The Abdus Salam
International Centre for Theoretical Physics

United Nations
Educational, Scientific and
Cultural Organization

IAEA
International Atomic Energy Agency

2022-22

Workshop on Theoretical Ecology and Global Change

2 - 18 March 2009

Predator-Prey Role Reversal in a Marine Benthic Ecosystem

HERNANDEZ DE RODRIGUEZ Maria Josefina
Universidad Central de Venezuela
Instituto de Zoologia Tropical
Facultad de Ciencias, Apartado 47058, 1041-A
Caracas
VENEZUELA

Predator-Prey Role Reversal in a Marine Benthic Ecosystem

Amos Barkai; Christopher McQuaid

Science, New Series, Vol. 242, No. 4875 (Oct. 7, 1988), 62-64.

Stable URL:
http://links.jstor.org/sici?sici=0036-8075%2819881007%293%3A242%3A4875%3C62%3APRRIAM%3E2.0.CO%3B2-P

Science is currently published by American Association for the Advancement of Science.

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at http://www.jstor.org/about/terms.html. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at http://www.jstor.org/journals/aaas.html.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is an independent not-for-profit organization dedicated to creating and preserving a digital archive of scholarly journals. For more information regarding JSTOR, please contact support@jstor.org.

http://www.jstor.org/
Mon Feb 21 06:18:51 2005

Reports

Predator-Prey Role Reversal in a Marine Benthic Ecosystem

Amos Barkai and Christopher McQuaid*

Two closely located islands on the west coast of South Africa support widely different benthic communities. The biota at Malgas Island is dominated by seaweeds and by rock lobsters that consume settling mussels, thereby preventing the establishment of the mussels. They also prey on whelks, although one species, *Burnupena papyracea*, is protected from predation by a commensal bryozoan that covers its shell. Marcus Island has extensive mussel beds, but rock lobsters and seaweeds are virtually absent; whelks (mostly *Burnupena* spp.) occur at high densities. Rock lobsters transferred to Marcus Island were overwhelmed and consumed by the whelks, reversing the normal predator-prey relation between the two species. These two contrasting communities persisted during 4 years and may represent multiple states of the same ecosystem. This effective change of roles between a prey species and its chief predator may provide an intrinsic mechanism to maintain these states following the initial exclusion of the predator.

Perhaps the most conspicuous feature of shallow subtidal communities on hard substrata is the high degree of spatial variability of both species composition and standing stocks (*1*). One of the most extensively studied and important causes of spatial variability is the localized effect of predation, including grazing (*2*), and several cases have been described of "keystone predators" that maintain a balance within the overall community between their preferred prey and species that are competitively dominated by these prey species (*3*). Removal or exclusion of such species often changes the community structure drastically and may result in the development of an "alternative stable state" (*4*). Evidence for the occurrence of alternative stable states in natural populations has been criticized—for example, external interference such as predator removal is required to maintain them (*5*). We do not address the question of whether or not "alternative stable states" are a real phenomenon. We do, however, describe a case in which some perturbation appears to have removed a key benthic predator, causing the community to shift to a totally different configuration; this new configuration appears to include an intrinsic mechanism for continued exclusion of the key predator without external interference.

Marcus and Malgas islands are 4 km apart in the Saldanha Bay area of South Africa (17°58′E; 33°02′S). Apart from normal patchiness, the shallow benthos of the two islands is radically different in the trophic levels that dominate biomass and, consequently, in the predicted patterns of energy flow (*6*).

Both islands lie within a rock lobster reserve and experience similar conditions of water temperature, turbidity, and nutrient availability. However, rock lobsters are abundant at Malgas Island and conspicuously absent from Marcus Island (*6*). Benthic communities at Marcus Island are dominated by extensive beds of black mussels (*Choromytilus meridionalis*) as well as large populations of holothurians, sea urchins, and especially whelks, mostly *Burnupena* spp. In contrast, communities near Malgas Island are dominated by extremely high densities of rock lobsters, which form approximately 70% of the total benthic biomass, whereas most of its normal prey species are absent (*6*). Total whelk density at Malgas Island is much lower than at Marcus Island and only two species of whelks occur there: *Burnupena papyracea*, which has larger mean shell length than *B. papyracea* at Marcus Island (*7*), and *Argobuccinum pustulosum* (Table 1).

We examined two major questions: How do two species of whelks survive rock lobster predation at Malgas Island? Why do rock lobsters not recolonize Marcus Island despite the high availability of food?

Whelk survival at Malgas Island. Twelve rock lobsters were maintained in individual aquaria and fed on whelks (*Argobuccinum pustulosum* and *Burnupena* spp.). The rock lobsters usually attacked the whelks by chipping away the shell margin with their mouthparts. This method of feeding results in larger whelks, which have a thicker shell

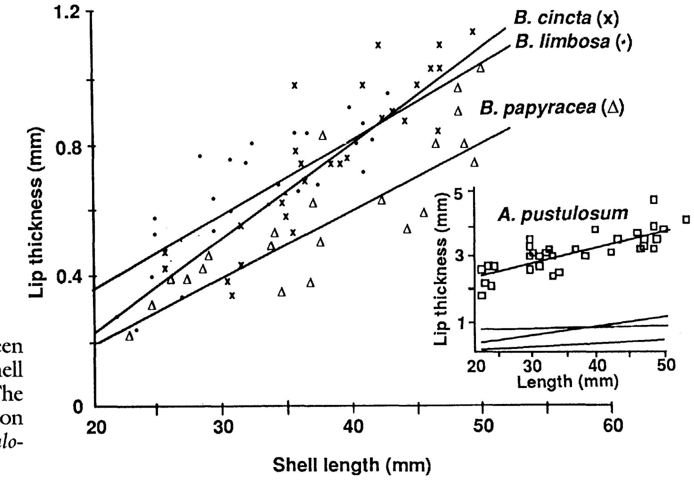

Fig. 1. The relation between shell lip thickness and shell length in *Burnupena* spp. The inset shows a comparison with *Argobuccinum pustulosum*.

Table 1. Mean density (and standard error) of whelk species (per square meter) at Marcus and Malgas islands.

Species	Marcus		Malgas	
	n	SE	*n*	SE
Argobuccinum pustulosum	12	6.1	40	8.5
Burnupena papyracea	141	4.1	14	4.7
Burnupena cincta	77	3.1	0	0.0
Burnupena limbosa	59	7.7	0	0.0
Total	289		54	

Marine Biology Research Institute, Zoology Department, Rondebosch 7700, University of Cape Town, Cape Town, South Africa.

---

*Present address: Department of Zoology and Entomology, Rhodes University, Grahamstown 6140, South Africa.

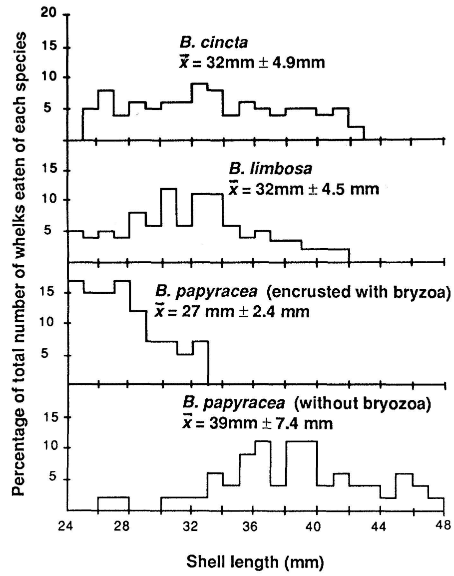

Fig. 2. Size distribution of *Burnupena* spp. eaten by rock lobsters during laboratory experiments.

lip that is less susceptible to predation. *Argobuccinum pustulosum* of all sizes were completely immune to predation because of their much thicker shells, and of the *Burnupena* spp. only individuals of less than 53 mm were eaten (Fig. 1). Subsequently, each rock lobster was offered three *Burnupena limbosa* and three *B. papyracea* of 25 to 50 mm; consumed whelks were replaced daily. The experiment was terminated after 10 days and repeated with *B. papyracea* and *B. cincta*. In each experiment *B. papyracea* was the less preferred prey (*8*). In addition, consumed *B. papyracea* were smaller than those of either *B. cincta* or *B. limbosa* (Fig. 2) (*9*).

Since the shell of *B. papyracea* is invariably covered by the commensal bryozoan *Alcyonidium nodosum* the feeding preference experiment was repeated for 31 days. This time each rock lobster was offered three normal *B. papyracea*, three from which the bryozoan covering had been removed, and three *B. cincta* (*10*). From a total of 242 whelks consumed, only 6.2% were uncleaned *B. papyracea* (*11*). There was, however, no statistically significant difference between the numbers of *B. cincta* and cleaned *B. papyracea* eaten (50.8% and 43.0%, respectively) (*12*). Maximum and mean size of *B. papyracea* eaten increased when the shells were cleaned (Fig. 2) (*13*) although the latter was still far below the mean size of *B. papyracea* at Malgas Island (*7*). The commensal bryozoans presumably reduce predation on *B. papyracea* by producing metabolites (*14*) that render whelks unpalatable to rock lobsters. Although this defense is not completely effective, the size of whelks taken is decreased. Thus, the species can survive at Malgas Island under a regime of intense predation that excludes all other members of its genus (Table 1).

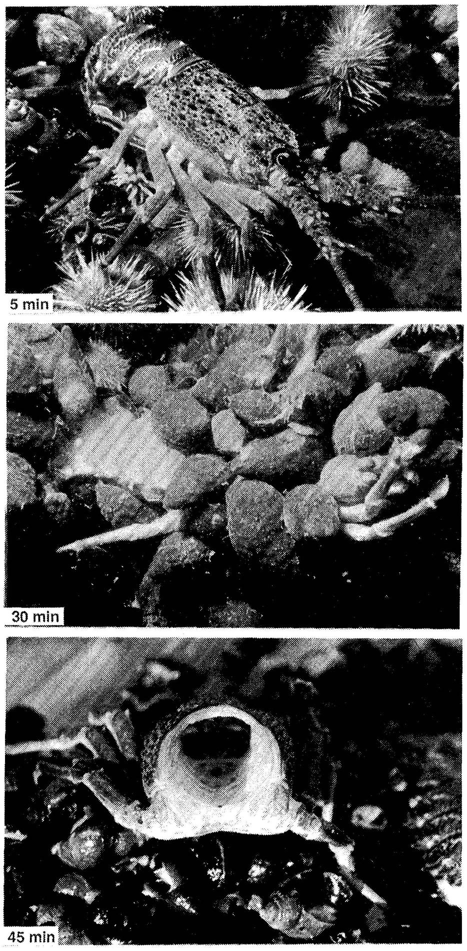

Fig. 3. Predation by *Burnupena* whelks of rock lobsters that were released at Marcus Island. Figures on plates give time after release.

Rock lobster exclusion from Marcus Island. The ability of *Jasus lalandii* to tolerate abiotic conditions at Marcus Island was examined by caging eight individuals at 10 m depth with eight control animals caged at Malgas Island. All caged animals at both islands survived until released more than 9 months later.

Subsequently 1000 rock lobsters from Malgas Island were tagged and transferred to Marcus Island after installing artificial shelters to provide suitable habitats (*15*). The result was immediate. The apparently healthy rock lobsters were quickly overwhelmed by large numbers of whelks. Several hundreds were observed being attacked immediately after release and a week later no live rock lobsters could be found at Marcus Island. As damage during tagging may have triggered the attacks the experiment was repeated five times with smaller numbers (~20) of unmarked rock lobsters. Pairs of animals were recovered at 15-minute intervals after release and the attached whelks were counted. The rock lobsters escaped temporarily by swimming, but each contact with the substratum resulted in several more whelks attaching themselves until weight of numbers prevented escape. On average each rock lobster was killed within 15 minutes by more than 300 *Burnupena* that removed all the flesh in less than an hour (Fig. 3).

Local rock lobster fishermen claim that *Jasus lalandii* populations at the two islands were similar until about 20 years ago. The original cause of their disappearance from Marcus Island is not known but may have been linked to a period of low oxygen near the island in the early 1970s (*16*). Physical conditions are now suitable for rock lobsters; the caged animals survived well. Predator removal often leads to a rapid increase in prey numbers (*17*), which is sometimes followed by a crash as the prey eliminate their own food resources (*18*). Mussels and whelks occur intertidally, providing them with a refuge from rock lobster predation. In the case of *B. papyracea*, the bryozoan *Alcyonidium nodosum* provides a further ref-

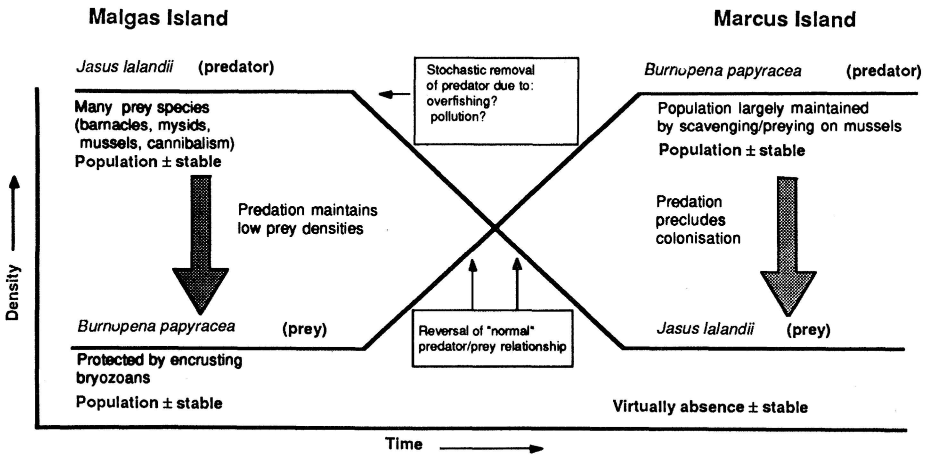

Fig. 4. Schematic summary of rock lobster and whelk predator-prey role reversal at Marcus and Malgas islands. Populations monitored have been stable for more than 4 years.

uge for subtidal populations, allowing the whelk to expand on the removal of predation pressure. In situ caging experiments indicate that *Burnupena* spp. cannot attack healthy mussels although they feed readily on damaged or dying mussels. Mussels in turn are filter-feeders that derive their food from the water column. The two populations are thus incapable of eliminating their own food source and can maintain high densities in the absence of their chief predator, the rock lobster. Thus *Burnupena* spp. can reverse their normal role as prey for rock lobsters and exclude the latter from Marcus Island (Fig. 4).

REFERENCES AND NOTES

1. W. P. Sousa, S. C. Schroeter, S. D. Gaines, *Oecologia* **48**, 297 (1981); J. H. Connell and M. J. Keough, in *Natural Disturbance: The Patch Dynamics Perspective*, S. T. A. Pickett and P. S. White, Eds. (Academic Press, New York, 1985), pp. 125–151; P. K. Dayton, *Ecol. Monogr.* **55**, 447 (1985); K. Hiscock, in *The Ecology of Rocky Coasts*, P. G. Moore and R. Seed, Eds. (Hodder & Stoughton, London, 1985), pp. 290–328.
2. P. A. Luckens, *N.Z. J. Mar. Fresh. Res.* **9** (no. 3), 379 (1975); S. D. Garrity and S. C. Levings, *Mar. Biol.* 72, 319 (1983); M. J. Tegner and A. Levin, *J. Exp. Mar. Biol. Ecol.* **73**, 1 (1983); P. K. Dayton *et al.*, *Ecol. Monogr.* **54**, 253 (1984); P. G. Fairweather, A. J. Underwood, M. J. Moran, *Mar. Ecol. Prog. Ser.* **17**, 143 (1984); A. J. Penny and C. L. Griffiths, *J. Exp. Mar. Biol. Ecol.* **75**, 19 (1984); R. N. Hughes, in *The Ecology of Rocky Coasts*, P. G. Moore and R. Seed, Eds. (Hodder & Stoughton, London, 1985), pp. 223–233; C. W. Thayer, *Science* **228**, 1526 (1985).
3. K. H. Mann and P. A. Breen, *J. Fish. Res. Board Can.* **29**, 603 (1972); C. A. Simenstad, J. A. Estes, K. W. Kenyon, *Science* **200**, 403 (1978); R. T. Paine, *Ecology* **49**, 667 (1980).
4. R. C. Lewontin, *Brookhaven Symp. Biol.* **22**, 13 (1969); J. P. Sutherland, *Am. Nat.* **108**, 859 (1974).
5. J. H. Connell and W. P. Sousa, *Am. Nat.* **121**, 789 (1983); *ibid.* **125**, 612 (1985).
6. A. Barkai, thesis, University of Cape Town, Cape Town, South Africa (1987); ——— and G. M. Branch, *S. Afr. J. Mar. Sci.*, in press.
7. t test; $P < 0.001$ (54 mm ± 6.9 mm at Malgas Island and 36 mm ± 7.5 mm at Marcus Island).
8. Chi-square test; $P < 0.001$ in both cases.
9. One-way ANOVA; $P < 0.05$.
10. It was not possible to perform a comparable experiment with *B. limbosa*, as the damaged shells of this species are difficult to distinguish from cleaned *B. papyracea* shells.
11. Significantly lower than 33% of the total; chi-square test; $P < 0.001$.
12. Chi-square test; $P > 0.05$.
13. Mean increased significantly, t test; $P < 0.001$.
14. S. M. Al-Ogily and E. W. Knight-Jones, *Nature* **265**, 728 (1977); J. S. Carle and C. Christophersen, *J. Am. Chem. Soc.* **102**, 5107 (1980).
15. These consisted of 2×0.5 ton, 1-m^3 concrete blocks with 200-cm diameter passages running through them.
16. G. G. Newman and D. E. Pollock, *S. Afr. J. Sci.* **69**, 27 (1973); N. D. Christie and A. Moldan, *Mar. Pollut. Bull.* **8** (no. 2), 41 (1977).
17. R. T. Paine, *Oecologia* **15**, 93 (1974).
18. N. G. Hairston, F. E. Smith, L. B. Slobodkin, *Am. Nat.* **94**, 421 (1960); G. Caughley, *Ecology* **51**, 53 (1970); D. R. Klein, in *Animal Populations in Relation to Their Food Resources*, A. Watson, Ed. (Blackwell, Oxford, 1970), pp. 25–46.

19. We thank G. M. Branch, R. Barkai, members of the Sea Fisheries Research Institute at Saldanha Bay, the Research Diving Unit of the University of Cape Town, and many friends and colleagues in the Zoology Department at the University of Cape Town, for assistance with this research.

2 March 1988; accepted 6 July 1988

Catastrophic Landslide Deposits in the Karakoram Himalaya

KENNETH HEWITT

In July 1986, three catastrophic landslides deposited about 20×10^6 cubic meters of debris on Bualtar Glacier in the Karakoram Himalaya. A sudden acceleration and superficial breakup of the glacier provided an opportunity to examine the fresh deposits in depth. Beneath a surface layer of large boulders, finer materials, mainly sand and silt, made up half of the total volume. The fine materials were formed during the rock avalanche from mostly intact, massive rock of the source zone. Velocity estimates suggest that this disaggregation occurred in less than 2 minutes. Coarse materials remained in bands of uniform lithology, but the fine materials had diffused throughout the landslides. A small amount of carbonate appears to have been calcined by frictional heating, presumably at the base of the initial sliding masses. These observations are relevant to understanding the mechanisms of catastrophic landslides. Other nearby rock avalanche deposits indicate that landslides are an important geomorphic process in the area and that they pose a continuing risk to human activity.

THREE LARGE ROCK AVALANCHES descended to the surface of Bualtar Glacier in the central Karakoram Himalaya between 29 and 31 July 1986 (*1*). Approximately 20×10^6 m^3 of debris were deposited on the ice (Fig. 1). The maximum descent of the first, most extensive landslide, Bualtar I, was 1490 m. It traveled 4.8 km horizontally and covered 4.1 km^2 of the ice (Fig. 2). Its debris remained fairly dry throughout. However, the second and third rock avalanches became saturated in the run-out zone, presumably from melted ice. Five months after the landslides, the glacier suddenly accelerated from measured flow rates of 0.6 to 0.8 m day^{-1} to more than 7.0 m day^{-1} in and below the debris-covered area. This surge carried the deposits 2 km down-valley between January and August 1987 (*2*) and broke the deposits up, which provided a rare opportunity to examine fresh rock avalanche deposits in complete sections.

The landslide sequence began midafternoon on 25 July with a large rockfall from just below where the three rock avalanches would originate. The timing of the rock avalanches is deduced from the occurrence of three major dustfall episodes, which were reported up to 25 km away, in the evening and night of 29, 30, and 31 July. The landslides were not observed in progress, nor found until a rainstorm cleared the air of their dust.

The source rocks, assigned to the Chalt Series of Cretaceous to Eocene age, are mainly schist and marble (*3*). Bedding planes, which dip at 50° or more and are subparallel to the slope, were the main surfaces of rupture and initial sliding. The breakout zone is also defined by major near-vertical joints. The landslides occurred during the melting of a larger than normal winter snowpack and during a period of heavy rainstorms. The regulation of meltwater supply by diurnal freeze-thaw cycles seems to have been the trigger for a sequence of failures on successive days and late in each day (*4*).

The actual movement of rock avalanches is rarely observed; therefore, aspects of their geometry that may indicate transport mechanisms are of special interest (Table 1). The geometry of Bualtar I places it in Hsu's "more mobile" class (*5*). Its average speed of descent to the glacier was approximately 62 m s^{-1}, and it had a velocity over the ice of at least 44 m s^{-1}. Its probable maximum velocity at impact with the glacier was 124 m s^{-1} more than 440 km hour^{-1}. Hence, the entire landslide was deposited in less than 100 s (*6*). Rock avalanche researchers have focused on mechanisms that can cause such mobility through reduced friction in the run-out zone. Some workers also emphasize conditions of initial sliding that promote rapid acceleration. The Bualtar deposits have a bearing on both questions.

The debris was spread over the glacier in

Snow and Ice Hydrology Project, Wilfrid Laurier University, Waterloo, Ontario, Canada N2L 3C5.