By experimentally manipulating the distribution and amount of habitat available for rocky-shore periwinkle snails, **Dr Patrick Doncaster** and his team are highlighting the consequences of the depletion and redistribution of an animal's resources of food and refuge shelter

Understanding the effects of habitat depletion

Habitat loss is a serious issue for any individual in terms of its ability to survive, forcing it to adapt quickly to a state of greater vulnerability as well as having adverse and unforeseen side-effects on the whole population. Indeed, habitat removal is one of the principal causes of species rarity and endangerment, and thus a major concern in the conservation of wildlife as well as a prime objective in the management of pest species. To tackle this growing and still relatively unexplored field of research, Patrick Doncaster's team is investigating responses by rocky-shore periwinkle snails to the depletion and redistribution of their resources of food and refuge shelter. Dr Doncaster elaborates:

"All living organisms exploit resources for survival and reproduction. Food resources provide the energy, and refuge resources the opportunity, to survive, grow and reproduce. It is a central tenet of ecology that the abundances of organisms are influenced by the supply of their resources – the users of a patchy world are themselves patchily distributed wherever they compete to exploit limiting resources. This process of competition combines with other processes such as predation and disease to determine the match between patterns of consumer abundance and patterns of resource-rich habitat.

"Where resources have become everywhere too thinly spread to support any exploitation by a population, extinction follows inevitably. Even these impoverished habitats can be rendered patchily habitable, however, by gathering the residue of resource into clumps to enable pockets of exploitation. This is an attractive idea for conservation management because the benefit arises without having to enrich the habitat overall. We have modelled the concept to explore its potential for applications across many scales of community structure. The next step is to test the model on natural systems."

The project is applying this concept to the slow moving – and thus easily examined – periwinkle snail *Melaraphe neritoides*, a marine gastropod that occupies the harsh tidal environment of the splash zone above mean high water. The tough conditions here of intermittent drought and heavy pounding by storm waves makes the rock-clinging periwinkle ideal for study. It must adapt rapidly to any change in the availability of holes and crevices, into which it packs in large numbers to weather scorching sun and battering storms. Refuges of holes, crevices and cracks are a limited resource for this species, and they present us with a microcosm and exemplar of the pressures that habitat depletion can impose on a species.

Dr Martin Skov is leading the fieldwork on the south coast of England. He says: "One of the advantages of working with periwinkles is that we can measure responses from large numbers of individuals that each move very little as adults – often no more than a few centimetres. This means we can fit many

This composite image reveals the typical habitat for the periwinkle snail which colonises the tidal splash zone of the upper rock wall, where the grey rock surface is blackened by biofilm experimental plots into one area and obtain good replication of our treatments of refuge density and dispersion."

The other key reason why the team are focusing on periwinkles is the global importance of their food supply, which is the biofilm that grows on rock surfaces as a mat of diatoms, cyanobacteria and other photosynthesising microbes. It has been postulated that rocky-shore biofilm is an important sequester of atmospheric carbon on a global scale, because it is so ubiquitous in the splash zone. Almost nothing is known, however, about the composition and photosynthetic physiology of the biofilm community or its responses to grazing by snails.

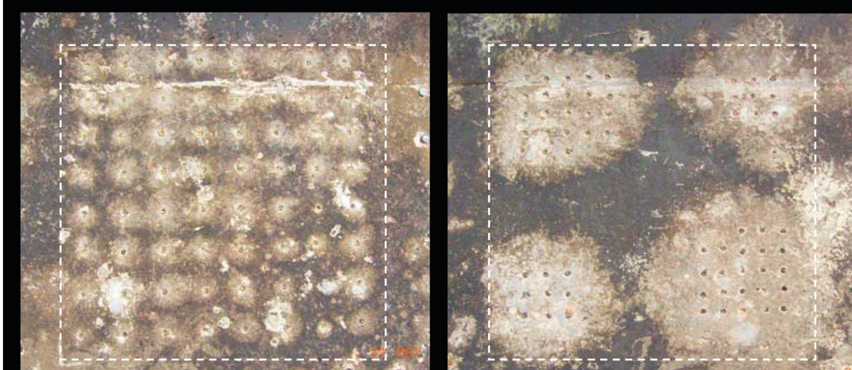
"Our field experimental manipulations are designed to redistribute refuges for snails as well as changing refuge density," explains Dr Doncaster. "By drilling new refuge holes in the bedrock in replicated designs we can interpret subsequent changes in the overall densities of periwinkles, and also in the distribution of their biofilm food, as responses to refuge availability. We expect that more holes will sustain more snails, but crucially also that a more patchy distribution of holes will sustain more snails."

The effects

The habitat treatments have produced intriguing responses in both the population sizes and the behaviours of the snails. Firstly, it was found that the periwinkles on a shore with generally low populations tended to achieve higher abundances in treatment plots where the holes were clumped together patchily than in plots with an even distribution of holes – as predicted by the project's models. In effect, more snails are attracted in to the refuge-rich patches than are lost from the intervening refuge-depleted areas. But this trend was conspicuously reversed on a much more densely populated shore, where a regular distribution of holes supported the highest abundances. In this heavily crowded environment, all available holes are occupied all of the time, and the biofilm can be grazed more efficiently around regularly spaced holes, thereby supporting more snails in each hole.

Secondly, the project found that snails occupying holes drilled into the rock would graze biofilm in a 'halo' all around each refuge. Constant grazing encouraged biofilm growth and prevented it from becoming shaded by encrusting dead cells. This gardening effect was so pronounced that the amount of living biofilm was measurably greater within halos than within the mat of unexploited biofilm away from holes. Except where holes were clumped together, the snails escaped overgrazing because limited numbers could pack into any one hole. Overexploitation is further averted by an innately inefficient method of raking up biofilm using a tongue armed with rows of sharp teeth. This 'radula' is common to all gastropod snails and its striping of the biofilm is easily visible in larger species such as limpets. The successive scrapes made by a grazing snail leave behind much of the microalgae to grow back over the scrape marks.

A periwinkle snail in its refuge surrounded by a 'halo' of grazed biofilm



Light-coloured halos in the darker biofilm produced by periwinkles grazing around 64 refuge holes drilled into ½ m^2 plots, in a regular pattern on the left and a patchy pattern on the right

What next?

The results of the project lead to vivid conclusions about the management of habitat for wildlife in general. Whereas the densest populations of periwinkles are achieved amongst evenly distributed resources, more vulnerable populations benefit from the resources being clumped into rich patches within the depleted habitat. Habitat loss threatens the persistence of many wildlife populations, and Dr Doncaster sees a clear need to understand its impacts on biodiversity. "As custodians of the world's natural resources, we must make informed decisions about how best to invest limited funds in sustaining wildlife populations. An ongoing debate amongst conservation managers concerns the relative merits of

Tracks made by a limpet grazing on bedrock. The parallel lines are 2mm long and each one is a scrape in the biofilm made by the toothed radula tongue possessed by all grazing gastropods

targeting a few biodiversity 'hotspots' where most difference can still be made, against spreading resources less partially across all ecosystems. Our work suggests that species close to extinction may benefit most from the former strategy of shifting resources out of doomed habitats into the still-saveable areas. In contrast, it is the highly abundant pest species that stand to gain most from an even spread."

Indeed, Dr Doncaster is keen to develop the work done on this project by further expanding its remit. "We would like to investigate the microalgal biofilm more fully, and the role of gastropod snails in carbon sequestration," he enthuses. "We have observed large inter-annual variations in biofilm production, which we think are regulated by weather events. For example, unseasonably warm periods in February 2008 caused a bleaching of the biofilm from which the biomass never fully recovered. Winter warming resulting from global climate change could therefore hinder carbon sequestering by microalgae. Any depletion of biofilm habitats will also have knock-on effects to the whole rocky-shore food web, since periwinkles and other gastropods are major grazers of rocky shores worldwide and important food sources to seabirds at low tide, and fish and crabs visiting on the tide. Further research on the rocky-shore biofilm will lead us to predictions about the effects of climate change on the ecological functioning of rocky shores." ★

Our field experimental manipulations are designed to redistribute refuges for snails as well as changing refuge density. By drilling new refuge holes in the bedrock in replicated designs we can interpret subsequent changes in the overall densities of periwinkles

At a glance

Full Project Title

Consumer responses to habitat depletion: food-refuge interactions in periwinkles

Project Partners

Dr Martin W. Skov
School of Biological Sciences
University of Southampton
Southampton
SO16 7PX

Dr Richard C. Thompson
Reader in Marine Ecology
School of Biological Sciences
University of Plymouth
Plymouth
PL4 8AA

Professor Stephen J. Hawkins
Head of College of Natural Sciences
Memorial Building
University of Bangor
Bangor, Gwynedd, LL57 2UW

Contact Details

Dr C. Patrick Doncaster,
Reader in Ecology,
School of Biological Sciences,
University of Southampton,
Boldrewood Campus,
Southampton SO16 7PX
T: +44 (0)23 8059 4352
F: +44 (0)23 8059 4459
E: cpd@soton.ac.uk
W: www.soton.ac.uk/~cpd/

Dr Patrick Doncaster

Project Coordinator

Patrick Doncaster has developed and tested theory to demonstrate population density triggers for the evolution of sexual from asexual reproduction, and non-senescing from senescing organisms. He has authored a textbook on experimental design, and is currently leading the development of mammalian wildlife corridors for Belize, funded by the UK Darwin Initiative.