

ODD SPECIES OUT AS PREDATORS REDUCE DIVERSITY OF CORAL-REEF FISHES

GLENN R. ALMANY^{1,3} AND MICHAEL S. WEBSTER²

¹*School of Marine Biology and Aquaculture, James Cook University, Townsville QLD 4811 Australia*

²*Department of Zoology, Oregon State University, Corvallis, Oregon 97331-2914 USA*

Abstract. When predators differentiate among prey species, they commonly select the most abundant species. Surprisingly, on coral reefs in Australia and the Bahamas, we found evidence to the contrary: using null models, we observed that generalist predators had a greater impact on less-abundant species, thereby reducing local species richness. Disproportionate effects on these rare species were evident during a narrow window of time between settlement and 1–2 days later, highlighting how interactions during or immediately following settlement may influence subsequent community structure. Differences in species richness between treatments that were established during this narrow window of time eventually disappeared from reefs in Australia but persisted on reefs in the Bahamas. Our results highlight an unexpected and largely unexplored ecological interaction whereby predators reduce prey diversity.

Key words: *oddy effect; predation; rarefaction; recruitment; settlement.*

INTRODUCTION

Understanding the causes and consequences of biodiversity patterns is critical to predicting and reversing ecological changes arising from biodiversity loss (Purvis and Hector 2000). Local patterns of diversity stem from a suite of ecological processes that partition a subset of the regional species pool into local communities. Consumers can play a pivotal role in maintaining high local diversity by preventing dominance by particular species (Paine 1966, Estes and Palminiano 1974), often via keystone predation (Power et al. 1996). Increased predation on dominant species is consistent with the prediction that consumers focus their effort on numerically abundant prey, leading to density-dependent prey mortality (Murdoch and Oaten 1975). Alternatively, some evidence suggests that, under certain circumstances, predators can have the greatest effects on species that are rare (Birkeland and Neudecker 1981, Hargreaves and Lebrasseur 1985, Spiller and Schoener 1998, Williams et al. 2003).

Coral reefs support the greatest species diversity of any marine ecosystem (Paulay 1997). Accelerating loss of coral cover and largely-unchecked harvesting of reef fishes have put coral reefs at high risk of large-scale biodiversity losses (Wilkinson 2002, Hughes et al. 2003). Studies of coral-reef fishes implicate predation as a critical component of population and community dynamics (Hixon 1991, Jones 1991). Abundant evidence suggests that predators can inflict density-dependent mortality on prey (Hixon 1991, Hixon and Webster 2002, Osenberg et al. 2002). Widespread density-dependent predation suggests that predators are

generally adept at identifying and exploiting prey of a given species when and where they are most common. When faced with the myriad of potential prey species found on coral reefs, predators that exhibit prey-switching behavior (*sensu* Murdoch and Oaten 1975) are predicted to have the greatest impacts on relatively common prey species, which could result in weaker impacts on relatively rare prey species.

Ultimately, how predators choose among multiple prey species can fundamentally alter the composition and diversity of prey communities (Hixon 1986). To illustrate some potential outcomes of predation, consider a hypothetical prey community in which prey species naturally differ in their relative abundance (Fig. 1A). A predator that chooses prey at random will tend to remove some species by chance as predation intensity increases (Fig. 1B). However, based on predator foraging theory and the widespread observation of density-dependent prey mortality, one might predict that predators would disproportionately consume the most abundant prey species (Murdoch and Oaten 1975, Hixon 1986, 1991), leading to higher prey diversity than random predation as the intensity of predation increases (Fig. 1C). Alternatively, predators could focus on rare species (Hixon 1986), leading to the rapid extirpation of rare species from the community (Fig. 1D). While these alternatives do not describe all the ways that predators might choose among prey species, they represent a set of testable alternatives using null models.

To generate a null model for the effects of random predation on prey communities, one can calculate a rarefaction curve for a control community in which predators have not yet removed any individuals (Fig. 1E, curve a). If predators then remove individuals at random with respect to species, communities should resemble a random draw from the control community (Fig. 1E, curve b). However, if predators focus on the

Manuscript received 20 October 2003; revised 10 March 2004; accepted 18 May 2004; final version received 14 June 2004. Corresponding Editor: G. E. Forrester.

³ E-mail: glenn.almany@jcu.edu.au

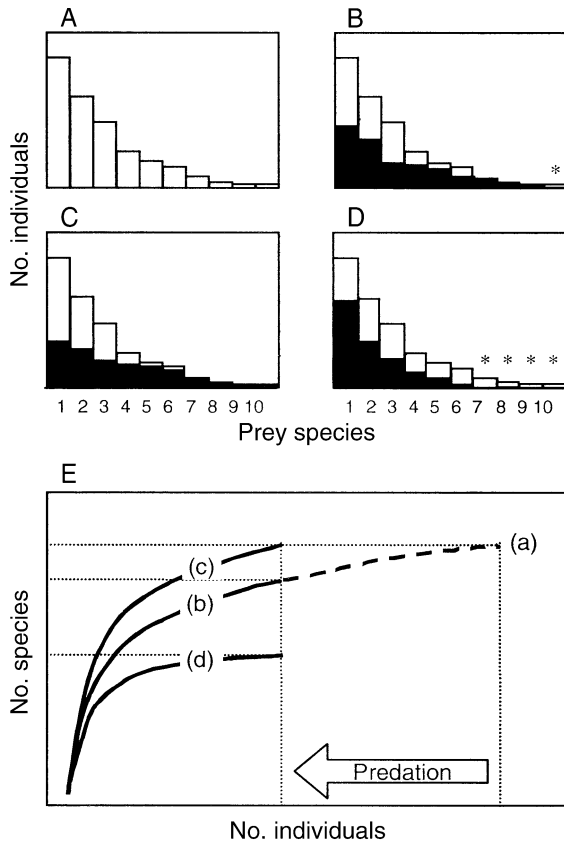


FIG. 1. Potential effects of predators on prey communities. (A) In a hypothetical community with 10 species that differ in abundance, predation could result in a variety of outcomes. Three possible outcomes are presented in panels (B)–(D), where black bars depict species composition following the removal of 50% of individuals via predation that is (B) random with respect to species, (C) disproportionate on common species, and (D) disproportionate on rare species. (E) Each of these predation scenarios result in quantitatively different rarefaction curves, with curves a–d corresponding to their respective communities in panels (A)–(D). Asterisks denote species removed by predators.

most abundant species, the resultant curve will have more species than predicted by the control curve for a given number of individuals (Fig. 1E, curve c). Alternatively, if predators disproportionately consume rare species, the resultant curve will have fewer species than predicted by the control curve (Fig. 1E, curve d). We used this null model approach to determine whether piscivores (fish that consume other fishes) exhibited random or nonrandom effects on the diversity of juvenile coral-reef fishes.

METHODS

Predator removal experiments and recruitment monitoring

Predator removal experiments were conducted near Lizard Island, Australia in the austral summer of 1999–2000, and Lee Stocking Island, Bahamas in the boreal

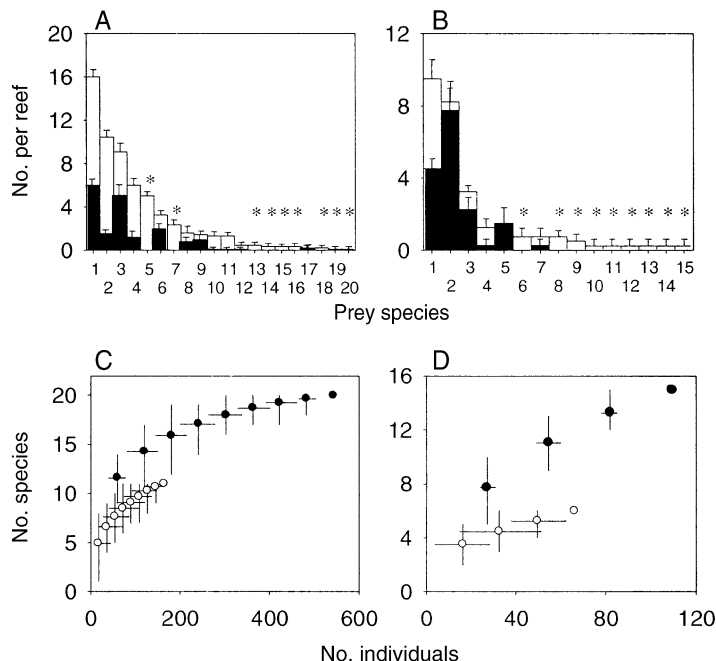
summer of 1997, on arrays of patch reefs consisting of live, translocated coral heads. Details about the size and composition of reefs in both arrays are available elsewhere (Webster 2002, Almany 2003). On 18 reefs in Australia and eight reefs in the Bahamas, we randomly assigned half at each site as resident predator-removal reefs and half as resident predator-present reefs. In Australia, predators consisted of one grouper (Serranidae: *Cephalopholis boenak*) and one dottyback (Pseudochromidae: *Pseudochromis fuscus*). Each reef with resident predators had four to six *C. boenak* and one to two *P. fuscus*, which reflected the natural range of predator densities observed on these reefs prior to manipulations. In the Bahamas, predators consisted of three groupers (*Cephalopholis cruentata*, *C. fulva*, and *Epinephelus striatus*) and two moray eels (Muraenidae: *Gymnothorax moringa* and *G. vicinus*). Each reef had two to seven groupers and none or one moray eel, which reflected the natural range of predator densities observed on these reefs prior to manipulation. In the Bahamas, we also removed territorial damselfishes (Pomacentridae: *Stegastes* spp.), as they interact with predators to influence recruit mortality and may also opportunistically prey on recently settled fishes (Carr et al. 2002, Almany 2003). We then removed all recently settled fishes and followed recruitment and subsequent persistence by censusing each reef every one (Bahamas) or two (Australia) days.

During each census, new recruits (fishes that settled since the previous census) were noted and distinguished from previously recruited fishes by size, coloration, behavior, and location. While the patch reefs we studied may represent suitable habitat for scores of species, the number of species we censused was limited to those that settled during our experiment, and were sufficiently conspicuous to census reliably. These included species from the following families: Acanthuridae (surgeonfish), Chaetodontidae (butterflyfish), Labridae (wrasse), Pomacentridae (damselfish), Pomacanthidae (angelfish), and Siganidae (rabbitfish). We did not attempt to measure recruitment of species that are typically cryptic and/or secretive (e.g., gobies and blennies) to ensure that our measure of recruitment was as accurate as possible for each species. Thus, our measures of recruitment and the effects of predators necessarily include only a subset of the families and species found naturally on these experimental reefs. We continued to measure recruitment (the sum of all new recruits) and persistence for 50 d in Australia and 44 d in the Bahamas, at which time we measured the final abundance of remaining fishes that had recruited during each experiment.

Rarefaction analyses

We calculated rarefaction curves to examine whether predators directionally changed the composition of fish communities (Gotelli and Entsminger 2001). Our null model approach asked whether communities subject to

FIG. 2. Effect of resident predators on the recruitment of prey species. Frequency histograms of cumulative recruitment (average per reef + 1 SE) in (A) Australia and (B) the Bahamas to reefs without resident predators (open bars) and with resident predators (filled bars) differed substantially, primarily due to the absence of numerous rare species on reefs with predators. Species are arranged with the most common recruits observed on reefs without predators on the left, and the most rare on the right, and asterisks indicate species present on reefs without resident predators, but absent from reefs with predators. For species identities, see the Appendix. Sample-based rarefaction curves of cumulative recruitment in both (C) Australia and (D) the Bahamas show that observed values of species richness on reefs with resident predators (open circles) were well below that predicted by random removal of samples from reefs without resident predators (filled circles). Error bars for rarefaction curves represent 95% confidence limits.



intense predation experienced species loss that was greater than, equal to, or lower than expected based on simulated random loss in control communities with experimentally reduced predation. We focused on how resident predators affected both recruitment and final abundance of prey fishes. To measure effects on recruitment, we compared the composition of prey fishes that recruited during the experiment on reefs with (treatment) and without (control) resident predators. To measure effects on final abundance, we compared the composition of prey fishes at the end of the experiment on reefs with (treatment) and without (control) resident predators. We utilized sample-based rarefaction for determining whether predation was random with respect to species or disproportionate on either rare or common species (Gotelli and Colwell 2001). Sample-based rarefaction curves were calculated by randomly removing samples (i.e., reefs) from the data sets for each treatment to calculate predicted richness for a given sample size. Per-sample predictions were then rescaled to the average number of individuals for a given sample size. Because the number of individuals included can vary for a given sample size, point predictions from rescaled sample-based rarefaction curves include variability in both the number of individuals and predicted richness. We calculated 95% confidence intervals for both abundance and predicted species richness for each sample size directly from the frequency distributions of 1000 rarefaction iterations.

RESULTS

We censused new recruits from a total of 20 species in Australia and 15 in the Bahamas (Appendix). While the individuals we designated "*Acanthurus* sp." from

Australia were likely a single species, we could not identify which species with certainty. *Siganus* sp. on reefs in Australia included two species that were difficult to distinguish at recruitment (*S. doliatus* and *S. corallinus*), but visually distinct later.

Our results focus on the effects of predators on recruitment, defined as the number of newly settled fishes observed on reefs during censuses every 1–2 d, and the final abundance of these fishes after 44–50 d of cumulative recruitment. Predators had a greater effect on rare species at recruitment. In both Australia (Fig. 2A) and the Bahamas (Fig. 2B), numerous species that recruited to reefs without predators were absent from reefs with predators. Reefs with predators tended to have lower recruit species richness than predicted based on the random removal of samples (Australia, Fig. 2C; Bahamas, Fig. 2D). The disproportionate absence of many rare species on predator-occupied reefs indicates that predators had rapid, highly nonrandom effects on diversity at recruitment in both Australia and the Bahamas. Differences in species richness between treatments that were established at the time of recruitment were no longer present after 50 d in Australia (Fig. 3A, C), but were still present after 44 d in the Bahamas (Fig. 3B, D).

DISCUSSION

Among the group of conspicuous prey species we censused, we observed greater effects of predators on the recruitment of relatively rare species, resulting in species richness well below that predicted by random predation null models. Because we could not accurately census cryptic prey species, we were unable to determine if disproportionate predator impacts on rare spe-

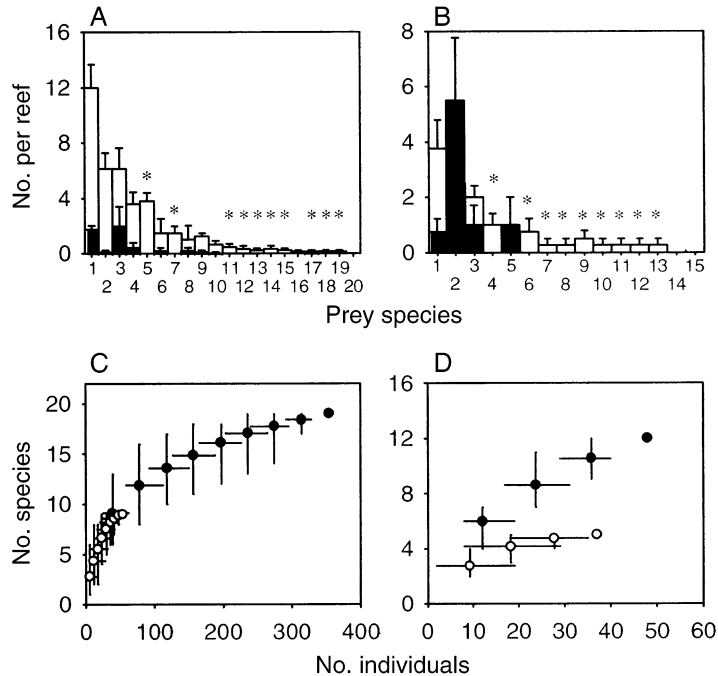


FIG. 3. Effect of resident predators on the final abundance of prey species. Frequency histograms show final abundance (average per reef + 1 SE) of each species in (A) Australia and (B) the Bahamas to reefs without resident predators (open bars) and with resident predators (filled bars). Species are arranged with the most common recruits observed on reefs without predators on the left, and the most rare on the right, and asterisks indicate species present on reefs without resident predators, but absent from reefs with predators. For species identities, see the Appendix. Sample-based rarefaction curves of final abundance show that in (C) Australia, species richness on reefs with resident predators (open circles) was comparable to that predicted by random removal of samples from reefs without resident predators (filled circles). In contrast, in (D) the Bahamas, observed values of species richness on reefs with resident predators (open circles) were well below that predicted by random removal of samples from reefs without resident predators (filled circles). Error bars for rarefaction curves represent 95% confidence limits.

cies occurred for all species that naturally settled to experimental reefs. Nonetheless, the remarkable similarity in the response of censused prey species in Australia and the Bahamas suggests that elevated impacts of predators on rare species may be a widespread phenomenon in reef fish communities.

To implicate predators as the cause of these patterns requires the assumption that the pool of larval settlers (both abundance and species composition) arriving at reefs in both treatments was similar. We argue that larval settlement was likely to be similar across reefs because of the close proximity of experimental reefs relative to the dispersal capabilities of larvae, which likely insured that all reefs were exposed to a similar water mass and thus a similar pool of larvae. Furthermore, random interspersing of treatments within each array would greatly reduce the possibility of any spatial bias in settlement. However, our experimental design does not allow for conclusions about what type of interaction (e.g., direct vs. indirect) led to greater effects on rare species. For example, predators could have had indirect effects on settlement, perhaps because settlement-stage larvae can detect, and actively avoid, reefs with predators. However, a recent study using the same reef array in the Bahamas that tested whether settlement differed among reefs with and without caged predators (i.e., predators that could be detected by settling larvae, but could not directly consume newly settled fishes) found no evidence for differential settlement, indicating that differences between reefs with and without predators likely stem from direct interactions between predators and prey during or following settlement (Almany 2003). Such interactions could result in either direct consumption of

prey or the movement of prey elsewhere. Presettlement movement remains a possible explanation for the recruitment effects in this study because diurnally released settlement-stage larvae have been observed to occasionally re-enter the pelagic environment following interactions with predators on reefs (Leis and McCormick 2002). However, once settled, there is little evidence that recruits reenter pelagic environments (Kaufman et al. 1992, Holbrook and Schmitt 1997). By the end of our experiments, disproportionate effects on rare species were no longer evident in Australia, while they remained in the Bahamas, indicating that post-recruitment interactions may or may not obscure patterns established at recruitment.

If the patterns we observed at recruitment were the result of consumption by predators, why would predators disproportionately prey on rare species? We propose two general mechanisms that may underlie this phenomenon. First, rarity could have covaried with some other factor(s) that increased susceptibility of rare species to predators (e.g., size, behavior, or escape ability). An intriguing possibility is that rare species on experimental reefs were common in other habitats and experimental reefs provided those species with only marginal, high-risk habitat, such that predation on rare species would tend to reinforce species-habitat associations. Second, predators may be more efficient when they attack less-common prey; focusing on rare species may allow predators to more easily pursue and capture a particular individual within a crowd. This hypothesis represents a community-level manifestation of the "oddity effect" in which predators actively select uncommon individuals

that differ in some way from common prey (Mueller 1975, Landeau and Terborgh 1986).

This study highlights an unexpected and largely unexplored ecological interaction whereby predators can shape local patterns of diversity. Predator-induced directional changes in diversity and community composition were evident during an exceptionally narrow window of time during and immediately following settlement. Our results raise the question of whether similar interactions occur in other high-diversity communities, and point to future studies aimed at determining whether and how small-scale predator/prey interactions influence ecosystem-level patterns of species composition.

ACKNOWLEDGMENTS

We thank Mark Hixon and Geoff Jones for the use of their experimental reef arrays in the Bahamas and Australia. Sean Connolly, Kealoha Freidenburg, Tess Freidenburg, Nicholas Gotelli, Bruce Menge, Philip Munday, Karen Overholtzer, Eric Sanford, David Skelly, and two anonymous reviewers provided helpful comments and suggestions on this manuscript. Financial support was provided by NSF Pre-Doctoral Fellowships, PADI Project AWARE, Sigma Xi, NSF International Research Fellowship Program, Fulbright Scholar Program, NSF grants (OCE-96-17483 and OCE-00-93976) and NURP-NOAA grants (CMRC-95-3042 and 97-3109) to M. Hixon, and by the David and Lucile Packard Foundation through PISCO (The Partnership for Interdisciplinary Studies of Coastal Oceans).

LITERATURE CITED

- Almany, G. R. 2003. Priority effects in coral reef fish communities. *Ecology* **84**:1920–1935.
- Birkeland, C., and S. Neudecker. 1981. Foraging behavior of two Caribbean chaetodontids: *Chaetodon capistratus* and *C. aculeatus*. *Copeia* 1981:169–178.
- Carr, M. H., T. W. Anderson, and M. A. Hixon. 2002. Biodiversity, population regulation, and the stability of coral-reef fish communities. *Proceedings of the National Academy of Sciences (USA)* **99**:11241–11245.
- Estes, J. A., and J. F. Palmisano. 1974. Sea otters: their role in structuring nearshore communities. *Science* **185**:822–833.
- Gotelli, N. J., and R. K. Colwell. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters* **4**:379–391.
- Gotelli, N. J., and G. L. Entsminger. 2001. EcoSim: null models software for ecology. Version 7.58. Acquired Intelligence, Inc. and Kesey-Bear, Burlington, Vermont, USA.
- Hargreaves, N. B., and R. J. Lebrasseur. 1985. Species selective predation on juvenile pink (*Oncorhynchus gorbuscha*) and chum salmon (*O. keta*) by coho salmon (*O. kisutch*). *Canadian Journal of Fisheries and Aquatic Sciences* **42**:659–668.
- Hixon, M. A. 1986. Fish predation and local prey diversity. Pages 235–257 in C. A. Simenstad and G. M. Cailliet, editors. *Contemporary studies on fish feeding*. Junk, Dordrecht, The Netherlands.
- Hixon, M. A. 1991. Predation as a process structuring coral reef fish communities. Pages 475–508 in P. F. Sale, editor. *The ecology of fishes on coral reefs*. Academic Press, San Diego, California, USA.
- Hixon, M. A., and M. S. Webster. 2002. Density dependence in reef fish populations. Pages 303–325 in P. F. Sale, editor. *Coral reef fishes: dynamics and diversity in a complex ecosystem*. Academic Press, San Diego, California, USA.
- Holbrook, S. J., and R. J. Schmitt. 1997. Settlement patterns and process in a coral reef damselfish: in situ nocturnal observations using infrared video. Pages 1143–1148 in H. Lessios and I. G. Macintyre, editors. *Proceedings of the Eighth International Coral Reef Symposium, Panama*. Volume 2. Smithsonian Tropical Research Institute, Balboa, Republic of Panama.
- Hughes, T. P., et al. 2003. Climate change, human impacts, and the resilience of coral reefs. *Science* **301**:929–933.
- Jones, G. P. 1991. Postrecruitment processes in the ecology of coral reef fish populations: a multifactorial perspective. Pages 294–328 in P. F. Sale, editor. *The ecology of fishes on coral reefs*. Academic Press, San Diego, California, USA.
- Kaufman, L., J. Ebersole, J. Beets, and C. C. McIvor. 1992. A key phase in the recruitment dynamics of coral reef fishes: post-settlement transition. *Environmental Biology of Fishes* **34**:109–118.
- Landeau, L., and J. Terborgh. 1986. Oddity and the “confusion effect” in predation. *Animal Behaviour* **34**:1372–1380.
- Leis, J. M., and M. I. McCormick. 2002. The biology, behavior and ecology of the pelagic, larval stage of coral reef fishes. Pages 171–199 in P. F. Sale, editor. *Coral reef fishes: dynamics and diversity in a complex ecosystem*. Academic Press, San Diego, California, USA.
- Mueller, H. C. 1975. Hawks select odd prey. *Science* **188**:953–954.
- Murdoch, W. W., and A. Oaten. 1975. Predation and population stability. *Advances in Ecological Research* **9**:1–132.
- Osenberg, C. W., C. M. S. Mary, R. J. Schmitt, S. J. Holbrook, P. Chesson, and B. Byrne. 2002. Rethinking ecological inference: density dependence in reef fishes. *Ecology Letters* **5**:715–721.
- Paine, R. T. 1966. Food web complexity and species diversity. *American Naturalist* **100**:65–75.
- Paulay, G. 1997. Diversity and distribution of reef organisms. Pages 298–353 in C. Birkeland, editor. *Life and death of coral reefs*. Chapman and Hall, New York, New York, USA.
- Power, M. E., D. Tilman, J. A. Estes, B. A. Menge, W. J. Bond, L. S. Mills, G. Daily, J. C. Castilla, J. Lubchenco, and R. T. Paine. 1996. Challenges in the quest for keystones. *BioScience* **46**:609–620.
- Purvis, A., and A. Hector. 2000. Getting the measure of biodiversity. *Nature* **405**:212–219.
- Spiller, D. A., and T. W. Schoener. 1998. Lizards reduce spider species richness by excluding rare species. *Ecology* **79**:503–516.
- Webster, M. S. 2002. Role of predators in the early post-settlement demography of coral-reef fishes. *Oecologia* **131**:52–60.
- Wilkinson, C., editor. 2002. *Status of coral reefs of the world: 2002*. Australian Institute of Marine Science, Townsville, Australia.
- Williams, L. R., C. M. Taylor, and M. L. J. Warren. 2003. Influence of fish predation on assemblage structure of macroinvertebrates in an intermittent stream. *Transactions of the American Fisheries Society* **132**:120–130.

APPENDIX

A table of rank abundances of prey species that recruited to experimental reefs in Australia and the Bahamas is presented in ESA's Electronic Data Archive: *Ecological Archives* E085-094-A1.