

Trophic links and condition of a temperate reef fish: comparisons among offshore oil platform and natural reef habitats

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ABSTRACT: We explored habitat-related variability in the composition and density of small invertebrate prey of microcarnivorous reef fishes among 2 artificial (offshore oil platform) and 2 natural reef habitats in the Santa Barbara Channel, USA, and the consequences of this variability to the condition of a resident reef fish, the painted greenling *Oxylebius pictus*. Amphipod crustaceans comprised the highest proportion of potential prey at all sites, but the amphipod assemblage from the platforms contained a high percentage (>50% by number) of 2 exotic species, *Caprella mutica* and *Erichthonius brasiliensis*, that were either absent or rare on the natural reefs. At the platforms, 80 to 90% of the caprellid amphipods consisted of *C. mutica*. Densities of amphipods varied among sites and were 10 to 100× higher at one of the platforms compared with the other sites. Amphipods comprised 89 to 98% (by number) of painted greenling diet. Fish condition factor (*K*) was correlated with absolute and per capita amphipod prey biomass. Our results fit a scenario described for some lotic systems where exotic amphipod species proliferate in the invaded habitat. Fish harvest the exotic species with positive effects on fish condition. The potential negative effects of the exotic species on the native amphipod assemblage thus contrast with a positive effect on the condition of a higher level consumer. Our findings suggest that trophic pathways on other types of artificial structures colonized by exotic species may also differ from those of the natural reef habitat.

KEY WORDS: Food web · Exotic species · Offshore oil platform · *Caprella mutica* · *Erichthonius brasiliensis* · Condition factor · *Oxylebius pictus* · Artificial reef

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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 (Coma et al. 2000, Menge 2000).

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

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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. Worldwide, there are nearly 7000 of these structures (Hamzah 2003); 27 oil and gas platforms are located on the Pacific offshore continental shelf (POCS) of central and southern California (Schroeder & 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 the relative abundance and density of the constituent species, may differ dramatically from those in natural habitats (Wolfson et al. 1979, Love et al. 2003). Additionally, exotic species (e.g. Cohen et al. 2005) have been found to occur at a higher abundance at platforms than on 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 & Cloern 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 for 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 2 offshore oil platforms and 2 natural rocky reefs in the Santa Barbara Channel. Specifically, we tested 3 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, is not associated with the abundance and composition of available prey resources.

We examined the latter 2 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). It is demersal, solitary, and nonmigratory with small home ranges or territories as post-settlement fish (<10 m², DeMartini 1976) and is predicted to feed exclusively on small benthic invertebrates resident on the platform or reef (Hobson & Chess 2001).

MATERIALS AND METHODS

Study sites. This study was conducted in the Santa Barbara Channel at 2 offshore oil and natural gas platforms and 2 inshore natural rocky reef outcrops (Fig. 1). We sampled Platform Holly (Venoco) 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, DCOR) located 7 km offshore of Carpinteria, California (34° 20' N,

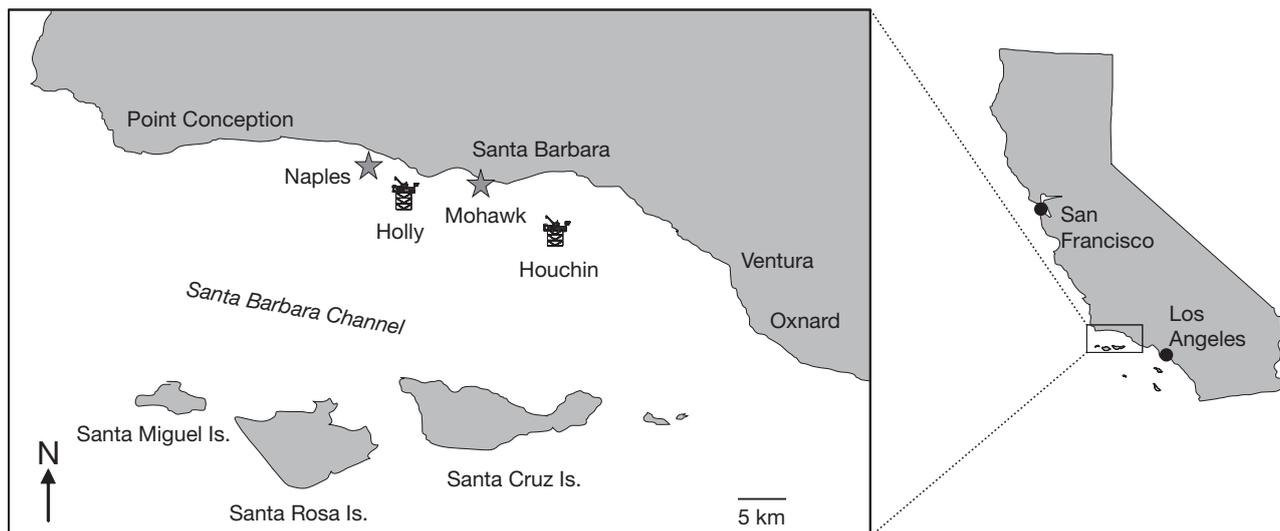


Fig. 1. Location of study sites; (🏠) Offshore oil and gas platforms Holly and Houchin; (★) natural rocky reefs Naples and Mohawk

119° 33' W), in a water depth of 49 m. The bottom size (Holly, 36 × 48 m; Houchin, 38 × 38 m) 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 to 11 m, 5 km NW of Platform Holly. Mohawk Reef (34° 23' N, 119° 43' W) is located 0.2 km offshore in 7 to 9 m of water, 16 km NW of Platform Houchin.

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* and *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 bladed 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 × 20 cm quadrats at depths of 7 to 9 m at each site. Four quadrats were situated randomly along 3 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 & Schmitt 1992). Invertebrates were identified to different levels of tax-

onomic resolution based on the abundance and diversity of the different taxa and the taxonomic expertise available using the description of 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 species to family. The 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 h to determine dry weight, then combusted at 450°C for 4 h 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 to 20 per site) were collected using hand nets in the same area at which 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 standard length (SL), which were ~2 yr 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: $\alpha_i = (r_i/p_i)/\Sigma(r_i/p_i)$, where α_i is the Chesson 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 and $\Sigma\alpha_i = 1$. 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, where m is the number of prey types.

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) = $10^n \cdot W/L^3$ for fish from each site, where W = wet weight (g), L = length (mm), and n = the exponent employed to bring K close to 1. 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 3 dates each during August to September 2003 and April to March 2004. Sampling was conducted along 8 transects ($30 \times 2 \times 2$ m, 920 m³) 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 ordination (nMDS) to examine assemblage patterns (Primer Version 5). 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 a non-parametric permutation test based on Bray-Curtis dissimilarity matrices that is useful for comparing benthic assemblages because no assumptions are required for the data (Clarke & Warwick 1994). We identified those taxa contributing most to statistically 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 the 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). In this analysis, site was the categorical random effect variable with length as the covariate. Parametric analyses were conducted using Systat 11.0 and SPSS 11.5 software.

RESULTS

Composition of small invertebrate assemblage

Amphipod crustaceans comprised the highest proportion of the small invertebrate assemblage at all sites (Fig. 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%), tanaidaceans (9%), small bivalves (7%), and gastropods (7%).

There were statistically significant differences in the assemblages of small invertebrates among sites ($p = 0.001$, 1-way ANOSIM: Table 1). Inspection of nMDS plots (Fig. 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,

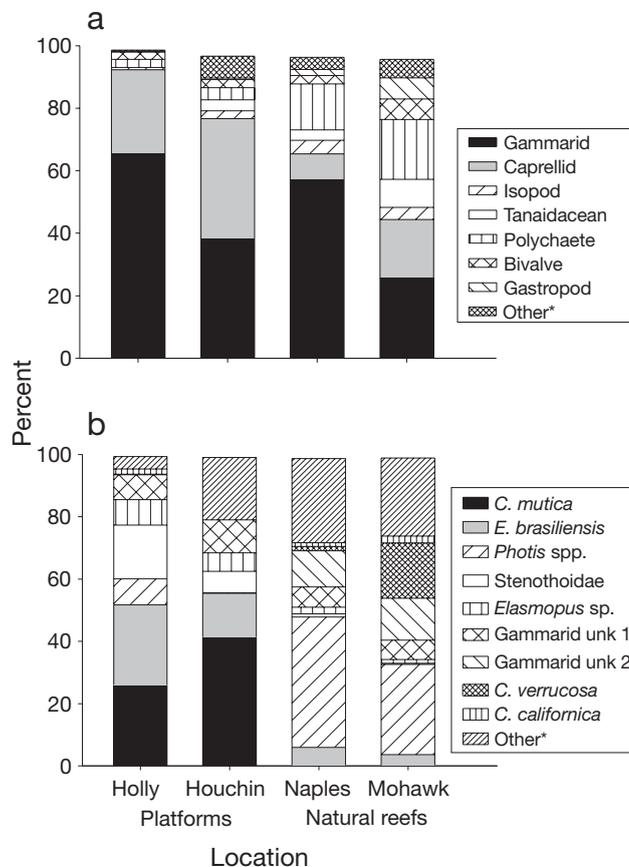


Fig. 2. Relative abundance of small invertebrate taxa in benthic samples; (a) 7 most abundant higher taxa; (b) 9 most abundant amphipod taxa. (a) Data averaged over time for samples taken approximately monthly from April 2003 to September 2004; Other*: grouped data for 17 other taxonomic categories. (b) Data averaged over time from samples taken in December 2003, and April, June and September 2004; *Caprella mutica*, *C. verrucosa*, *C. californica* are caprellid amphipods, remaining taxa are gammarids; Other*: grouped data for 30 other gammarid and caprellid amphipod taxa

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 in italics, natural reefs in normal type. R values closer to 1 indicate greater assemblage dissimilarity between sites

Comparison	Total small invertebrates		Amphipods	
	R	p	R	P
<i>Holly</i> vs. Naples	0.290	0.001	0.909	0.001
<i>Holly</i> vs. Mohawk	0.726	0.001	0.885	0.001
<i>Houchin</i> vs. Naples	0.090	0.001	0.796	0.001
<i>Houchin</i> vs. Mohawk	0.324	0.001	0.772	0.001
<i>Holly</i> vs. <i>Houchin</i>	0.258	0.001	0.258	0.001
Naples vs. Mohawk	0.296	0.001	0.245	0.001

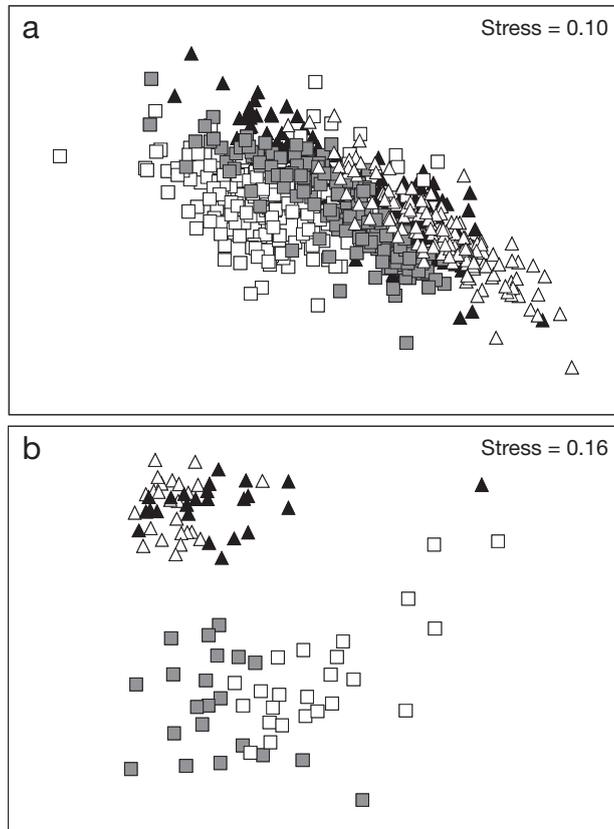


Fig. 3. Non-metric multidimensional scaling of invertebrate assemblages by (a) higher taxonomic group for combined samples taken approximately from April 2003 to September 2004, and (b) gammarid and caprellid amphipod taxa only in samples taken in December 2003, and in April, June and September 2004. Platforms = (Δ) Holly, (\blacktriangle) Houchin; Reefs = (\blacksquare) Naples, (\square) Mohawk. Stress values indicate degree of distortion of ordination from the dissimilarity rankings; values of <0.2 are considered adequate representations of the data (Clarke & Warwick 1994)

Fig. 2a). SIMPER analysis indicated that variation in proportions of gammarid and caprellid amphipods were the 2 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 (Figs. 2b, 3b). Amphipod assemblages at the platforms differed markedly from those on 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 (Fig. 2b). In contrast, *C. mutica* was absent from samples from Mohawk Reef and extremely rare at Naples Reef. Although statistically significant differences existed in all pairwise site comparisons ($p < 0.01$, ANOSIM: Table 1), the nMDS plots (Fig. 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), widely distributed in the NE Atlantic and Mediterranean Sea (Myers & McGrath 1984), contributed most to the dissimilarity (39 to 45% combined) of amphipod assemblages between platforms and natural reefs. *E. brasiliensis* was primarily associated with the platform habitat and was uncommon at the two natural reefs.

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 3 mo preceding (or overlapping) the sampling of painted greenling for the determination of condition factor in September 2003 and April 2004.

There were statistically significant differences among sites in the densities of potential amphipod prey (Fig. 4). Densities of gammarid amphipods were statistically significantly higher at Platform Holly compared with the other sites prior to both the September ($p < 0.001$, $F = 54.264$, $df = 3, 132$; $p < 0.001$, Tukey's post hoc test) and April ($p < 0.001$, $F = 46.697$, $df = 3, 133$, $p < 0.001$, Tukey's post hoc test) sampling of fish (Fig. 4a). In these analyses, the effects of time were also tested because statistically significant differences among sites could be confounded by a site \times time

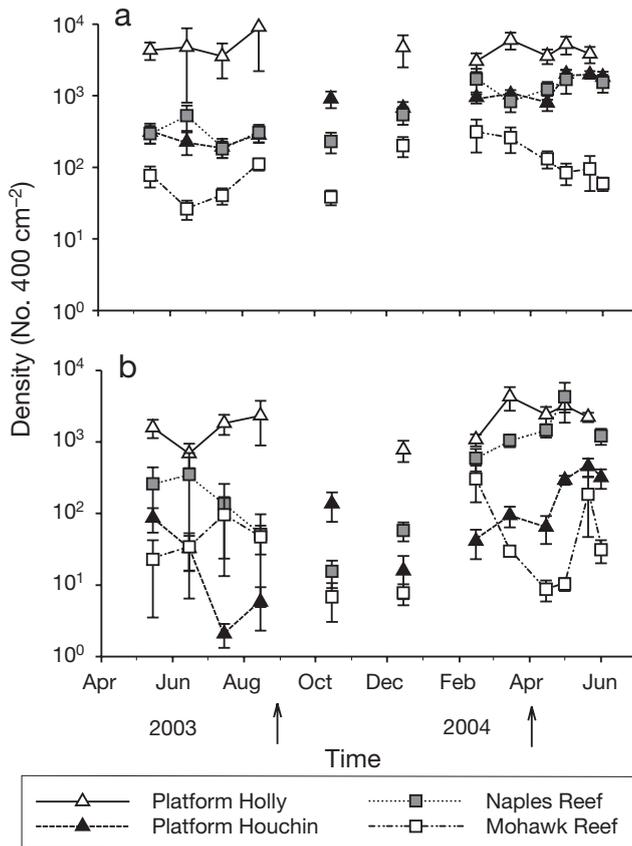


Fig. 4. Mean \pm 1 SE density of (a) gammarid and (b) caprellid amphipods at platform and natural reef study sites. $n = 12$ quadrats per site in each month; arrows indicate time of fish sampling; lines connect samples taken 1 mo apart. Note differences in log scales of y -axes among plots

interaction; however, there was no interaction between site and time ($p > 0.1$). Densities of gammarid amphipods were approximately $100\times$ higher at Platform Holly than Mohawk Reef, but similar between Platform Houchin and Naples Reef ($p = 0.55$, Tukey's post hoc test).

Densities of caprellid amphipods were also statistically significantly higher at Platform Holly than at the other sites prior to the September 2003 ($p < 0.001$, $F = 68.072$, $df = 3, 132$; $p < 0.001$, Tukey's post hoc test) sampling of fish (Fig. 4b). However, there was a statistically significant site \times time interaction in caprellid density prior to the April 2004 ($p = 0.002$, $F = 3.620$, $df = 6, 133$) sampling of fish. This was due to a precipitous decline in caprellid densities at Mohawk Reef from February to April (Fig. 4b). Again, densities of caprellids were often 10 to $100\times$ higher and less variable over time at Platform Holly than at the other sites (Fig. 4b). The most abundant caprellid amphipod on both Platforms Holly and Houchin was the exotic species *Caprella mutica*. Densities of *C. mutica* on the 2 plat-

forms 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 (Fig. 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 (Fig. 5).

There were statistically significant differences in several pairwise comparisons in the relative proportion of prey types in fish stomachs in September and April ($p < 0.05$, 1-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 (Fig. 5). In April, gammarid and caprellid amphipods were about equal in 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.

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) (Fig. 6). In contrast, there was weaker or no selection ($\alpha_i = 0.1$

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

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

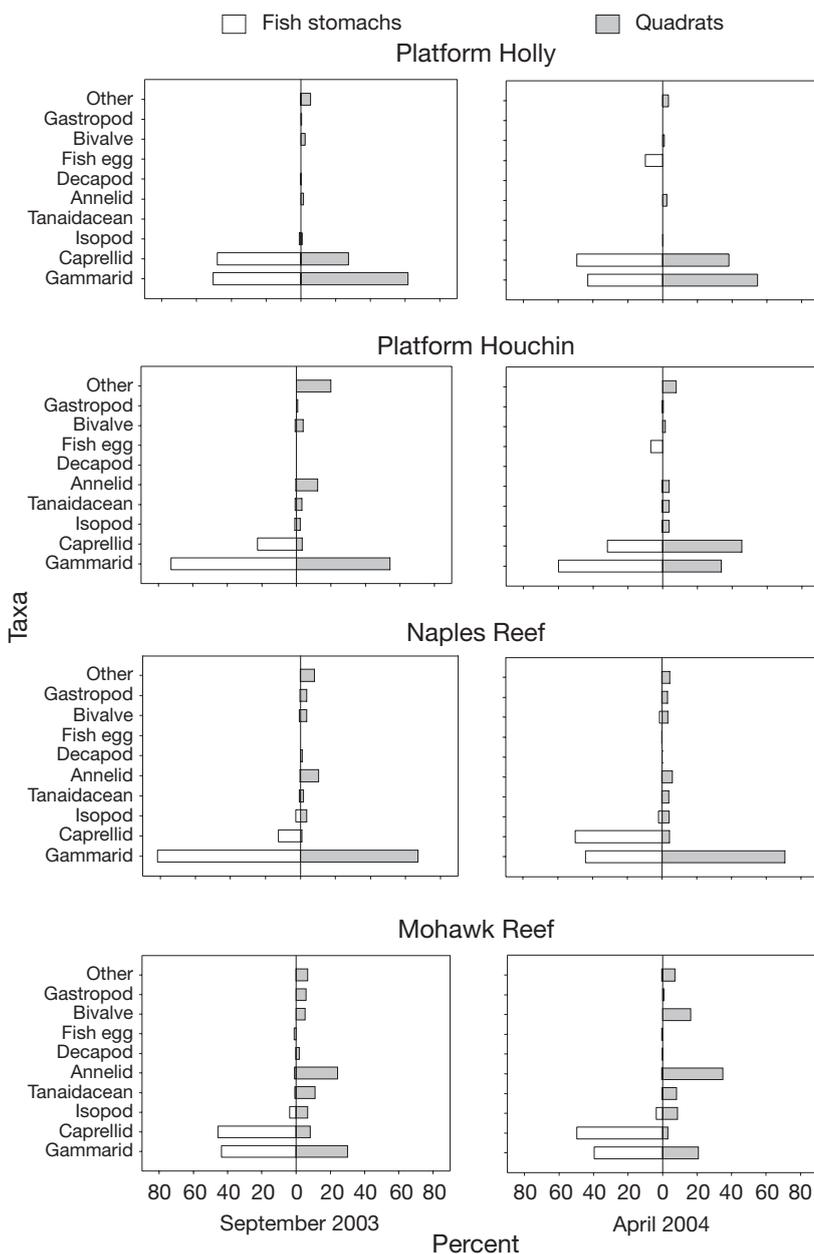


Fig. 5. Relative abundance of small invertebrates in stomachs of painted greenling *Oxylebius pictus* and in benthic samples in September 2003 and April 2004. $n = 10$ to 20 painted greenling stomachs, $n = 12$ quadrats per site. Other: small sipunculids, pycnogonids, brittle stars, cumaceans, nudibranchs,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

to 0.4) of gammarid amphipods. From 29 to 38% ($n = 144$ to 503 total summed by site) 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.

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 statistically 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's post hoc test: Fig. 7). In April, painted greenling weighed more at a given length at the 2 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's post hoc test: Fig. 7).

Fulton's condition factor (K) reflected the statistically 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's post hoc test: Fig. 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's post hoc test: Fig. 8).

Relationship between prey resources and fish condition

We explored relationships between prey abundance and condition factor K of painted greenling using 2 approaches (Fig. 9). Since amphipods comprised $\geq 90\%$ 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 400 cm^{-2} , at each site (Fig. 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 (Fig. 9b).

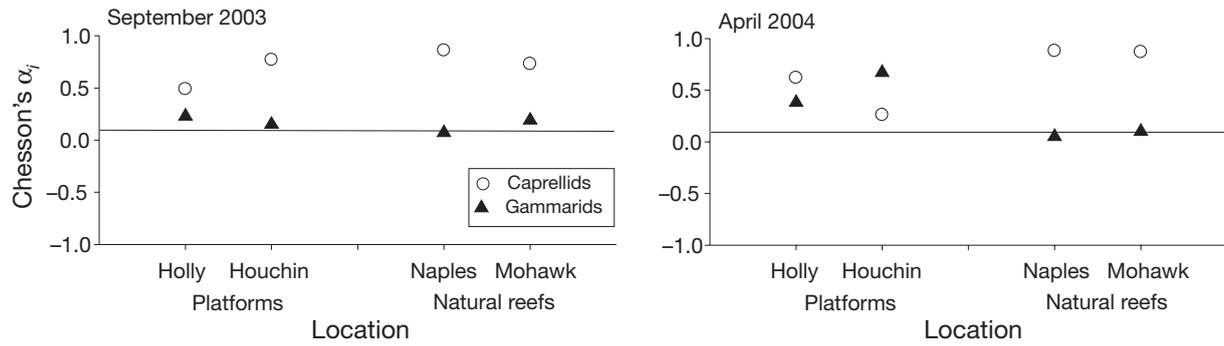


Fig. 6. *Oxylebius pictus*. Chesson's selectivity index (α_i) for caprellid and gammarid prey ingested by painted greenling in September and April at all sites. $\alpha_i = 0.1$ indicates no selection (when $\alpha_i = m^{-1}$, $m = 10$ prey types), $\alpha_i > 0.1$ indicates selection, $\alpha_i < 0.1$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

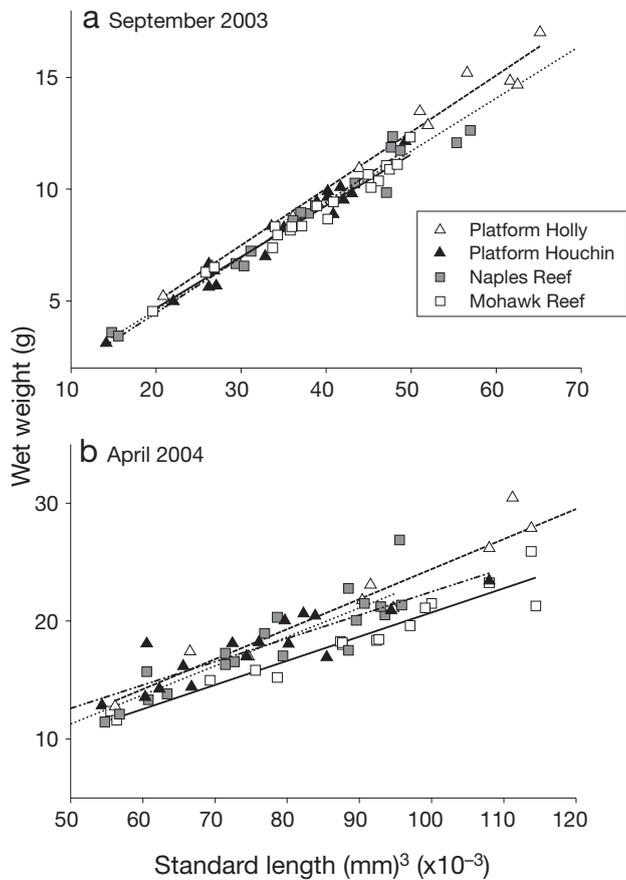


Fig. 7. *Oxylebius pictus*. Relationship between blotted wet weight and standard length cubed ($\times 10^{-3}$) for painted greenling sampled in (a) September 2003 ($n = 10$ to 19 fish per site) and (b) April 2004 ($n = 15$ to 20 fish per site), note the differences in scales of y-axes. Regression lines are 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, $y = 0.205x + 0.250$, $r^2 = 0.92$

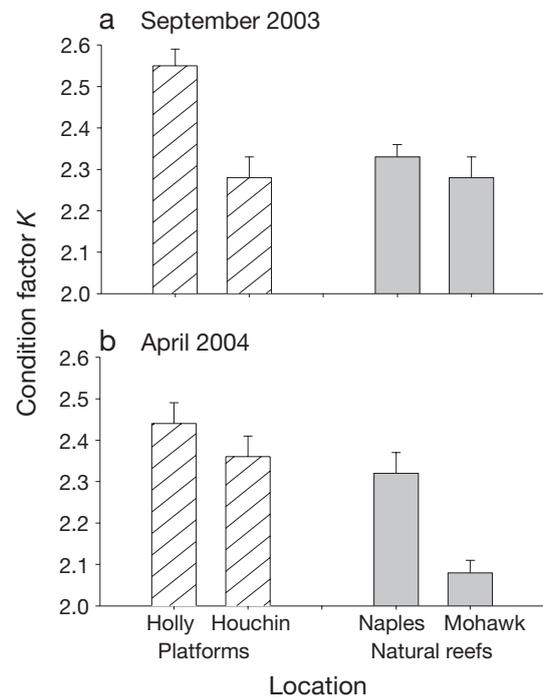


Fig. 8. *Oxylebius pictus*. Mean + 1 SE Fulton's condition factor (K) for painted greenling at Platforms Houchin and Holly, and Mohawk and Naples Reefs in (a) September 2003 and (b) April 2004

There was a statistically 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 (Fig. 9a). There was also a statistically significant positive relationship between K and per capita amphipod biomass for the September ($r^2 = 0.33$, $p < 0.001$) and April ($r^2 = 0.12$, $p < 0.01$) samples (Fig. 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).

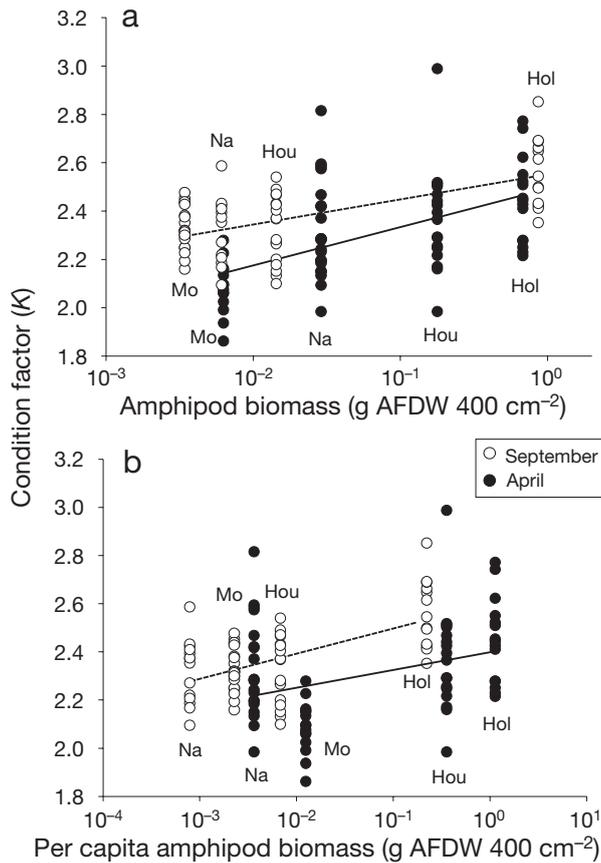


Fig. 9. *Oxylebius pictus*. Relationship between condition factor K and (a) amphipod biomass and (b) per capita amphipod biomass, at oil platform and natural reef study sites. Hol: Platform Holly; Hou: Platform Houchin; Na: Naples Reef; Mo: Mohawk Reef. Regression lines are (a) (----) September, $y =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

DISCUSSION

Habitat-related variation in invertebrate prey

Previous studies have shown that the composition and abundance of larger epibenthic invertebrate species associated with offshore platforms differ from those 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 at the platforms; however, amphipod crustaceans comprised an important component (>40% by individual) of all assemblages (Fig. 2a). At finer taxonomic resolution, pronounced habitat-related differences existed in the composition of the amphipod assemblage (Fig. 2b). Notably, exotic spe-

Table 3. *Oxylebius pictus*. Mean \pm 1 SE (no. 100 m⁻²) in September 2003 and April 2004 at the 4 study sites

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

cies (*Caprella mutica* and *Erichthonius brasiliensis*) comprised >50% of the amphipod individuals at the platform sites; these species were rare or absent on the 2 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) (Fig. 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, 1992).

Diet and food preference of painted greenling

Although considerable data are available on the diet of microcarnivorous fish (e.g. Quast 1968, Bray & Ebeling 1975, Schmitt & Holbrook 1984, Holbrook & Schmitt 1992), fewer studies have explored 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 to 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 & Ebeling 1975, Schmitt & Holbrook 1984, Holbrook & Schmitt 1992). Our study shows that the taxonomic composition of amphipods differed 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 for extraction than amphipod crustaceans. For example, the annelid found in the stomachs of painted greenling from Mohawk Reef was the sand castle worm *Phragmatopoma californica*. This colonial polychaete lives in tubes constructed of sand grains that must be broken open by the fish to feed on 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 the morphology and the 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 pers. obs.). In contrast, gammarid amphipods have a more compact body form and occur throughout the matrix of attached organisms, which is likely to provide 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 the potential effects on food web structure and higher trophic levels (Groscholz 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 et al. 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 has positive effects on individual fish 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 those of the natural reef habitat.

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LITERATURE CITED

- Alpine AE, Cloern JE (1992) Trophic interactions and direct physical effects control biomass and production in an estuary. *Limnol Oceanogr* 37:946–955
- Anderson TW, Sabado BD (1995) Correspondence between food availability and growth of a planktivorous temperate reef fish. *J Exp Mar Biol Ecol* 189:65–76
- Arimoto I (1976) Taxonomic studies of caprellids (Crustacea, Amphipoda, Caprellidae) found in the Japanese and adjacent waters. *Spec Publ Seto Mar Biol Lab Ser III* 1–229
- Berumen ML, Pratchett MS, McCormick MI (2005) Within-reef differences in diet and body condition of coral-feeding butterflyfishes (Chaetodontidae). *Mar Ecol Prog Ser* 287: 217–227
- Blake JA, Watling L, Scott PV (1997) Taxonomic atlas of the benthic fauna of the Santa Maria Basin and the Western Santa Barbara Channel, Vol 12. The Crustacea Part 3. The Amphipoda. Santa Barbara Museum of Natural History, Santa Barbara, CA
- Bolger T, Connolly PL (1989) The selection of suitable indices for the measurement and analysis of fish condition. *J Fish Biol* 34:171–182
- Bram J, Page HM, Dugan JE (2005) Spatial and temporal variability in early successional patterns of an invertebrate assemblage at an offshore platform. *J Exp Mar Biol Ecol* 317:223–237
- Bray RN, Ebeling AW (1975) Food, activity, and habitat of three 'picker-type' microcarnivorous fishes in the kelp forests off Santa Barbara, California. *US Natl Mar Fish Serv Fish Bull* 73:815–829
- Bulleri F, Airoidi L (2005) Artificial marine structures facilitate the spread of a non-indigenous green alga, *Codium fragile* ssp. *tomentosoides*, in the north Adriatic Sea. *J Appl Ecol* 42:1063–1072
- Buschbaum C, Gutow L (2005) Mass occurrence of an introduced crustacean (*Caprella* cf. *mutica*) in the south-eastern North Sea. *Helgol Mar Res* 59:252–253
- Chesson J (1983) The estimation and analysis of preference and its relationship to foraging models. *Ecology* 64: 1297–1304
- Clarke KR, Warwick RM (1994) Change in marine communities: an approach to statistical analysis and interpretation. Plymouth Marine Laboratory, Plymouth
- Clifton KE (1995) Asynchronous food availability on neighboring Caribbean coral reefs determines seasonal patterns of growth and reproduction for the herbivorous parrotfish *Scarus iserti*. *Mar Ecol Prog Ser* 116:39–46
- Cohen AN, Harris LH, Bingham BL, Carlton JT and 8 others (2005) Rapid assessment survey for exotic organisms in southern California bays and harbors, and abundance in port and non-port areas. *Biol Invasions* 7:995–1002
- Coma R, Ribes M, Gili JM, Zabala M (2000) Seasonality in coastal benthic ecosystems. *Trends Ecol Evol* 15:448–453
- Coulas RA, McIssac HJ, Dunlop W (1998) Selective predation on an introduced zooplankter (*Bythotrephes cederstroemi*) by lake herring (*Coregonus artedii*) in Harp Lake, Ontario. *Freshw Biol* 40:343–355
- Custer CM, Custer TW (1996) Food habits of diving ducks in the Great Lakes after the zebra mussel invasion. *J Field Ornithol* 67:86–99
- DeMartini EE (1976) The adaptive significance of territoriality and egg cannibalism in the painted greenling, *Oxylebius pictus* Gill, a northeastern Pacific marine fish, PhD dissertation, Department of Zoology, University of Washington (available from University Microfilms, 300 North Zeeb Road, Ann Arbor, Michigan 48106)
- DeMartini EE, Anderson ME (1980) Comparative survivorship and life history of painted greenling (*Oxylebius pictus*) in Puget Sound, Washington and Monterey Bay, California. *Environ Biol Fish* 5:33–47
- Elliot J (1992) The role of sea anemones as refuges and feeding habitats for the temperate fish *Oxylebius pictus*. *Environ Biol Fish* 35:381–400
- Forrester G E (1990) Factors influencing the juvenile demography of a coral reef fish. *Ecology* 71:1666–1681
- Grosholz E (2002) Ecological and evolutionary consequences of coastal invasions. *Trends Ecol Evol* 17:22–27
- Hamzah BA (2003) International rules on decommissioning of offshore installations: some observations. *Mar Policy* 27: 339–348
- Hobson ES, Chess JR (2001) Influence of trophic relations on form and behavior among fishes and benthic invertebrates in some California marine communities. *Environ Biol Fish* 60:411–457
- Holbrook SJ, Schmitt RJ (1986) Food acquisition by competing surfperch on a patchy environmental gradient. *Environ Biol Fish* 16:135–146
- Holbrook SJ, Schmitt RJ (1992) Causes and consequences of dietary specialization in surfperches: patch choice and intraspecific competition. *Ecology* 73:402–412
- Jones GP (1986) Food availability affects growth in a coral reef fish. *Oecologia* 70:136–139
- Kelleher B, Bergers PJM, van den Brink FWB, Giller PS, van der Velde G, Bij de Vaate A (1998) Effects of exotic

- amphipod invasions on fish diet in the Lower Rhine. Arch Hydrobiol 143:363–382
- Kelly DW, Dick JTA (2005) Introduction of the non-indigenous amphipod *Gammarus pulex* alters population dynamics and diet of juvenile trout *Salmo trutta*. Freshw Biol 50: 127–140
- Lambert CC, Lambert G (2003) Persistence and differential distribution of nonindigenous ascidians in harbors of the Southern California Bight. Mar Ecol Prog Ser 259: 145–161
- Le Cren ED (1951) The length–weight relationship and seasonal cycle in gonad weight and condition in the perch (*Perca fluviatilis*). J Anim Ecol 20:201–219
- Lemke AM, Stoeckel JA, Pegg MA (2003) Utilization of the exotic cladoceran *Daphnia lumholtzi* by juvenile fishes in an Illinois River floodplain lake. J Fish Biol 62:938–954
- Love MS, Schroeder DM, Nishimoto MM (2003) The ecological role of oil and gas platforms and natural outcrops on fishes in southern and central California: a synthesis of information. OCS Study MMS 2003–032, US Department of the Interior, USGS, Seattle, Washington
- Menge BA (2000) Top–down and bottom–up community regulation in marine rocky intertidal habitats. J Exp Mar Biol Ecol 250:257–289
- Munday PL (2001) Fitness consequences of habitat use and competition among coral–dwelling fishes. Oecologia 128: 585–593
- Myers AA, McGrath D (1984) A revision of the north–east Atlantic species of *Erichthonius* (Crustacea: Amphipoda). J Mar Biol Assoc UK 64:379–400
- Page HM, Dugan JE, Dugan DS, Richards JB, Hubbard DM (1999) Effects of an offshore oil platform on the distribution and abundance of commercially important crab species. Mar Ecol Prog Ser 185:47–57
- Page HM, Dugan JE, Culver CS, Hoesterey JC (2006) Exotic invertebrate species on offshore oil platforms. Mar Ecol Prog Ser 325:101–107
- Quast JC (1968) Observations on food of the kelp bed fishes. In: North WJ (ed) The biology of giant kelp beds (*Macrocystis*) in California. Calif Dep Fish Game Fish Bull 139: 109–142
- Ruttenberg BI, Haupt AJ, Chiriboga AI, Warner RR (2005) Patterns, causes and consequences of regional variation in the ecology and life history of a reef fish. Oecologia 14: 394–403
- Schmitt RJ, Holbrook SJ (1984) Ontogeny of prey selection by black surfperch *Embiotoca jacksoni* (Pisces: Embiotocidae): the roles of fish morphology, foraging behavior, and patch selection. Mar Ecol Prog Ser 18:225–239
- Schroeder DM, Love MS (2004) Ecological and political issues surrounding decommissioning of offshore oil facilities in the Southern California Bight. Ocean Coast Manag 47: 21–48
- Smith RI, Carlton JT (eds) (1975) Light's manual: intertidal invertebrates of the central California coast, 3rd edn, University of California Press, Berkeley
- Spencer CN, McClelland BR, Stanford JA (1991) Shrimp stocking, salmon collapse and eagle displacement. BioScience 41:14–21
- Stachowicz, JJ, Whitlatch RB, Osman RW (1999) Species diversity and invasion resistance in a marine ecosystem. Science 286:1577–1579
- Stetter PSL, Witzel LD, Rudstam LG, Einhouse DW, Mills EL (2005) Energetic consequences of diet shifts in Lake Erie rainbow smelt (*Osmerus mordax*). Can J Fish Aquat Sci 62: 145–152
- Williams JE (2000) The coefficient of condition of fish. Chapter 13. In: Schneider JC (ed) Manual of fisheries survey methods. II: with periodic updates. Fish Spec Rep 25, Michigan Department of Natural Resources, Ann Arbor
- Willis KJ, Cook EF, Lozano–Fernandez M, Takeuchi I (2004) First record of the alien caprellid amphipod, *Caprella mutica*, for the UK. J Mar Biol Assoc UK 84:1027–1028
- Wolfson A, Van Blaricom G, Davis N, Lewbel GS (1979) The marine life of an offshore oil platform. Mar Ecol Prog Ser 1: 81–89
- Zar JH (2003) Biostatistical analysis, 4th edn. Pearson Education (Singapore), Delhi

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