conducted using Systat 11.0 (Systat software 2004) and SPSS 11.5 (SPSS 1989-2000).

RESULTS

Composition of the small invertebrate assemblage

Amphipod crustaceans comprised the highest proportion of the small invertebrate assemblage at all sites (Figure 2a). Mohawk Reef had the lowest proportion of amphipods (44% of individuals in the samples) and the highest proportion of other taxa, including polychaetes (19%), tanadiceans (9%), small bivalves (7%), and gastropods (7%).

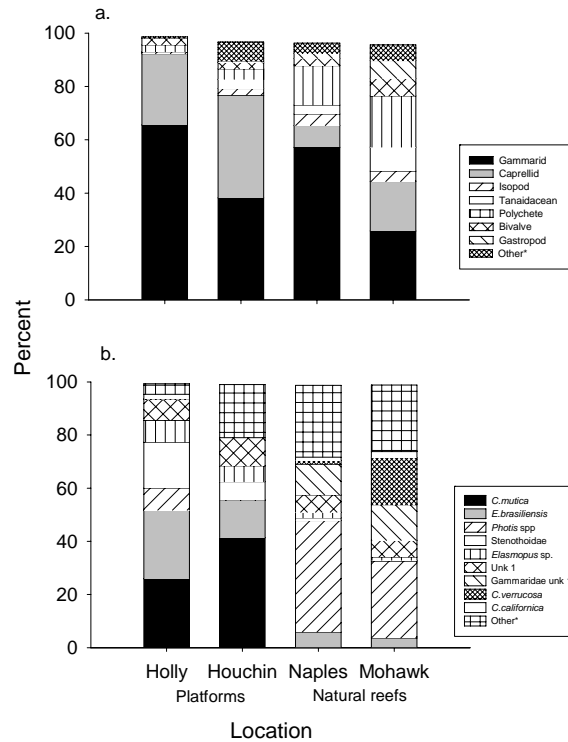


Figure 2. Relative abundance of small invertebrate taxa in benthic samples: a) the 7 most abundant higher taxa and b) the 9 most abundant amphipod taxa. Data for (a) averaged over time from samples taken approximate monthly from April 2003 to September 2004. *Grouped data for 17 other taxonomic categories. Data for (b) averaged over time from samples taken in December 2003, and April, June, and September 2004. *Grouped data for 30 other amphipod taxa.

There were significant differences in the assemblages of small invertebrates among sites ($P=0.001$, One-way ANOSIM: Table 1). Inspection of nMDS plots (Figure 3a) and R values from the ANOSIM analysis (Table 1) reveal that assemblages from Platform Holly and Mohawk Reef were the least similar (Table 1, Figure 2a). SIMPER analysis indicated that variation in proportions of gammarid and caprellid amphipods were the two most important contributors to the dissimilarity (60 to 85% combined) in all pairwise comparisons between sites (no other taxa ranked higher than 10%).

Differences were more apparent among sites when the amphipod assemblages were compared at a finer scale of taxonomic resolution (Figure 2b, 3b).

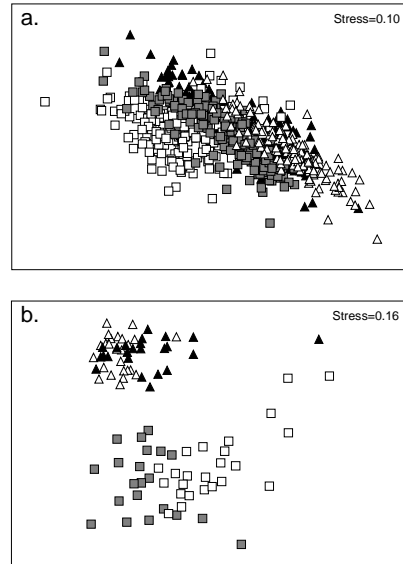


Figure 3. Non-metric multidimensional scaling of invertebrate assemblages by a) higher taxonomic group for combined samples taken approximately from April 2003 to September 2004 and b) lower taxonomic group for gammarid and caprellid amphipods in samples taken in December 2003, and April, June, and September 2004. Platforms: Holly (\triangle), Houchin (\blacktriangle); Reefs: Naples (\blacksquare), Mohawk (\square).

Amphipod assemblages at the platforms differed markedly from natural reefs and were characterized by a high proportion (>50%) of exotic species (Page et al. 2006). Notably, the caprellid, *Caprella mutica*, indigenous to the coastal waters of north-east Asia (Arimoto 1976), comprised 26% of the total amphipods and 90% of the caprellid amphipods at Platform Holly and 41% of the total amphipods and 80% of the caprellid amphipods at Platform Houchin (Figure 2b). In contrast, *C. mutica* was absent in samples from Mohawk Reef and extremely rare at Naples Reef. Although significant differences existed in all pairwise site comparisons ($P < 0.01$, ANOSIM: Table 1), the nMDS plots (Figure 3b) and R values from ANOSIM analysis (Table 1) indicated that the amphipod assemblages from the two platforms were more similar to each other than to the two natural reefs. SIMPER analysis indicated that *C. mutica*, and the exotic gammarid, *Erichthonius brasiliensis*, (Cohen et al. (2005) contributed most to the dissimilarity (39 to 45% combined) of amphipod assemblages between platforms and natural reefs. *E. brasiliensis* was primarily associated with platform habitat and was uncommon at the two natural reefs.

Table 1. Results of ANOSIM analysis comparing the assemblages of total small invertebrates, grouped by higher taxa, and amphipods only between sites. Data for total invertebrates grouped for samples taken approximately monthly from April 2003 to September 2004. Data for amphipods grouped for samples taken in December 2003, and April, June, and September 2004. Platforms indicated in italics. R values closer to 1 indicate greater assemblage dissimilarity between sites.

Comparison	Total small invertebrates		Amphipods	
	R	P	R	P
<i>Holly, Naples</i>	0.29	0.001	0.909	0.001
<i>Holly, Mohawk</i>	0.726	0.001	0.885	0.001
<i>Houchin, Naples</i>	0.09	0.001	0.796	0.001
<i>Houchin, Mohawk</i>	0.324	0.001	0.772	0.001
<i>Holly, Houchin</i>	0.258	0.001	0.258	0.001
Naples, Mohawk	0.296	0.001	0.245	0.001

Density of gammarid and caprellid amphipods

Here, we focus our analysis on amphipod crustaceans, which were important prey items of the painted greenling (see below). For this analysis, we used data from the three months preceding (or overlapping) the sampling of painted greenling for the determination of condition factor in September 2003 and April 2004.

There were significant differences among sites in the densities of potential amphipod prey (Figure 4). Densities of gammarid amphipods were significantly higher at Platform Holly compared with the other sites prior to both the September ($P < 0.001$, $F = 14.82$, $df = 3, 132$; $P < 0.001$, Tukey *post hoc* test) and April ($P < 0.001$, $F = 46.70$, $df = 3, 133$, $P < 0.001$, Tukey *post hoc* test) sampling of fish (Figure 4a). In these analyses, the effects of time were also tested because significant differences among sites could be confounded by a site x time interaction; however, there was no interaction between site and time ($P > 0.1$). Densities of gammarid amphipods were approximately 100x higher at Platform Holly compared with Mohawk Reef, but similar between Platform Houchin and Naples Reef ($P = 0.55$, Tukey *post hoc* test).

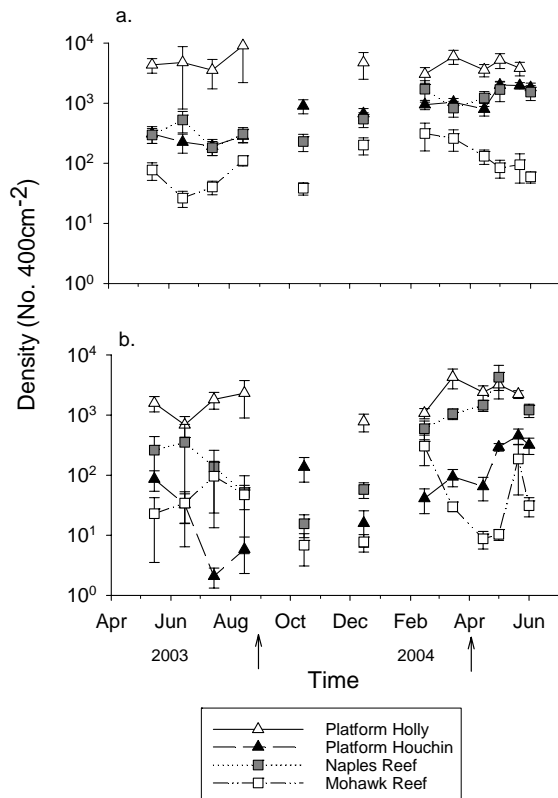


Figure 4. Density of a) gammarid and b) caprellid amphipods at platform and natural reef study sites. $n=12$ quadrats per site in each month. $\bar{x} \pm 1SE$. Arrows indicate time of fish sampling. Lines connect samples taken one month apart. Note the differences in log scale.

Densities of caprellid amphipods were also significantly higher at Platform Holly compared with the other sites prior to the September 2003 ($P < 0.001$, $F = 54.26$, $df = 3, 132$; $P < 0.001$, Tukey *post hoc* test) sampling of fish (Figure 4b). However, there was significant site \times time interaction in caprellid density prior to the April 2004 ($P < 0.001$, $F = 46.70$, $df = 3, 132$; $P < 0.001$, Tukey *post hoc* test) sampling of fish. This was due to a precipitous decline in caprellid densities at Mohawk Reef from February to April (Figure 4b). Again, densities of caprellids were often 10 to 100x higher and less variable over time at Platform Holly compared with the other sites (Figure 4b). The most abundant caprellid amphipod on both Platforms Holly and Houchin was the exotic species, *Caprella mutica*. Densities of *C. mutica* on the two platforms were much higher, several hundred individuals per 400 cm^2 , than densities of native caprellid species either on the platforms or natural reefs (Page et al. 2006).

Diet and food preference of painted greenling

Diet of painted greenling was similar across platform and natural reef sites with amphipod crustaceans comprising from 89 to 98% by number of the stomach contents (Figure 5). The diet of fish from Platform Holly was almost exclusively amphipods, whereas fish from the other sites had ingested a greater variety of prey, including isopods, tanaidaceans, polychaetes, bivalves, and gastropods (Figure 5).

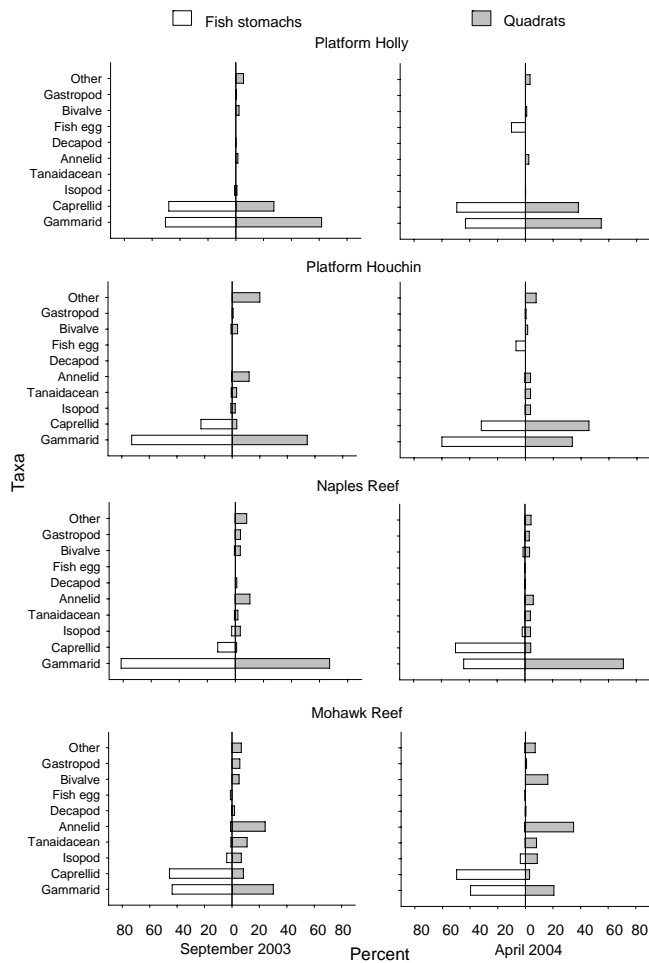


Figure 5. Relative abundance of small invertebrates in stomachs of painted greenling and in benthic samples in September 2003 and April 2004. n=10 to 20 painted greenling stomachs, n=12 quadrats per site. *Other includes small sipunculids, pycnogonids, brittle stars, cumaceans, nudibranchs, urchins, sea stars, anemones, and flatworms.

There were significant differences in several pairwise comparisons in the relative proportion of prey types in fish stomachs in September and April ($P < 0.05$, One-way ANOSIM: Table 2). However, a consistent pattern related to habitat (platform vs. natural reef) was not evident. In September, for example, gammarid and caprellid amphipods comprised about equal proportions of the stomach contents of fish from Holly and Mohawk Reef, whereas gammarids predominated in fish diet at Naples Reef and Platform Houchin (Figure 5). In April, gammarid and caprellid amphipods were of about equal importance to the diet of painted greenling at Platform Holly and Mohawk and Naples Reef (40 to 44%). However, gammarid amphipods comprised a higher proportion of the diet (60%) than caprellid amphipods at Platform Houchin.

Table 2. Results of ANOSIM analysis comparing the assemblages of small invertebrates in the stomachs of painted greenling between sites. Pairwise comparisons of fish sampled in September 2003 and April 2004 from platforms and natural reefs. Platforms indicated in italics. R values closer to 1 indicate greater assemblage dissimilarity between sites.

Comparison	September 2003		April 2004	
	R	P	R	P
<i>Holly</i> , Naples	0.622	0.001	0.554	0.002
<i>Holly</i> , Mohawk	0.048	0.137	0.163	0.041
<i>Houchin</i> , Naples	0.166	0.003	0.248	0.001
<i>Houchin</i> , Mohawk	0.225	0.002	0.170	0.050
<i>Holly</i> , <i>Houchin</i>	0.231	0.002	0.204	0.052
Naples, Mohawk	0.440	0.001	0.173	0.062

Although the relative proportion of gammarid and caprellid amphipods in the diet of painted greenling varied among sites, there was selection ($m^{-1}=0.1$, $\alpha_i=0.5$ to 0.9) for caprellid amphipods at all sites (with the exception of Platform Houchin in April 2004) (Figure 6). In contrast, there was weaker or no selection ($\alpha_i=0.1$ to 0.4) of gammarid amphipods. From 29 to 38% ($n=144$ to 503 total) of the caprellid amphipods in the stomachs of fish were identifiable to species. The exotic *Caprella mutica* comprised from 31 to 52% of these identified individuals at Platforms Holly and Houchin. As expected, *C. mutica* was not found in the stomachs of painted greenling from the natural reefs.

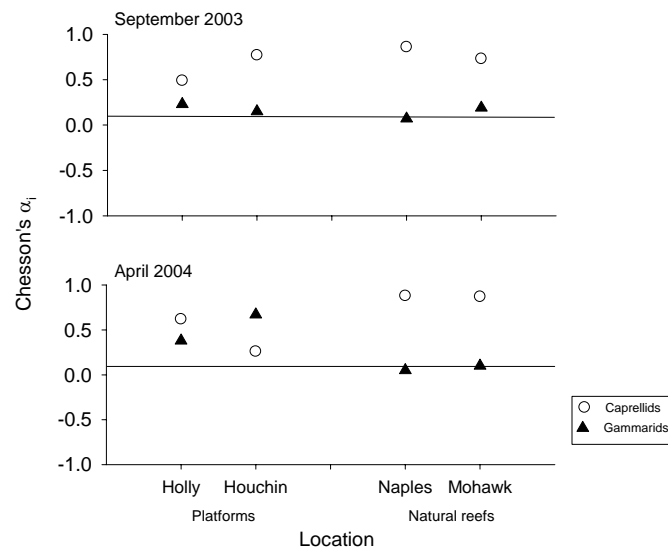


Figure 6. Chesson's selectivity index (α_i) for caprellid and gammarid prey ingested by painted greenling in September and April at all sites. $\alpha_i = 0.1$ indicates no selection (when $\alpha_i = m^{-1}$, $m=10$ prey types); $\alpha_i > 0.1$ indicates selection; $\alpha_i < 0.1$ indicates avoidance.

Index of fish condition

The relationship between length and weight of painted greenling varied among sites in both September and April. In September, painted greenling of a given size weighed significantly more at length at Platform Holly compared with fish from Platform Houchin and Naples and Mohawk Reefs ($P=0.410$, test for homogeneity of slopes; $P<0.001$, $F=7.018$, $df=3, 58$, ANCOVA; $P<0.01$, Tukey *post hoc* test: Figure 7). In April, painted greenling weighed more at length at the two platforms and Naples Reef compared to Mohawk Reef ($P=0.127$, test for homogeneity of slopes; $P=0.001$, $F=12.417$, $df=3, 53$, ANCOVA; $P\leq 0.001$, Tukey *post hoc* test: Figure 7).

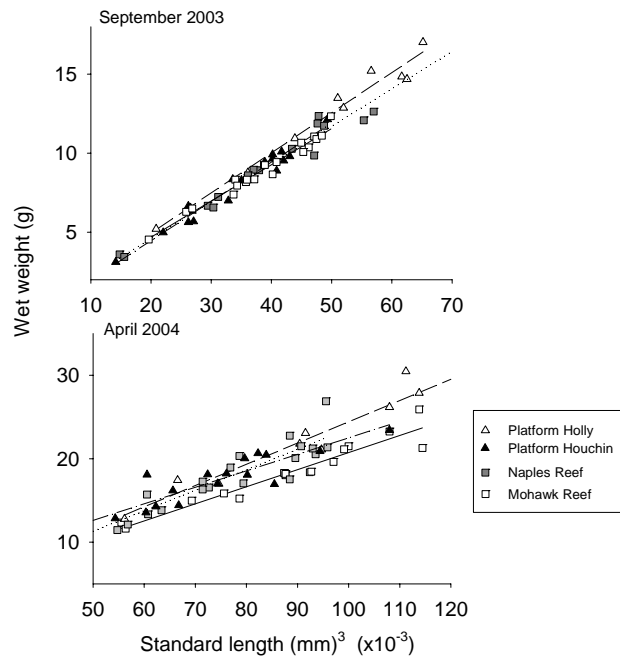


Figure 7. Relationship between blotted wet weight and standard length cubed ($\times 10^{-3}$) for painted greenling sampled in September 2003 ($n=10$ to 19 fish per site) and April 2004 ($n=15$ to 20 fish per site). Note the differences in scale of the y-axis. Regression lines: September, Platform Holly (---), $y=0.253x-0.130$, $r^2=0.98$; Platform Houchin (---), $y=0.249x-0.510$, $r^2=0.97$; Naples Reef (.....), $y=0.240x-0.139$, $r^2=0.99$; Mohawk Reef (—), $y=0.299x-0.089$, $r^2=0.97$; April, Platform Holly, $y=0.255x-1.077$, $r^2=0.91$; Platform Houchin, $y=0.198x+2.713$, $r^2=0.83$; Naples Reef, $y=0.247x+0.986$, $r^2=0.85$; Mohawk Reef, $y=0.205x+0.250$, $r^2=0.92$.

Fulton's condition factor (K) reflected the significant differences in body length and weight relationships observed among sites. In September, values of K were higher at Platform Holly compared with the other sites ($P=0.001$, $F=6.644$, $df=3, 59$; $P<0.01$, Tukey *post hoc* test: Figure 8). In April, values of K were lower at Mohawk Reef compared with the other sites ($P<0.001$, $F=11.579$, $df=3, 64$; $P<0.001$, Tukey *post hoc* test: Figure 8).

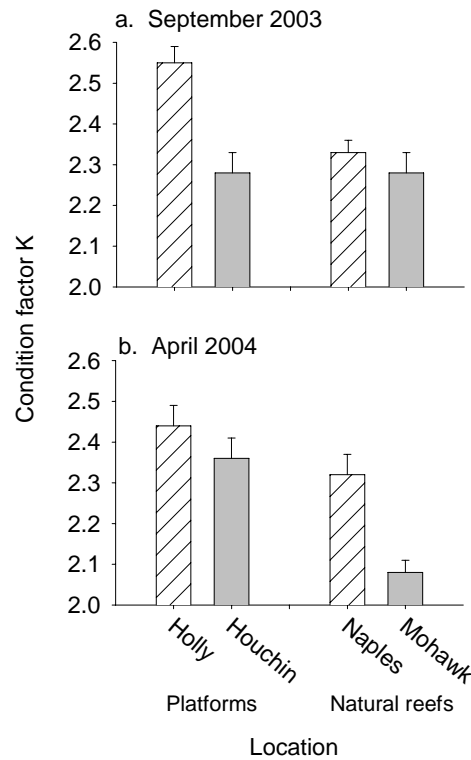


Figure 8. Fulton's condition factor (K) of painted greenling at Platforms Houchin and Holly, and Mohawk and Naples Reefs in a) September 2003 and b) April 2004. Mean values $1 \pm \text{SE}$.

Relationship between prey resources and fish condition

We explored relationships between prey abundance and condition factor K of painted greenling using two approaches (Figure 9). Since amphipods comprised $> \sim 90\%$ by number of the diet of painted greenling, we focused on this group of prey. First, we plotted condition factor K versus amphipod biomass, expressed as mean AFDW of amphipods per 400 cm^{-2} , at each site (Figure 9a). Second, we considered the possible influence of an interaction between painted greenling density and prey abundance on fish condition. We calculated amphipod prey availability per capita by dividing the biomass values of amphipods by the density of painted greenling (Table 3) at each site for each sampling period (Figure 9b).

Table 3. Density of painted greenling *Oxylebius pictus* (No. 100 m^{-2}) in September 2003 and April 2004 at the 4 study sites. Mean values $\pm 1\text{SE}$.

Site	September 2003	April 2004
Platform Holly	3.9 ± 0.8	0.6 ± 0.3
Naples Reef	7.7 ± 0.5	7.9 ± 0.3
Platform Houchin	2.1 ± 0.7	0.5 ± 0.3
Mohawk Reef	1.5 ± 0.2	0.5 ± 0.3

There was a significant positive relationship between K and amphipod biomass for both the September ($r^2=0.36$, $P<0.001$) and April ($r^2=0.28$, $P<0.001$) samples (Figure 9a). There was also significant positive relationships between K and per capita amphipod biomass for both September ($r^2=0.33$, $P<0.001$) and April ($r^2=0.12$, $P<0.01$) (Figure 9b). In both comparisons, K was higher in September as a function of amphipod biomass than in April ($P>0.1$, test for homogeneity of slopes; $P<0.001$, ANCOVA).

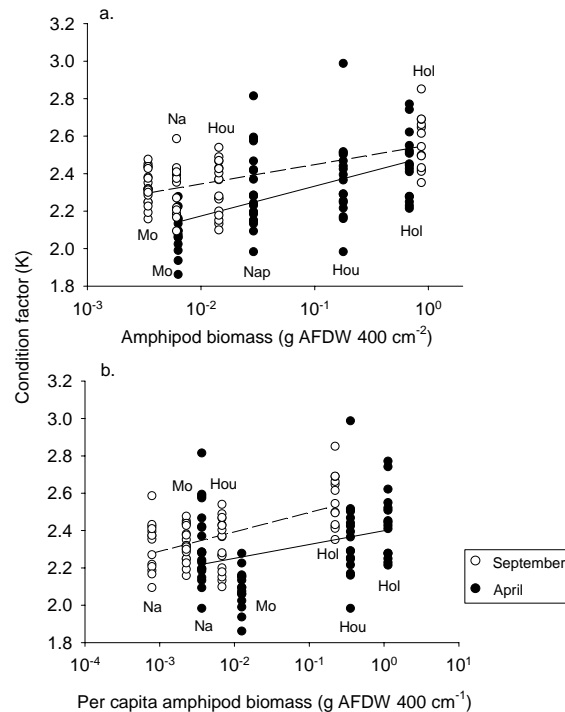


Figure 9. Relationship between condition factor K of painted greenling and a) amphipod biomass and b) per capita amphipod biomass, at the oil platform and natural reef study sites. Symbols: Hol-Platform Holly, Hou-Platform Houchin, Na-Naples Reef, Mo-Mohawk Reef. Regression lines: a) September (— —), $y=0.104*\log(x)+2.552$, $r^2=0.36$, $n=63$; April (—), $y=0.159*\log(x)+2.492$, $r^2=0.28$, $n=69$, b) September, $y=0.104*\log(x)+2.601$, $r^2=0.33$; April, $y=0.074*\log(x)+2.400$, $r^2=0.12$.

DISCUSSION

Habitat-related variation in invertebrate prey

Previous studies show that the composition and abundance of larger epibenthic invertebrate species associated with offshore platforms differs from that of natural reefs (e.g. Wolfson et al. 1979, Page et al. 1999). In the present study, these habitat-related differences in assemblage composition were extended to include the small invertebrates that are potential prey of microcarnivorous fishes. A greater proportion of potential non-amphipod prey were available on the natural reefs than the platforms; however, amphipod crustaceans comprised an important component (>40% by individual) of all assemblages (Figure 2a). At finer taxonomic resolution, pronounced habitat-related differences existed in the composition of the amphipod assemblage (Figure 2b). Notably, exotic species (*Caprella mutica*, *Erichthonius brasiliensis*) comprised

>50% of the amphipod individuals at the platform sites; these species were rare or absent on the two natural reefs.

The specific physical and biological factors that contribute to the successful colonization of offshore oil platforms by exotic amphipods are unknown, but this artificial environment is very different from that of natural reefs. Offshore platforms are located in an oceanic environment, which together with the platform structure may influence the development and composition of the invertebrate assemblage (Bram et al. 2005). Unlike natural reefs in the region, macroalgae are typically sparse on platforms, probably due to shading by the structure, and the matrix of attached organisms is dominated by sessile bivalves, barnacles, and anemones (Wolfson et al. 1979, Page et al. 1999). This assemblage may lack the predators and/or competitors or differ from natural reefs in some other characteristic that influences the establishment of exotic amphipod species (Stachowicz et al. 1999, Grosholz 2002).

Prey abundance also varied among sites, but relationships to habitat type (platform vs. natural reef) were less clear than for assemblage composition. Densities of potential prey were highest at an offshore platform (Holly) and lowest at a natural reef (Mohawk) with overlap in prey densities between the second platform (Houchin) and the other natural reef (Naples) (Figure 4). The high density of *Caprella mutica* contributed to the overall high prey density at Platform Holly compared with the other sites. This amphipod was present at densities higher than other caprellid species either on the platforms or natural reefs (Page et al. 2006) and has been reported to occur at high densities on artificial surfaces in other geographical locations (Willis et al. 2004, Buschbaum & Gutow 2005). In contrast, the lower densities of potential prey observed at Mohawk Reef may be related to the physical setting of this reef, which is located in shallow water, close to shore (0.2 km) and exposed to higher wave turbulence and sediment movement than the other sites. Physical disturbance could influence the abundance of small invertebrates at this site directly through dislodgement or burial or indirectly through effects on the composition of the epibenthic assemblage on or in which small invertebrates occur. Spatial variation in prey availability associated with habitat characteristics (e.g. the abundance of red foliose algae) has been reported for other natural reefs in the region (Holbrook & Schmitt 1986, Holbrook & Schmitt 1992).

Diet and food preference of painted greenling

Although considerable data are available on the diet of microcarnivorous fish (e.g. Quast 1968, Bray & Ebling 1975, Schmitt & Holbrook 1984, Holbrook & Schmitt 1992), fewer studies explore how fish diet varies among reefs, including artificial structures. The diet of painted greenling was comparable among our sites in that it consisted almost entirely of amphipod crustaceans (89-98% by number). In this regard, our results were similar to those reported for this fish elsewhere on natural reefs (Elliot 1992). Gammarid and caprellid amphipods are in general important components of the diet of microcarnivorous reef fishes (Bray & Ebling 1975, Schmitt & Holbrook 1984, Holbrook & Schmitt 1992). Our study shows that the taxonomic composition of amphipods differed significantly among platforms and natural reefs, and this variability was reflected in the diets of painted greenling.

The strong selection for amphipod prey suggests that other prey types were less available or preferred or required greater effort to extract than amphipod crustaceans. For example, the annelids found in the stomachs of painted greenling from Mohawk Reef were the sand castle worm, *Phragmatopoma californica*. This tube-dwelling polychaete lives in large colonies that must be broken open to access the worms. During fish surveys, painted greenling fish were observed tearing into colonies of this worm at Mohawk Reef.

Based on a comparison of stomach contents and prey availability, there was also strong selection of caprellid over gammarid amphipods by painted greenling at the natural reefs in both September and April and at Platform Houchin in September. The selection of caprellid over gammarid amphipods may be related to differences in morphology and microhabitats used by these taxa. Caprellid amphipods, including the exotic *Caprella mutica*, are typically found on the exposed surface of attached organisms and macroalgae and protrude into the water column, presenting a conspicuous profile to a visually orientated microcarnivore, such as painted greenling (Page, personal observation). In contrast, gammarid amphipods have a more compact body form and occur throughout the matrix of attached organisms, which likely provides a refuge from predation. In addition, the gammarid taxa included tubicolous forms (*Photis* sp., *Erichthonius brasiliensis*) that may be less apparent or accessible to visual predators than free-living amphipod taxa (Schmitt & Holbrook 1984). It is also possible that the apparent selection of caprellid over gammarid amphipods was a consequence of selective foraging in patches of habitat that contained high densities of caprellids (Holbrook & Schmitt 1992).

Fish condition and prey resources

Condition of a resident reef fish, the painted greenling, was correlated with absolute and per capita biomass of amphipod prey. Much of the small invertebrate biomass at the platforms consisted of the exotic *Caprella mutica*, and this amphipod comprised a high proportion of fish diet at these sites. Predators may harvest exotic species if the native prey is scarce or the new prey species is abundant, conspicuous, and/or accessible (Kelleher et al. 1998, Lemke et al. 2003). *C. mutica* is a large abundant caprellid species that occurs on the surface of epibenthic invertebrates and algae at the platforms making it readily accessible to microcarnivorous fish such as painted greenling.

An important concern regarding the impacts of exotic species on ecosystems is their potential effects on food web structure and higher trophic levels (Grosholz 2002). These effects can be detrimental, if the exotic prey is less nutritious than native prey or otherwise harmful to the fish predator (Stetter et al. 2005), neutral with no obvious effect on the predator population (Coulas et al. 1998), or positive, if the exotic prey benefits the predator (Lemke et al. 2003, Kelly & Dick 2005). Our results appear most similar to the latter scenario as described for exotic amphipod invasions of lotic ecosystems. In this scenario, the amphipod invader(s) proliferates in the novel habitat, achieving high densities. The exotic amphipod(s) may displace native amphipod species (Kelleher 1998, Kelly & Dick 2005), a phenomenon that could have occurred at the platforms, but no data are available with which to evaluate this possibility. Because the exotic amphipod is abundant and accessible, fish harvest the exotic species, which then comprises a high proportion of fish diet and may provide a food subsidy in invaded areas. This food subsidy provides positive effects on fish individual performance. The potential negative effects of the invader on

native invertebrate species richness and abundance thus contrast with a positive effect on the condition of a higher level consumer. Greater prey availability could also influence other life history and fitness attributes of painted greenling not measured in this study, including growth and reproductive rates, territory or home range size, and activity budgets (e.g. time spent in foraging and intraspecific interactions).

In conclusion, we found that bottom up processes may be influenced by habitat type in that a high proportion of the diet of a reef fish at the platforms consisted of exotic species. Because exotic prey is abundant, this prey may provide a food subsidy to resident microcarnivorous fish with positive effects on fish condition relative to natural reefs. The extent to which our findings are generalizable to other types of artificial structures, including those constructed specifically to enhance local invertebrate and fish populations is unknown. However, given the proclivity for artificial structures to be colonized by exotic species (Lambert & Lambert 2003, Bulleri & Airoidi 2005, Cohen et al. 2005), the trophic pathways on these structures may also be very different from natural reef habitat.

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The Department of the Interior Mission

As the Nation's principal conservation agency, the Department of the Interior has responsibility for most of our nationally owned public lands and natural resources. This includes fostering sound use of our land and water resources; protecting our fish, wildlife, and biological diversity; preserving the environmental and cultural values of our national parks and historical places; and providing for the enjoyment of life through outdoor recreation. The Department assesses our energy and mineral resources and works to ensure that their development is in the best interests of all our people by encouraging stewardship and citizen participation in their care. The Department also has a major responsibility for American Indian reservation communities and for people who live in island territories under U.S. administration.



The Minerals Management Service Mission

As a bureau of the Department of the Interior, the Minerals Management Service's (MMS) primary responsibilities are to manage the mineral resources located on the Nation's Outer Continental Shelf (OCS), collect revenue from the Federal OCS and onshore Federal and Indian lands, and distribute those revenues.

Moreover, in working to meet its responsibilities, the **Offshore Minerals Management Program** administers the OCS competitive leasing program and oversees the safe and environmentally sound exploration and production of our Nation's offshore natural gas, oil and other mineral resources. The **MMS Royalty Management Program** meets its responsibilities by ensuring the efficient, timely and accurate collection and disbursement of revenue from mineral leasing and production due to Indian tribes and allottees, States and the U.S. Treasury.

The MMS strives to fulfill its responsibilities through the general guiding principles of: (1) being responsive to the public's concerns and interests by maintaining a dialogue with all potentially affected parties and (2) carrying out its programs with an emphasis on working to enhance the quality of life for all Americans by lending MMS assistance and expertise to economic development and environmental protection.