DISTURBANCE INFLUENCES OYSTER COMMUNITY RICHNESS AND EVENNESS, BUT NOT DIVERSITY

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Abstract. Foundation species in space-limited systems can increase diversity by creating habitat, but they may also reduce diversity by excluding primary space competitors. These contrasting forces of increasing associate diversity and suppressing competitor diversity have rarely been examined experimentally with respect to disturbance. In a benthic marine community in central California, where native oysters are a foundation species, we tested how disturbance influenced overall species richness, evenness, and diversity. Surprisingly, overall diversity did not peak across a disturbance gradient because, as disturbance decreased, decreases in overall species evenness opposed increases in overall species richness. Decreasing disturbance intensity (high oyster abundance) led to increasing species richness of sessile and mobile species combined. This increase was due to the facilitation of secondary sessile and mobile species in the presence of oysters. In contrast, decreasing disturbance intensity and high oyster abundance decreased the evenness of sessile and mobile species. Three factors likely contributed to this decreased evenness: oysters reduced abundances of primary sessile species due to space competition; oysters supported more rare mobile species; and oysters disproportionately increased the relative abundance of a few common mobile species. Our results highlight the need for further studies on how disturbance can differentially affect the evenness and richness of different functional groups, and ultimately how these differences affect the relationship between overall diversity and ecosystem function.

Key words: biodiversity; competition; foundation species; intermediate disturbance hypothesis; mobile species; Olympia oysters; positive interactions; species richness and evenness.

INTRODUCTION

Understanding how species diversity is maintained at the local scale has been among the foremost challenges for community ecologists (Hutchinson 1959, MacArthur and MacArthur 1961, Paine 1966, Connell 1978, Huston 1979, Menge and Branch 2001, Bruno et al. 2003). According to nonequilibrium models, like the intermediate disturbance hypothesis (IDH), local diversity can be maintained by intermediate levels of natural disturbance (Connell 1978, Huston 1979, Petraitis et al. 1989). Low and high levels of disturbance are expected to be less effective in maintaining diversity because the former enable competitive exclusion and the latter directly eliminate many species. Intermediate levels of disturbance, however, maximize diversity (Fig. 1) by enabling the coexistence of potential competitors and stress tolerant species (Connell 1978, Sousa 1979).

In formulating IDH, researchers studied the effects of disturbance on basal (sessile) species such as trees, corals, and marine algae (Connell 1978, Sousa 1979). While many experimental and observational studies

provide a good understanding of how disturbance maintains the diversity of basal species, we know less about how disturbance influences the diversity of associate species such as herbivores, mutualists, parasites, and predators that live within or on basal species (Sousa 1979, Bruno et al. 2003). Disturbance can directly affect the diversity of associate species by removal or death, but it may also indirectly affect the diversity of associate species by altering the diversity of basal species. As outlined in the diversity–trophic structure hypothesis (DTSH), high diversity of basal species will increase resource diversity for associate species (Hutchinson 1959, Knops et al. 1999). Similarly, basal species diversity may also increase the diversity of structure or habitat available to associate species (Johnston and Odum 1956, Murdoch et al. 1972). If we combine IDH and DTSH, we would predict that the diversity of basal and associate species (i.e., overall diversity) peaks under intermediate levels of disturbance (Fig. 1).

The combined model of IDH and DTSH relies on the assumption that basal diversity determines the diversity of associate species. Strong correlations between basal and associate diversity have been found for trees and birds (Johnston and Odum 1956, MacArthur and MacArthur 1961), plants and lizards (Pianka 1967), as well as plants and insects (Murdoch et al. 1972). While these correlations only indirectly support the model's

Fig. 1. Conceptual model of the effect of disturbance on species diversity. The intermediate disturbance hypothesis (IDH) predicts that basal species diversity (solid line) will peak under intermediate levels of disturbance. The combination of IDH and the diversity–trophic structure hypothesis (DTSH) predicts that high diversity of basal species will increase resource diversity for associate species and maximize overall diversity under intermediate levels of disturbance (dashed line). Positive interaction theory (facilitation) predicts that the structural complexity of a dominant basal species will increase the diversity of associate species and maximize overall diversity under low disturbance (dotted line).
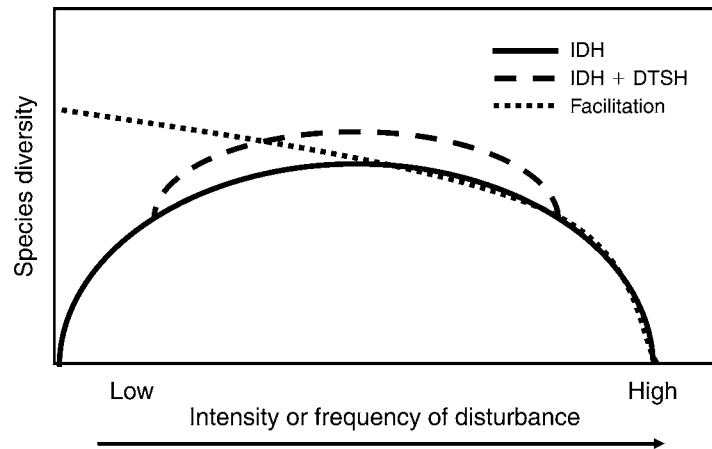
assumption, experimental increases and deceases in species richness of grassland plants significantly affected the richness of insect communities and directly support the assumption of this model (Siemann et al. 1998, Knops et al. 1999).

Alternatively, overall diversity can be greatest with low levels of disturbance if the quantity of structure, rather than the quality or diversity of structure, ultimately determines associate species diversity. In agreement with IDH, low levels of disturbance may allow a few basal species to occupy a limiting resource (e.g., space), decreasing the diversity of basal species (Connell 1978; Fig. 1). But theory based on positive interactions suggests that these dominant basal species, by acting as "foundation species" (Dayton 1975), can increase the diversity of associate species (Suchanek 1986, Bruno et al. 2003). For example, low diversities of canopy-forming plants or reef-building invertebrates often support high diversities of insects, birds, marine invertebrates, or fishes (Callaway and Walker 1997, Stachowicz 2001). Foundation species may increase associate diversity by creating large amounts of physical structure that provide refuge from predation, ameliorate physical stress, augment food supply, or increase the surface area of available habitat (Parker et al. 2001, Bruno et al. 2003, Grabowski et al. 2005). The physical structure of foundation species may also generate interstitial spaces that isolate associate species, decrease competition for resources, and increase species evenness (Huston 1979, Bruno et al. 2003). If these increases in diversity of associate species exceed decreases in diversity of basal species, then overall diversity will peak at low rather than intermediate disturbance (Fig. 1).

A classic example of a dominant basal species that is also a foundation species comes from studies of algal mats on intertidal boulders in southern California. The alga, *Gigartina canaliculata*, is a strong competitor for space whose nonselective removal by seasonal wave disturbance restarts algal succession, maximizing algal diversity at intermediate disturbance levels (Sousa 1979, 2001). The diversity of mobile invertebrates living within algal mats, however, was greater with low than with intermediate disturbance because *G. canaliculata* has more surface area or structural refuge than all other algal species (Dean and Connell 1987). Thus, foundation species may increase associate diversity merely by increasing the surface area of available habitat (Dean and Connell 1987, Parker et al. 2001).

Much of the previous work on disturbance and diversity has been either nonexperimental or has focused on the diversity of individual groups within a community (e.g., Johnston and Odum 1956, Murdoch et al. 1972, Sousa 1979, Dean and Connell 1987). Most studies have also examined how disturbance affects the number of species (richness) in a community, paying less attention to the relative abundance of species (evenness) (Mackey and Currie 2001). Recent research suggests that efforts focused solely on species richness may be misleading if richness and evenness show different responses. For example, an examination of how seed additions and grazing history affect the diversity of grassland plants found that seed addition increased species richness but decreased species evenness, thereby generating no net diversity effect (Wilsey and Polley 2003). Despite the historical focus on IDH and the renaissance of positive interaction studies investigating associate species, we lack experimental tests of how overall species richness, evenness, and diversity vary along a disturbance gradient (Bruno et al. 2003).

The present study experimentally tested the effects of disturbance intensity on the diversity (richness and evenness) of both basal and associate species in a community dominated by oysters. Olympia oysters (*Ostreola conchaphila = Ostrea lurida*) are native to estuaries of western North America and exist on hard substrate such as rocks and cobbles (Baker 1995). Because hard substrate is limited in soft sediment estuaries, oysters may strongly compete with other basal species (hereafter primary sessile species) for space on cobbles. At the same time, Olympia oysters increase structure on cobbles and likely function as a foundation species for associate species including amphipods and

polychaetes (hereafter mobile species) as well as sponges and algae that live on the oysters (hereafter secondary sessile species) (Baker 1995). Most research on oysters has occurred in estuaries of eastern North America; these studies showed that oysters (*Crassostrea virginica*) function as a foundation species by providing a refuge from predation or physical stress and increasing the amount of habitat available for associate species (Arve 1960, Wells 1961, Meyer and Townsend 2000, Grabowski 2004, Grabowski et al. 2005). Unlike *C. virginica* reefs that create habitat on soft sediment and positively affect diversity, Olympia oysters occur on hard substrate and may negatively impact the diversity of other basal species while benefiting associate species diversity. Consequently, cobbles with Olympia oysters provide a model system for experimentally testing how disturbance influences overall diversity.

In this study, we examined how disturbance simultaneously affects the diversity of primary sessile, secondary sessile, and mobile species living on intertidal cobbles dominated by Olympia oysters. We also investigated how the responses of the different functional groups (i.e., mobile vs. sessile) influence the behavior of overall diversity across a disturbance gradient. Because species diversity is a statistic with two important components, species richness and evenness, we also focused on how disturbance affected both the richness and evenness of each functional group. We explicitly tested three hypotheses: (1) richness and evenness of primary sessile species are highest at intermediate levels of disturbance intensity; (2) richness and evenness of associate species (secondary sessile and mobile species) are highest at low levels of disturbance intensity and high oyster cover; and (3) overall diversity is highest at low levels of disturbance intensity because increases in the richness and evenness of associate species compensate for corresponding decreases in basal species.

METHODS

Study system

The Olympia oyster is a protandrous hermaphrodite that is native to eastern Pacific estuaries from Alaska to Baja California Sur, Mexico. Juvenile oysters settle on hard substrate, grow to ~6 cm, and create loose reefs (~0.10 m tall) within low intertidal and shallow subtidal portions of estuaries (Baker 1995). Olympia oysters compete with sessile organisms for available substrate (Baker 1995), and we have indirect evidence that these oysters are competitive dominants. Olympia oysters can live for several years and occur across broad areas of shoreline (~20 km) at our study site with densities up to 40 oysters per 0.25 m². These oysters also coexist with soft-bodied and ephemeral sessile species (e.g., tunicates and algae), while the only other long-lived space competitor, the mussel *Mytilus galloprovincialis*, occurs higher in the intertidal than oysters (D. L. Kimbro, *personal observation*). The Olympia oyster is also the dominant bivalve fossil found in estuaries throughout its range (Baker 1995), suggesting that these oysters have historically been an important space holder in Pacific coast estuaries.

We conducted this experiment at Shell Beach State Park (38°07′ N, 122°52′ W) on the west side of Tomales Bay, California, ~18 km from the mouth of bay. Tomales Bay is an estuary created by a submerged river valley on the San Andreas Fault, whose physical and biological characteristics have been well described (Hearn and Largier 1997). Although Olympia oysters can exist subtidally (Baker 1995), oysters in Tomales Bay occur within a narrow intertidal zone consisting of cobbles scattered along a sandy beach at +0.5 to −1.0 m Mean Lower Low Water (MLLW). The oyster zone occurs above seagrass (*Zostera marina*) beds and below zones of mussels (*M. galloprovincialis*) and barnacles (*Balanus glandula*).

Our intertidal surveys show that oysters in Tomales Bay have an average size and density of 29.27 ± 0.40 mm and 12.83 ± 0.77/0.30 m², respectively. At our study location, mean densities of oysters at +0.5 m MLLW and −1.0 m MLLW were 4.68 ± 3.44 and 5.16 ± 3.41/0.10 m², respectively. Oysters occur on cobbles that have a median surface area (length × height) of 32 cm² and cover 65% of the sandy intertidal. These cobbles are often overturned by winter waves that indiscriminately remove sessile species and create areas with various successional stages.

Experimental design

A 50-m transect was placed parallel to the tide line at 0.0 m above MLLW within the oyster zone at Shell Beach in May 2003. Along the transect, we randomly selected 30 cobbles dominated by oysters (65–100% oyster cover) and permanently marked 0.15 × 0.15 m quadrats on each cobble with Z-Spar Marine Epoxy (Z-Spar, Los Angeles, California, USA) and stainless steel screws. Quadrats were randomly assigned to three treatments (n = 10 quadrats) varying in the intensity of disturbance and subsequent nonselective mortality of organisms: (1) high disturbance, with all organisms removed, (2) intermediate disturbance, with organism cover reduced to 25–50%, and (3) low disturbance, with no organisms removed (organism cover = 65–100%). Primary sessile species were removed with a small hammer and chisel. Because oysters dominated the cobbles, disturbance treatments mostly affected oysters and organisms attached to oysters. These treatments simulate natural disturbances (e.g., waves and overturning rocks) that remove organisms from hard substrate, generate additional space, reduce the structural complexity of rocks, and create a nonequilibrium system of cobbles differing in successional stage.

Our experiment proceeded in the following order: disturbance treatments were applied in May 2003; point contact surveys were conducted for sessile species diversity (morning low tide, 15 August 2003); transient mobile invertebrates were sampled (afternoon high tide,

15 August 2003); structural complexity of quadrats was calculated, and quadrats were harvested to sample resident mobile species (low tide, 16 August 2003).

Sessile species diversity patterns

In each quadrat, we estimated the abundance of sessile species by recording the identity and position of species at 25 randomly generated points. The point contact survey generated richness (R) and evenness (E) data describing the composition of primary, secondary, and total (i.e., primary + secondary) sessile species. We defined primary sessile species as those attached directly to the rock surface and secondary sessile species as organisms attached to primary sessile species. Because some primary sessile species were also observed as secondary sessile species, these two groups were not mutually exclusive (Appendix A). We combined both of these groups to analyze patterns of diversity for total sessile species. The evenness of the three assemblages of sessile species was calculated for each quadrat as $E = H'/\ln(R)$ where H' is the Shannon-Wiener Diversity Index and R is species richness.

Quantifying structural complexity

We estimated the complexity of biogenic structure within quadrats by laying twine along the contours of sessile organisms and measuring the length of twine (centimeters) needed to span opposing sides of the quadrat. We calculated mean structural complexity (pre-removal mean) from estimates of three twine lengths for each quadrat. We made these measurements prior to removing the biogenic structure, which was necessary for sampling the diversity of mobile species (see *Methods: Mobile species diversity*), and then repeated these measurements immediately after the removals for a post-removal mean. We subtracted the post-removal from the pre-removal mean and divided this difference by the pre-removal mean. This calculation estimates the percentage reduction in structural complexity of the cobble due to loss of biogenic structure.

Mobile species diversity

After sampling sessile species (point contact surveys), we scraped off all the organisms within each quadrat to sample resident mobile organisms at low tide. Samples were put on ice, returned to the laboratory, preserved in 10% buffered formalin, and later transferred to 70% ethanol. Samples were split in two parts by sieving the sample through 4.0-mm (macro samples) and 0.5-mm (micro samples) sieves. We split macro samples by evenly distributing the contents on a sieve, flipping a coin, and randomly selecting half for analysis. In the randomly chosen macro sample, epifauna and sediment were removed from sessile species in water under a dissecting microscope. These organisms were added to the micro sample, which was then divided in half using a plankton splitter. All mobile organisms within the micro sample were counted under a dissecting microscope.

To provide data for transient mobile species, some quadrats were also sampled during high tide ($\sim$1.5 m depth at 0.0 m above MLLW) using SCUBA. We suction sampled each quadrat for 30 s to collect as many mobile organisms as possible. All mobile organisms were identified to the lowest practical taxonomic level, and these identifications were verified by regional systematic experts.

Overall species diversity

We produced values of overall richness by adding the number of sessile and mobile species in each quadrat. In contrast, overall evenness and diversity (i.e., Shannon-Wiener index) values concern two functional groups (sessile and mobile) that were sampled with different methods (sessile, percent cover; mobile, individual counts). As a result, we calculated ratios of functional group richness for each quadrat (e.g., sessile R/overall R). The evenness and diversity of each functional group was then multiplied by its respective ratio, producing weighted evenness and diversity values for sessile and mobile species. We added these weighted values to produce "estimated" overall evenness and diversity values (e.g., (mobile evenness $\times$ 0.70) + (sessile evenness $\times$ 0.30)). We conducted simulations to justify the estimated overall diversity and evenness indices (Appendix B).

Statistical analyses

Although our experimental design contained 10 replicates of each treatment, we lost three experimental units (one intermediate and two low disturbance) due to the overturning of rocks and death of all sessile organisms, and we misplaced three other experimental units. As a result, the study contained 24 experimental units for data on primary sessile species (low, $n = 6$; intermediate, $n = 9$; and high, $n = 9$). For three quadrats (high disturbance), abundances of sessile species were recorded as zero because the point-contact survey failed to sample resident organisms. Consequently, these quadrats lacked evenness data and were excluded from the evenness analyses.

To protect against Type I error rate, we conducted a multivariate analysis of variance (MANOVA) to determine if functional groups changed significantly in richness across the disturbance levels (Scheiner and Gurevitch 2000). Where multivariate analysis indicated a significant effect at $P \leq 0.05$, univariate analysis of variance (ANOVA) was performed on each response variable (i.e., richness of total, primary, secondary, and mobile species; Underwood 1981). These steps were repeated for the evenness and overall species diversity data.

Further exploring the richness and evenness patterns of sessile species, we focused on how the seven (out of 10) most numerous sessile species changed in relative abundance across disturbance treatments. As above, we used MANOVA and ANOVA to analyze the responses of each species. Using only a subset of the sessile species enabled us to conduct a MANOVA on relative
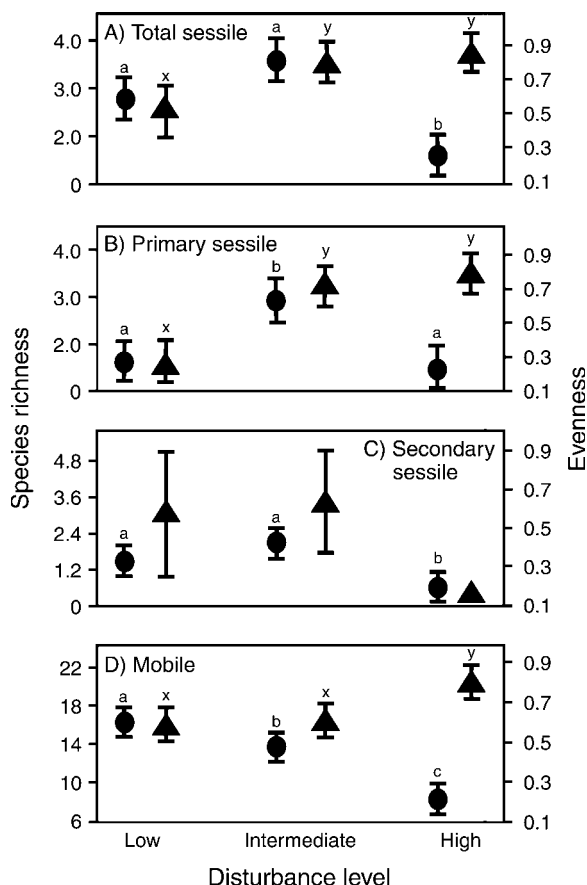
FIG. 2. Plots of species richness (circles) and species evenness (triangles), shown as mean ± SE, of three disturbance treatments (low, intermediate, and high) for the following four groups: (A) total sessile species, (B) primary sessile species, (C) secondary sessile species, and (D) mobile species. Richness and evenness values for a given disturbance are staggered to clearly distinguish error bars. Different lowercase letters above error bars indicate significant differences among treatments for richness (a–c) and evenness (x–z) according to Tukey's post hoc test of means.

abundances because their total was <100%. For the three most abundant sessile species, the relationship between structural complexity and percent cover of each organism in a quadrat was quantified using linear regression. Similar to the analyses for sessile species, patterns of mobile species were investigated by focusing on changes in number and relative abundance of the 10 most numerous mobile species. While this approach may overlook the effects of rare species, these 10 species comprise 96% of the total number of individuals present in all of our samples.

When necessary, we transformed our data to comply with parametric assumptions using arcsine square-root or log-transformations. Data failing to meet the assumptions were analyzed using a Welch ANOVA, which allows testing means that have unequal standard deviations. The nonparametric Wilcoxon/Kruskal-Wallis test was used for data containing unequal

variances. We used Tukey's or Ryan's Q method for all post hoc tests of means. We present the means and 95% confidence intervals for analyses involving transformed data. Statistical analyses were conducted using JMP 4.0 (SAS Institute 2001) and SAS statistical software (SAS Institute 2002–2003).

RESULTS

Species assemblage of Olympia oyster community

We found a diverse assemblage of species ($n = 47$) within the Olympia oyster habitat (Appendix A). Mollusca (12 species), Arthropoda (11 species), and Polychaeta (10 species) comprised 70% of the taxa present. Seventeen species were sessile and likely competitors for space with Olympia oysters, while the remaining 30 species were mobile organisms that lived on or among Olympia oysters. The richness of the different functional groups (i.e., total sessile, primary sessile, secondary sessile, and mobile species) changed significantly across disturbance treatments (MANOVA, Wilk's lambda, $F_{8,34} = 5.94$, $P = 0.0001$). Evenness values for the four functional groups also significantly differed among the three treatment levels (MANOVA, Wilk's lambda, $F_{8,28} = 3.39$, $P = 0.008$).

Sessile species diversity

The mean richness of all sessile species asymptotically increased from high to low disturbance (Fig. 2A, Appendix C). Mean evenness of all sessile species decreased from high to low disturbance, with the low disturbance mean differing from means of intermediate and high disturbance (Fig. 2A, Appendix C).

In contrast to the results for total sessile species, mean richness of primary sessile species unimodally changed across treatments (Fig. 2B, Appendix C). Mean richness peaked at intermediate disturbance and remained low at either disturbance extreme, while mean evenness of primary sessile species was greatest at high and intermediate disturbances (Fig. 2B, Appendix C).

The richness of secondary sessile species also varied significantly among the disturbance treatments, with low and intermediate treatments having greater values than the high disturbance treatment (Fig. 2C, Appendix C). Mean evenness of secondary sessile species was greater in low and intermediate treatments than in the high disturbance treatment (Fig. 2C, Appendix C). The percentage of free space available for sessile species also increased with disturbance intensity (Appendix C).

As a group, relative abundances varied significantly across treatments for the seven most common sessile species (MANOVA, Wilk's lambda, $F_{14,30} = 7.88$, $P = 0.0001$). ANOVAs for individual species showed that oysters increased, while algae and a nonnative sponge decreased in relative abundance as disturbance attenuated (Fig. 3A, Appendix D). The relative abundance of a tube building polychaete (Eunicidae) unimodally changed, and the relative abundance of three other species remained constant across the disturbance gradient.
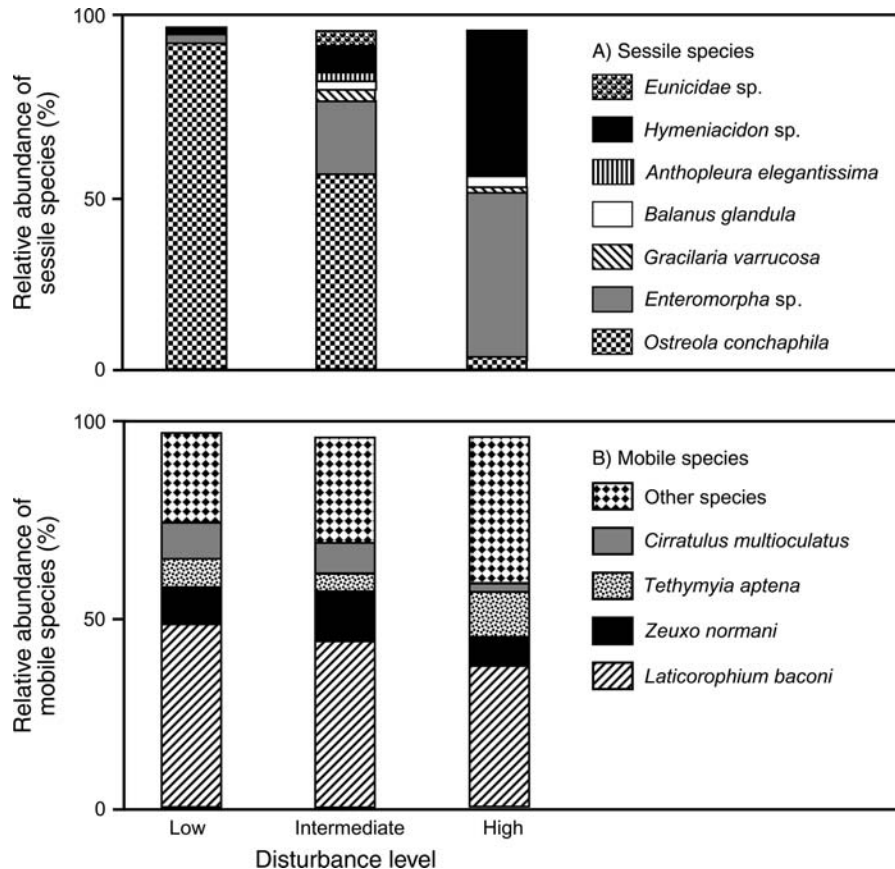
FIG. 3. Histograms showing changes in relative abundance of (A) sessile species and (B) mobile species as a function of disturbance. For (A) sessile species, relative abundances of four species in the treatments varied with decreasing disturbance: one species increased, two species decreased, and one species changed unimodally. Three species did not change in relative abundance as disturbance decreased (see Appendix D). For (B) mobile species, relative abundances of five species in the treatments changed with decreasing disturbance: three species increased, one species decreased, and one species varied unimodally. Five species remained constant in relative abundance as disturbance decreased (see Appendix F).

Quantifying structural complexity

Structural complexity (centimeters) increased linearly as oyster percent cover increased ($n = 20$, $R^2 = 0.33$, $P = 0.008$, $y = 2.53x + 0.52$). There was no relationship between structural complexity and the abundance of a green alga (*Enteromorpha/Ulva* sp., $n = 20$, $R^2 = 0.01$, $P = 0.71$, $y = 0.42x + 1.09$) or a nonnative sponge (*Hymeniacidon* sp., $n = 20$, $R^2 = 0.07$, $P = 0.27$, $y = -1.57x + 1.47$).

Mobile species diversity patterns

The richness of mobile species increased with decreasing disturbance and increasing oyster cover (Fig. 2D). The mean evenness of mobile species decreased from high to low disturbance, while the density of mobile species showed a pattern similar to the richness data (Appendix C). Although these data were collected at low tide, results were consistent with additional data (suction samples) taken from a subset of quadrats at high tide (Appendix C). Because limited high tide sampling

essentially confirmed low tide results, we do not discuss it further here.

The abundance of the 10 most common mobile species varied significantly among treatments (MANOVA, Wilk's lambda, $F_{20,26} = 3.83$, $P = 0.0008$). ANOVAs for individual species revealed that the abundance of six species significantly increased with decreasing disturbance (Fig. 4, Appendix E). Relative abundances of five species in the treatments changed, but not uniformly, as disturbance decreased (MANOVA, Wilk's lambda, $F_{20,26} = 3.54$, $P = 0.002$, Fig. 3B and Appendix F). Fourteen common mobile species accounted for 95% and 100% of the individuals in low/intermediate and high disturbance treatments, respectively. The 12 species present only with oysters accounted for a maximum of 5% of the individuals in all samples. Ranking the relative abundances of each species by treatment illustrates that the ordering of species changes across treatments and that several rare species enter the community as disturbance decreased (Appendix G).
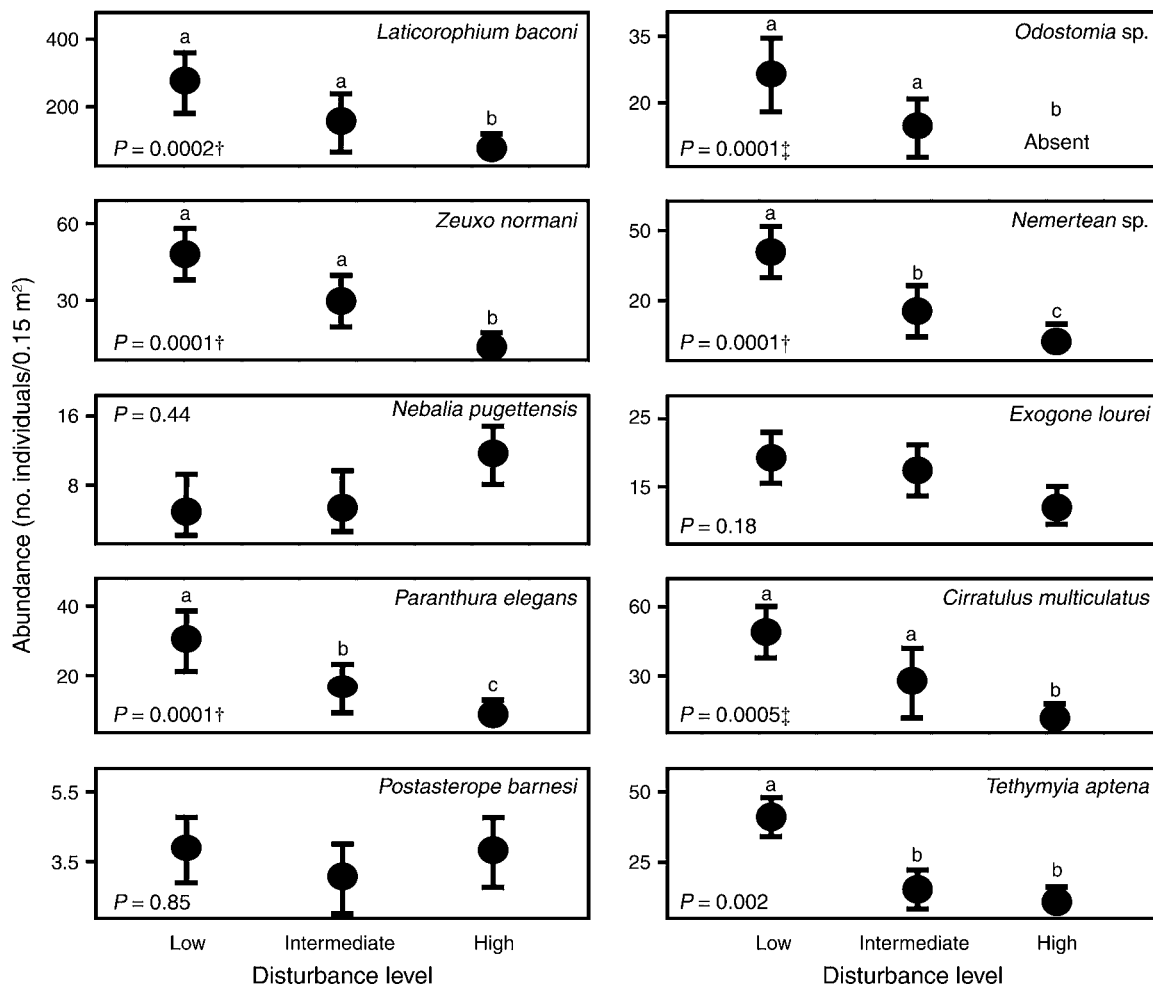
FIG. 4. Plots of mean abundance (with 95% confidence intervals) for the 10 most common mobile species as a function of decreasing disturbance. Means were compared using Tukey's post hoc test. Different lowercase letters over error bars indicate treatments that differ significantly. *P* values represent results of ANOVA (see Appendix E).

† Log$_{10}$-transformed.

‡ Nonparametric Wilcoxon/Kruskal-Wallis test using chi-square test statistic.

Overall species diversity patterns

The richness, evenness, and diversity of all taxa combined differed significantly among the disturbance treatments (MANOVA, Wilk's lambda, $F_{6,30} = 5.56$, $P = 0.0006$). Mean richness of all taxa increased from high to low disturbance treatments (Fig. 5A, Appendix C). In contrast, mean evenness of all taxa decreased from high to low disturbance (Fig. 5A, Appendix C). The combination of these opposing patterns of species richness and evenness resulted in no change of overall species diversity across disturbance treatments (Fig. 5B, Appendix C).

DISCUSSION

Contrary to predictions from the diversity–trophic structure hypothesis (DTSH), theory based on positive interactions, and our most important hypothesis (third), overall diversity (Shannon-Wiener index) in a space-limited environment remained constant across an experimental disturbance gradient. In addition, overall species richness was highest under low disturbance with high oyster structure, suggesting that the structure of basal species, rather than the diversity of basal species, may better predict associate species richness. In contrast, overall species evenness peaked under high disturbance intensity with low oyster structure. From previous environmental stress models (e.g., Connell 1978, Bruno and Bertness 2001, Menge and Branch 2001), we infer that decreasing the intensity of disturbance interacted with competition among basal species and facilitation among associate species to increase overall richness and decrease overall evenness. Because these components of diversity (i.e., richness and evenness) had opposing patterns across a disturbance gradient, overall diversity remained constant.

To support our previous inferences, we now discuss the results with respect to our first two hypotheses. Consistent with the intermediate disturbance hypothesis (IDH) and our first hypothesis, the richness of primary sessile species peaked in the intermediate disturbance treatments. High disturbance treatments were dominated by bare space (mean = 62%) and opportunistic species such as a green alga (*Enteromorpha* sp.) and a nonnative sponge (*Hymeniacidon* sp.) that recruited rapidly after disturbance. Because oysters grow rapidly after settling and have persisted in Tomales Bay over a long time period (Baker 1995; D. L. Kimbro, *unpublished data*), we suggest that oysters competitively excluded opportunistic basal species, reducing species richness and evenness under low disturbance (mean free space available = 9%). An alternative to the IDH interpretation is that oysters facilitated the presence of other basal species that could not persist in high disturbance treatments without oysters. But the species present in intermediate disturbance treatments were absent in low disturbance treatments, suggesting that oysters diminished rather than facilitated the richness and evenness of other primary sessile species.

In agreement with our second hypothesis and theory based on positive interactions, high oyster structure in low disturbance treatments significantly increased the number of mobile individuals by almost an order of magnitude while more than doubling the number of species. Oysters also appear to have facilitated the richness of secondary sessile species, potentially explaining why the total richness of all sessile species did not show a strong unimodal relationship. Research in the rocky intertidal of California also demonstrated that a foundation species, the mussel *Mytilus californianus*, can acquire a limiting resource (space) without reducing the diversity of basal species if other basal species settle on secondary substratum (mussel shell) (Lohse 1993).

The results of our second hypothesis contribute to the literature addressing how foundation species influence associate diversity through the provision of habitat (Bruno and Bertness 2001, Stachowicz 2001, Bruno et al. 2003, and references therein). Because associate species richness and individual numbers peaked under low disturbance and high oyster structure, our data reinforce previous findings about the abundance of structure and associate diversity (Pianka 1967, Murdoch et al. 1972, Parker et al. 2001). This richness outcome, however, contradicted the prediction from DTSH that the richness of basal species determines the richness of associate species. With these results, we conclude that the abundance of structure produced by basal species like oysters is more important than the diversity of basal species producing the structure.

Although the second hypothesis was supported by the richness data for mobile species, it was not supported by the species evenness data. There are three possible explanations for the negative relationship between oyster abundance and mobile species evenness. First, a
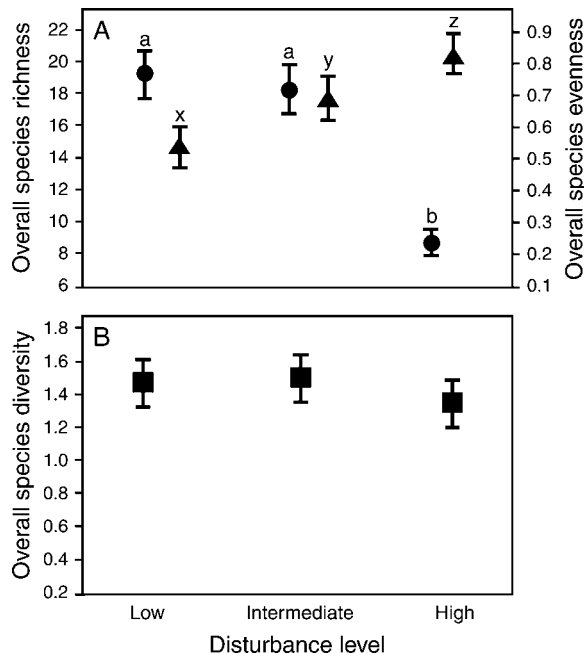

Fig. 5. Plots of treatment means ($\pm$SE) for (A) overall species richness (circles) and evenness (triangles), as well as (B) overall diversity (squares). Different lowercase letters over error bars indicate significant treatment differences using Tukey's post hoc test for richness (a–c) and evenness (x–z). Diversity was calculated using the Shannon-Wiener diversity index (see Appendix C).

foundation species may confer greater competitive advantage to one or a few species (Hartnett and Wilson 1999, Stachowicz 2001). In this case, lower evenness would be due to increases in number and relative abundance of competitively dominant invertebrates and to decreases in competitively subordinant invertebrates. The potential subordinant invertebrates (e.g., amphipods, isopods, harpactoids, and cirratulids) in this study can have several generations in four months, thus enough time was provided for competition to decrease their population growth rates and evenness (Grosse and Pauley 1989, Duffy et al. 2005). The populations of all mobile invertebrates, however, grew in abundance as oyster structure increased. These data suggest that competition, which may have caused sublethal effects, fails to fully explain why evenness decreased under low disturbance and high oyster structure (Coen et al. 1981, Peterson 1991).

The second explanation for the mobile evenness result involves a simple sampling effect (Dean and Connell 1987). Low disturbance treatments with greater oyster structure yielded more mobile individuals, likely increasing the occurrence of rare species and decreasing evenness (Dean and Connell 1987). Our data are consistent with this second explanation because 12 (out of 28) rare species occurred in treatments with intermediate oyster structure and four additional rare species occurred in treatments with high oyster structure.

A third possible explanation for the decrease in mobile evenness is suggested by work in seagrass communities (e.g., Parker et al. 2001): increased oyster structure may disproportionately facilitate a few mobile invertebrates. As suggested before, abundances of mobile species peaked under low disturbance, most likely as a response to oyster surface area (i.e., sampling effect). If a sampling effect alone decreased evenness, we would expect abundances of common species to increase evenly, maintaining proportional relationships among these invertebrates. But only three of the 10 common species increased in relative abundance under low disturbance, while five other common species remained constant. Consequently, species ordering on rank-abundance plots shifted among disturbance treatments. We suggest that positive interactions helped decrease the evenness of mobile invertebrates under low disturbance and high oyster structure. Additional experiments, however, are required to mechanistically understand the relative importance of our three explanations.

Our study has limitations and one concerns the experiment's duration. Prematurely ending experiments can limit the generality of results because outcomes often change through time (Luttbeg et al. 2003). While this experiment lasted only four months, four components of natural history make this time scale appropriate. First, Olympia oysters can recruit to cobbles in Tomales Bay during the spring and autumn (Baker 1995). We conducted the experiment in between the two recruitment windows to maintain the effects of our disturbance treatments with respect to oysters. Second, recruitment of other sessile species within Tomales and nearby Bodega Bay is highest during this time period (A. Chang, *unpublished data*; J. Stachowicz, *unpublished data*). Third, the experiment was conducted during the upwelling season (spring–summer) of northern California, which provides high levels of food for filter feeders (Largier et al. 1993). These high food levels then promote high growth and competition for space among sessile species. Finally, preliminary data on oyster demography demonstrates that oysters grow quickly after settlement, reaching 64% of adult body size during the time frame of this experiment (D. L. Kimbro, *unpublished data*). Thus, we timed the experiment to maintain treatment differences and to allow high recruitment of interspecific organisms as well as competition for space.

Another limitation of our study concerns the distribution of natural disturbances in relation to our disturbance treatments. Our experimental design used a discrete distribution of disturbance treatments while IDH originally discussed a continuous distribution of disturbance (Connell 1978). Inaccurately placing discrete treatments along the disturbance continuum could inhibit us from correctly interpreting any results with regard to IDH. In addition, disturbances in nature rarely occur in isolation (Huston 1979, Sousa 2001), and experimental cobbles could have experienced other disturbances (e.g., predation and wave disturbance). In

fact, recent field and laboratory research suggests that a nonnative whelk (*Urosalpinx cinera*) consumes oysters at our study site (D. L. Kimbro and E. D. Grosholz, *unpublished data*). Despite these potential confounding factors, the distribution of oyster percent cover on cobbles at the end of the experiment spanned a similar range of values found on natural cobbles (Appendix H). These similar distributions suggest that the discrete treatments were correctly positioned along the disturbance continuum. Further, additional natural disturbances would shift treatments to the right on the disturbance gradient (see Fig. 1); had we minimized these disturbances, we may have found higher oyster structure, and thus higher overall species richness and lower overall evenness under low disturbance treatments.

While our study has limitations, one of its strengths is the attention given to species evenness at two organizational levels. First, evenness of the overall community contradicted our most important hypothesis (third) and helped generate the surprising result of overall diversity. Second, overall evenness comprises the unexpected result of mobile species evenness, whose uncertain causes indicate a need for future research. In other study systems, species evenness has been argued to strongly affect local diversity and ecosystem functioning (Fox 1979, Cardinale et al. 2002, Dangles and Malmquist 2004). Despite these recognitions, research on the relationships between disturbance–diversity and diversity–ecosystem function focuses predominantly on species richness (Mackey and Currie 2001, Covich et al. 2004). But, as demonstrated in this study, species richness and evenness can respond differently to experimental treatments (Wilsey and Polley 2003). Thus, the focus on species richness may prevent us from better understanding natural and experimental patterns involving diversity.

In conclusion, ecologists have long recognized that natural disturbances can maintain and organize the diversity of communities (Sousa 2001). Natural and anthropogenic disturbances, however, are now affecting ecosystems at increasing intensities, frequencies, and scales (Sousa 2001, Harley et al. 2006). Accurately predicting the consequences of these disturbances will improve our ability to mitigate and conserve natural habitats (Harley et al. 2006). In this study, we demonstrated that the effect of disturbance on the diversity of basal species does not predict the diversity of another functional group or the overall community. Although disturbance did not quantitatively affect overall diversity, we found that disturbance qualitatively influenced overall diversity, likely by altering structural complexity, the strength of competition among basal species, and positive interactions for associate species. We suggest that understanding the qualitative effects of disturbance on overall diversity, and the effects of overall diversity on key ecosystem processes, requires investigating the richness and evenness of different

functional groups. Because communities along our disturbance gradient were qualitatively very different with respect to a foundation species, we also suggest that investigating the forces controlling the distribution, abundance, and morphological variation of foundation species will help inform resource managers trying to conserve or restore habitat diversity (Stachowicz 2001).

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APPENDIX A

Taxa present in the Olympia oyster community (*Ecological Archives* E087-145-A1).

APPENDIX B

Estimating overall diversity from the mean of mobile and sessile species diversity *(Ecological Archives* E087-145-A2).

APPENDIX C

ANOVA results for 16 different response variables (*Ecological Archives* E087-145-A3).

APPENDIX D

Changes in the relative abundance of the seven most abundant sessile species (*Ecological Archives* E087-145-A4).

APPENDIX E

Variation in absolute abundance of the 10 most abundant mobile species (*Ecological Archives* E087-145-A5).

APPENDIX F

Effect of disturbance on the percentage composition of mobile species in a quadrat (*Ecological Archives* E087-145-A6).

APPENDIX G

Ranked relative abundance (mean) of mobile species in each treatment (*Ecological Archives* E087-145-A7).

APPENDIX H

Histograms of oyster percent cover on cobbles from study site (a) and from experiment (b) (*Ecological Archives* E087-145-A8).