Description of the rocky intertidal communities and Norway rat behavior on Rat Island, Alaska in 2003

Carolyn M. Kurle

Correspondence to: Carolyn Kurle
Ecology and Evolutionary Biology Department
Long Marine Laboratory
University of California
Santa Cruz, California 95060
Email: Kurle@biology.ucsc.edu
Phone: 831.459.4581
FAX: 831.459.3383

Introduction

The introduction of non-indigenous animal species is recognized as one of the primary components of global change and a leading threat to biodiversity (Vitousek et al. 1996, Chapin III et al. 2000). Recognizing, studying, and managing the threats caused by immigrant species is one of the leading fields of interest within conservation biology and its importance has been increasingly emphasized since it was first described by Elton in 1958 (Coblentz 1990, Soule 1990, Parker et al. 1999). Non-indigenous species (NIS) are also commonly referred to as exotic, alien, invasive, or introduced species and they can cause a biological invasion when they are transported to and proliferate and persist in a range previously not inhabited by that species (Elton 1958). The numbers of NIS have increased by orders of magnitude in the last 500 years with most expansion happening in the last 200 years. This significant increase in the invasion of NIS worldwide is directly related to expansion of human related transport (di Castri 1989) and the increasing dominance of humans over all of earth's ecosystems (Vitousek et al. 1997).

A common problem associated with NIS is their propensity to disrupt native ecosystems through habitat change, predation, and/or disease and this frequently leads to the severe reduction, extinction, or other alteration of native species. Species on oceanic islands are particularly vulnerable to invasion due to many factors (Vitousek 1988, Simberloff 2000). These include impoverishment (islands contain fewer species thus occupying fewer habitats leaving room for invaders to colonize), limited island size with few refuges (islands are smaller then continents and therefore provide less of a buffer if a species' habitat is disrupted or taken over by an invader), and lower genetic diversity which makes species more susceptible to introduced pathogens. In addition to islands being especially fragile and prone to devastation when invaded, they are also very important to the world's biodiversity because they harbor high numbers of endemic species and a disproportionate percentage of the earth's endangered and recently extinct species are from islands (Simberloff 2000). Therefore, it is crucial that effects of NIS on native island populations be at the forefront of ecological research so that conservation scientists can best determine how to manage and protect island species and ecosystems.

One of the most prevalent and devastating NIS are introduced rats (Atkinson 1985, Moors et al. 1989). They have invaded 82% of the world's major islands and island groups (Atkinson 1985) and evidence of their deleterious effects on island endemic vegetation, birds, and other animals is fairly extensive (Atkinson 1985, Moors et al. 1989, Gaston 1994, Bertram and Nagorsen 1995, Lovegrove 1996, Pickering and Norris 1996, Towns 1996, Brown et al. 1998, Robinet et al. 1998, Brook 1999, Innes et al. 1999, Pye et al. 1999, Martin et al. 2000, Taylor et al. 2000). The Aleutian Islands in Alaska are no exception and there are currently at least 17 major islands within the archipelago that contain introduced Norway rats (*Rattus norvegicus*) (Bailey 1993) from shipwrecks and military presence. It is known that rats negatively affect bird populations on the Aleutian Islands (Jones et al. 2001, Major and Jones 2002, 2005), but their wider affects on other communities are unknown. This report describes the rocky intertidal species present on Rat Island and is a small part of a larger study investigating the impacts of introduced rats on the rocky intertidal and marine bird community assemblages throughout the Aleutian Islands.

Several studies have focused on the effects of rats on island flora and fauna, with emphasis on the detriment their predation causes endemic nesting seabird populations, and a small number of studies have examined their specific effects on seabird abundance in the Aleutian Islands (Jones et al. 2001, Major and Jones 2002). There is also evidence that rats may forage directly on intertidal invertebrates. Studies from Chile (Navarrete and Castilla 1993) and England (Drummond 1960) indicate that rat predation on intertidal marine invertebrates occurs at measurable levels and may have an important structuring effect on intertidal communities. My work seeks to determine if there is evidence for direct rat predation on intertidal invertebrates in the Aleutian Islands. In addition, little is known about rat impacts beyond direct predation and my larger dissertation research addresses an alternative hypothesis for how rats may indirectly structure the rocky intertidal communities on the Aleutians.

Specifically, my research investigates whether rats introduced onto the Aleutian Islands have directly reduced marine bird populations through predation and thereby indirectly affected marine intertidal community structure through reduced predation by the marine birds. On an island without rats, marine birds such as Glaucous-winged gulls (*Larus glaucescens*) and Black Oystercatchers (*Haematopus bachmani*) breed without disruption and they forage largely on marine intertidal invertebrates (Irons et al. 1986, Andres and Falxa 1995). Their predation significantly reduces numbers of intertidal herbivores such as snails, sea urchins, and limpets (Wootton 1997). With fewer intertidal herbivores, there is decreased grazing on marine algae which creates extensive algal cover (Wootton 1992, 1995). My hypothesis is that the introduction of rats into this system causes a significant reduction in the number of gulls and oystercatchers which leads to an increase in numbers of intertidal invertebrates. The increase in herbivory by the invertebrates causes a subsequent reduction in the amount of fleshy algal cover thereby significantly altering the intertidal ecosystem. Surveys of intertidal species on islands with and without introduced rodent predators will help determine the extent to which rat presence affects intertidal habitat and community structure. Therefore, I am providing baseline survey data of intertidal species on islands with introduced rats for comparison with comparable surveys on islands without rats and for possible follow-up studies anticipated after proposed rat eradication in the future. In line with those goals, this report documents the intertidal communities on the north

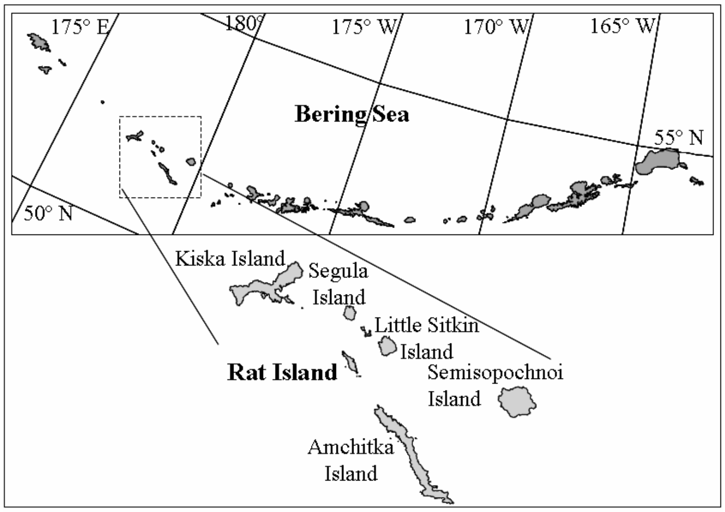

Figure 1. The Aleutian Islands, Alaska. The featured islands comprise the Rat Island Group in the western third of the Archipelago.

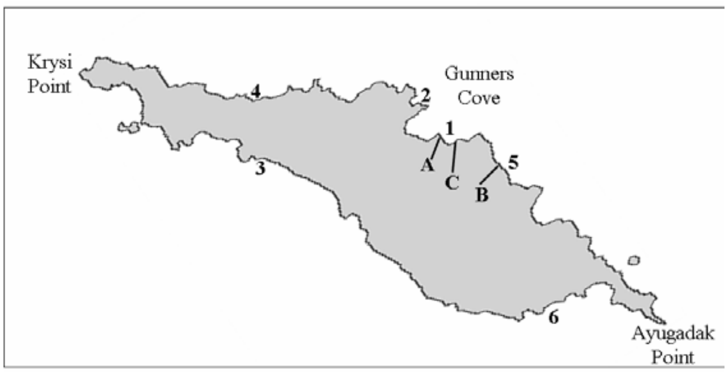

Figure 2. Rat Island, Alaska. The intertidal survey sites are indicated by the numbers 1-6 and the rat behavioral observation sites are indicated by the letters A-C.

and south sides of Rat Island, Alaska. In addition, I conducted behavioral surveys of rats at night and trapped and collected tissues from a number of rats and their possible prey items for stable carbon and nitrogen isotope analysis in an attempt to ascertain where and on what they were foraging. The isotope data and the full comparison of intertidal communities on islands with and without rats appears in upcoming publications.

Methods

Categorization of rocky intertidal species

Rat Island is located in the western Aleutian Archipelago (Figure 1). To comprehensively categorize the rocky interdial on Rat Island, we performed surveys at 6 areas around the island (Figure 2), with 4 sites located on the north side of the island and 2 on the south side. Surveys consisted of taking systematic photos of the rocky intertidal in the low zone (characterized by *Alaria* and *Laminaria* spp. of algae; corresponds to Zone 4 in Kozloff 1983), middle zone (characterized by *Fucus* and *Halosaccion* spp. of algae; corresponds to Zone 3 in Kozloff 1983),
and high zone (characterized by acorn barnacles and *Porphyra* sp. of algae; corresponds to Zone 2 in Kozloff 1983). Photos were taken every 5 meters for approximately 30 meters in each of the

zones described above and each photo captured an area 26.5 cm by 16.5 cm in size. One photo of each site was taken with full algal cover and a second photo was taken of the exact site with the overlying algae removed with a knife. This allowed for both an estimate of algal cover and estimates of percent cover and counts of species that would otherwise be hidden beneath the algal cover.

Digital photos were then analyzed using Adobe Photoshop 6.0. A grid was overlayed on each photo with grid line preferences set to 2.5 inches and species were counted if they were encompassed by a 6 by 9 rectangle made up of the grid lines. This rectangle translated into a photo area that was 26.5 x 16.5 cm or 437.25 square centimeters. Species were either counted as percent cover or estimated as number of individuals per square meter depending upon how the species covered an area. For example, sponges cover an area in such a way that it is impossible to count individuals, and so their percent cover was estimated. Percent cover species were assessed by counting items if they fell beneath a grid intersection and then dividing that number of intersections by the total number of intersections on a grid (54). To estimate actual numbers of species, I counted the occurrence of each individual within the 6 by 9 rectangle that portrayed 437.25 square centimeters of intertidal and then I estimated individual numbers per square meter. Species counted as percent cover were acorn barnacles, geniculate and encrusting coralline algae, sponges, tunicates, and all fleshy algal species. I only present species if they covered over 1% of area. Not all numbers from the percent cover estimates add to 100% because some areas contained rock, sand, or invertebrate species that were not counted as percent cover. Species counted as individuals per quadrat were anemones, chitons, herbivorous snails, isopods, limpets, mussels, sea cucumbers, sea stars, and sea urchins. Data were not sufficient to perform statistical analyses between the north and south sides of the island, but are presented as estimates of algal and other species percent cover and invertebrate counts per square meter.

Rat behavior and foraging ecology assessments

Rat behavior was observed at three sites on Rat Island using scan sampling with night vision binoculars for three consecutive nights of August 3, 4, and 5, 2003 (see Figure 2 for site locations). Beginning at dusk and ending at dawn, rats were observed every half hour, counted, and their behavior categorized. Scans took place in the center of the beach and were conducted for approximately 25 meters in all directions (i.e., towards the water into the intertidal, towards the berm, and in both directions along the center of the beach).

Fifteen to 20 snap traps were baited and set at 5-10 meter intervals on beaches along the terrestrial vegetation line for one trap night each at three locations (sites A, B, and C shown in Figure 2) on Rat Island. Rats were collected the following morning, sexed, and dissected to collect tissues appropriate for stable carbon and nitrogen isotope analyses. Appropriate prey items were also collected for isotopic comparison with rat tissues for estimation of rat foraging ecology. See Appendix I for a complete list of all tissues collected.

Results

Percent cover of fleshy algae

Photos of the algal cover in the intertidal before the algae were cut away allowed for estimates of the percent cover of fleshy algal species present in each of the three zones on the north and south sides of Rat Island. The low intertidal zones on the north and south sides were dominated by *Alaria* (42.9% and 22.2%, respectively) and *Laminaria* (56.8% and 22.2%, respectively) spp. of algae, with a trend towards a higher percentage of each species on the north side. Geniculate coralline algae were also present on the south side (3.9%). The middle intertidal

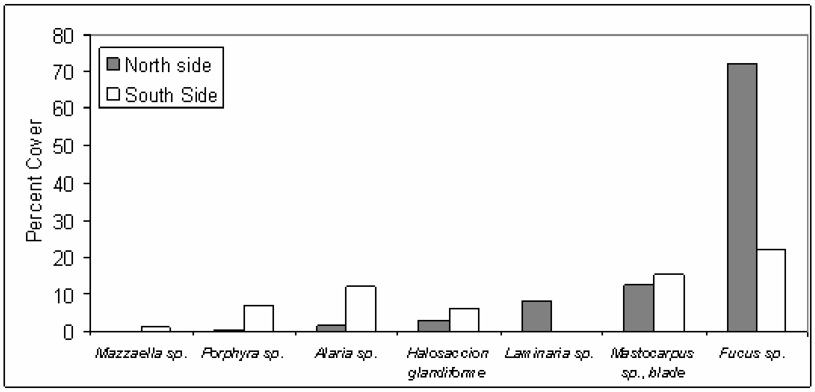

Figure 3a. Percent cover of algal species in the high zone of the rocky intertidal on the north and south sides of Rat Island. Numbers may not add to 100% due to the presence of rock, sand, or non-algal species.

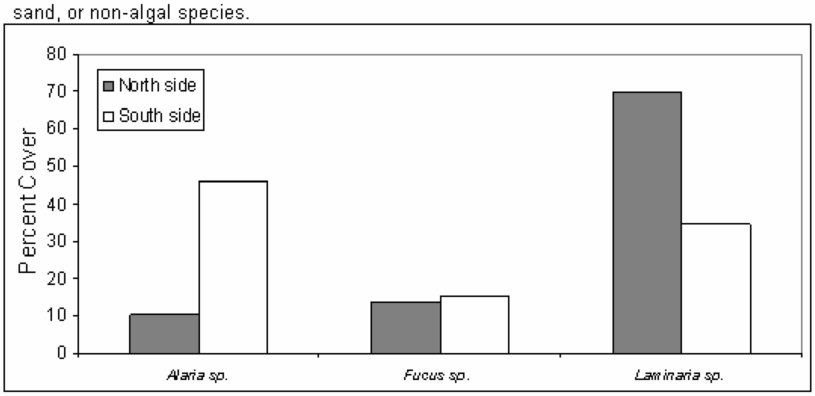

Figure 3b. Percent cover of algal species in the middle zone of the rocky intertidal on the north and south sides of Rat Island. Numbers may not add to 100% due to the presence of rock, sand, or non-algal species.

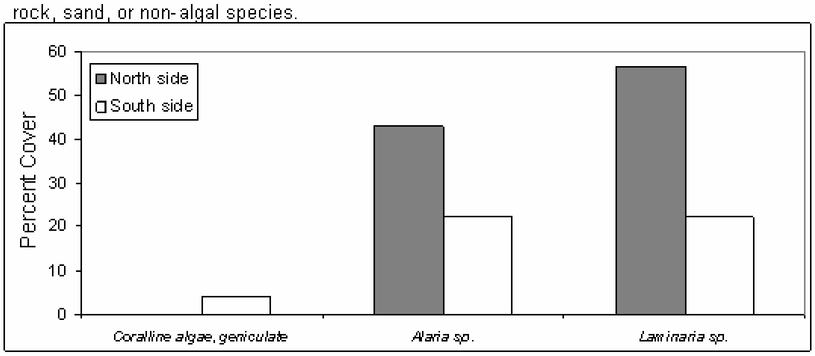

Figure 3c. Percent cover of algal species in the low zone of the rocky intertidal on the north and south sides of Rat Island. Numbers may not add to 100% due to the presence of rock, sand, or non-algal species.

zones on the north and south sides of Rat Island contained three primary algal species including *Alaria* sp. (10.3% and 45.8%, respectively), *Laminaria* sp. (69.5% and 34.4%, respectively), and *Fucus* sp. (13.9% and 15.2%, respectively). Finally, the high intertidal zones on the north and south sides of the island contained primarily *Fucus* sp. (72.3% and 22.2%, respectively), with several other species present in smaller quantities including *Mastocarpus* sp. in blade form (12.3% and 15.2 %, respectively), *Laminaria* sp. (8.3% on the north side), *Halosaccion glandiforme* (3.0% and 6.2%, respectively), *Alaria* sp. (1.3% and 12.2%, respectively), *Porphyra* sp. (.3% and 6.8%, respectively), and *Mazzaella* sp (1.2% on the south side) (Figures 3a – 3c).

Percent cover of invertebrates and coralline algae

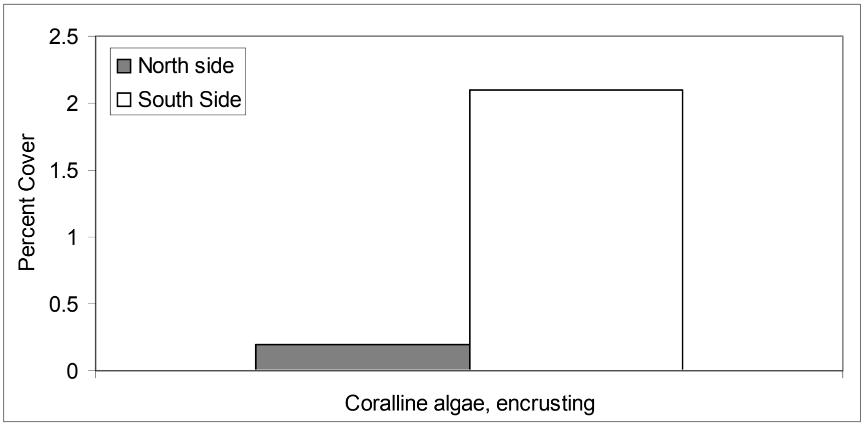

Figure 4a. Percent cover of non-fleshy algal species in the high zone of the rocky intertidal on the north and south sides of Rat Island following removal of fleshy algae. Numbers do not add to 100% due to the presence of rock, sand, and/or other species not counted as percent cover.

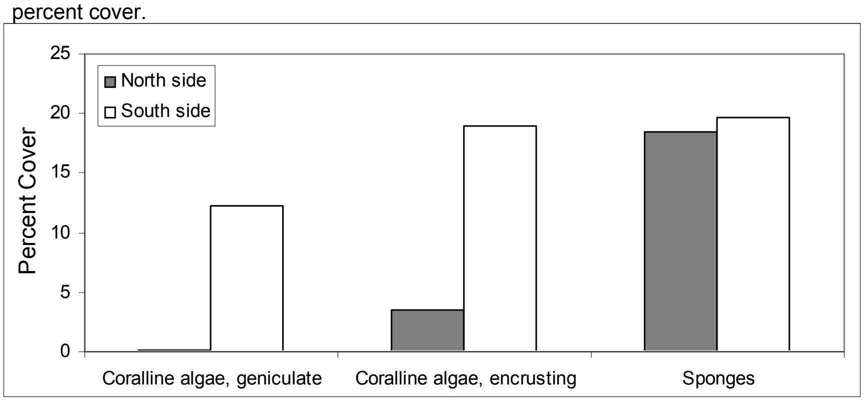

Figure 4b. Percent cover of non-fleshy algal species and invertebrates in the middle zone of the rocky intertidal on the north and south sides of Rat Island following removal of fleshy algae. Numbers do not add to 100% due to the presence of rock, sand, and/or other species not counted as percent cover.

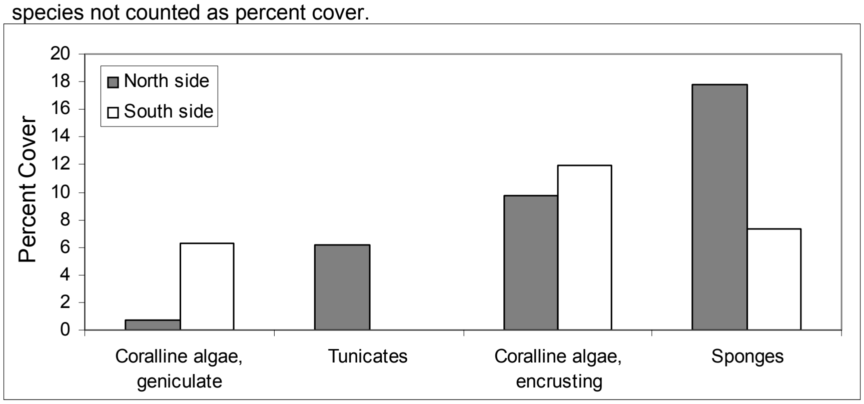

Figure 4c. Percent cover of non-fleshy algal species and invertebrates in the low zone of the rocky intertidal on the north and south sides of Rat Island following removal of fleshy algae. Numbers do not add to 100% due to the presence of rock, sand, and/or other species not counted as percent cover.

The percent cover of several invertebrate and coralline algae species were estimated after the overlying algae were removed with a knife. The low intertidal zones on the north and south sides of Rat Island contained several species of sponges (17.8% and 7.3%, respectively), encrusting coralline algae (9.7% and 11.9%, respectively), tunicates (6.2% on the north side), and geniculate coralline algae (0.7% and 6.3%, respectively). The middle intertidal zones on the north and south sides of the island showed similar species composition including sponges (18.4%and 19.7%, respectively), encrusting coralline algae (3.5% and 18.9%, respectively), and geniculate coralline algae (0.1% and 12.3%, respectively). Finally, the high intertidal zone on the north and south side contained very little in the way of cover with only encrusting coralline algae present (.2% and 2.1%, respectively) (Figures 4a – 4c).

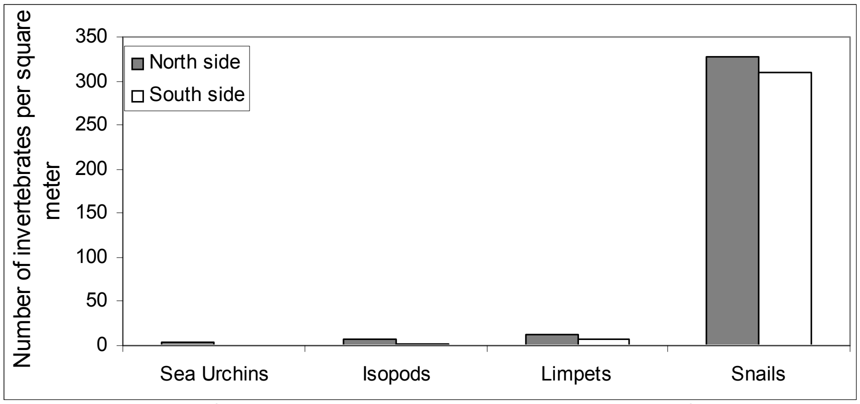

Figure 5a. Number of invertebrates per square meter in the high zone of the rocky intertidal on the north and south sides of Rat Island following removal of fleshy algae.

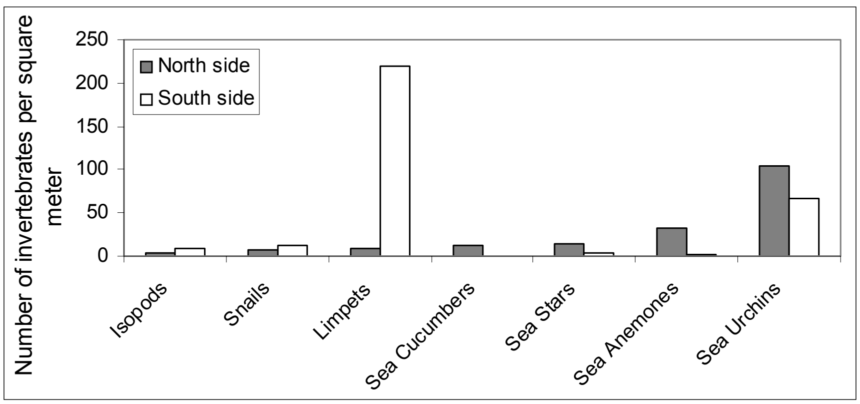

Figure 5b. Number of invertebrates per square meter in the middle zone of the rocky intertidal on the north and south sides of Rat Island following removal of fleshy algae.

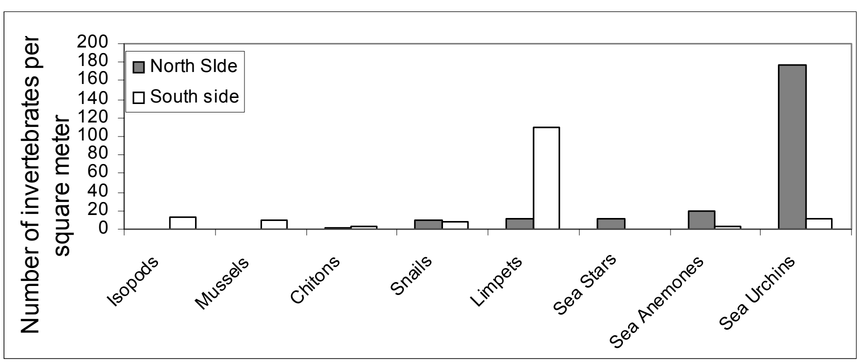

Figure 5c. Number of invertebrates per square meter in the low zone of the rocky intertidal on the north and south sides of Rat Island following removal of fleshy algae.

Counts of invertebrates per square meter

Invertebrates were counted and their numbers estimated per square meter (PSM). Several invertebrate types were present in the low intertidal zones on the north and south sides of Rat Island including sea urchins (*Strongylocentrotus polyacanthus*; 176.4 and 11.4 PSM, respectively), sea anemones (19.5 and 3.8 PSM, respectively), sea stars (11.0 PSM on the north side), limpets (11.0 and 110.6 PSM, respectively), herbivorous snails (10.5 and 7.6 PSM, respectively), chitons (2.2 and 3.8 PSM, respectively), mussels (0.8 and 9.5 PSM, respectively), and isopods (13.4 PSM on the south side). The middle intertidal zones on the north and south sides of the island contained sea urchins (*S. polyacanthus*; 105.0 and 67.2 PSM, respectively), sea anemones (33.0 and 1.4 PSM, respectively), sea stars (14.7 and 4.3 PSM, respectively), sea cucumbers (12.4 PSM on the north side), limpets (8.2 and 220.3 PSM, respectively), herbivorous snails (7.1 and 12.9 PSM, respectively), and isopods (2.9 and 8.6 PSM, respectively). The high intertidal zones on the north and south sides of Rat Island were dominated by herbivorous snails (327.2 and 309.3 PSM, respectively) and also held limpets (11.7 and 7.6 PSM, respectively), isopods (7.4 and 2.5 PSM, respectively), and sea urchins (*S. polyacanthus*; 2.9 PSM on the north side) (Figures 5a – 5c).

Norway rat behavior and foraging ecology

A total of 41 scans were conducted and 164 rats observed in all of the scans combined. The dominant behavior witnessed was rats foraging for amphipods in the dead algae sitting at the tide line on the beach (typically referred to as "beach wrack") and 57.3% of the rats were observed in this behavior during 51.2% of scans. Other behaviors included standing or running on the beach (10.4% of rats during 26.8% of scans), digging or foraging in or on the *Fucus* sp. (9.8% of rats during 19.5% of scans), and standing or running on the rocks near the *Fucus* sp. (4.9% of rats in 14.6% of scans) or through the *Fucus* sp. (3.0% of rats in 9.8% of scans). All observed behaviors can be seen in Table 1.

Stable carbon and nitrogen isotope analysis is being conducted to further estimate rat foraging ecology and a list of tissue samples taken for isotope analysis appears in Appendix I. The comprehensive analysis of the larger study examining 17 Aleutian Islands without rats and 15 with rats will be presented in a future publication and a list of the islands surveyed appears in Appendix II.

Table 1. Rat behavior observed at three sites on Rat Island using scan sampling with night vision binoculars for three nights. A total of 41 scans were conducted and 164 rats observed.

Rat Behavior	Percentage of rats observed in this behavior	Percentage of scans where a rat was observed in this behavior
Foraging on amphipods in beach wrack	57.3%	51.2%
Running or standing on beach	10.4%	26.8%
Foraging or digging in *Fucus* sp.	9.8%	19.5%
Foraging in the rocks on the beach	6.7%	4.9%
Running or standing on rocks in *Fucus* sp. zone	4.9%	14.6%
Running or standing on *Fucus* sp.	3.0%	9.8%
Standing or digging in the *Honkenya peploides*	1.8%	7.3%
Running through the beach wrack	1.8%	4.9%
Running through the river	1.8%	4.9%
Foraging or digging in the sand	1.2%	4.9%
Foraging or digging under log near the berm	1.2%	4.9%
No rats observed	NA	24.4%

Discussion

As mentioned previously, my survey of Rat Island is a small part of a larger project designed to investigate the effects of introduced rats on intertidal community compositions on the Aleutian Islands. Preliminary analyses of the larger study examining the differences in the rocky intertidal community assemblages indicate notable differences between islands with and without rats supporting my hypothesis outlined above. The pattern appears to be one of increased algal cover on islands without rats and increased numbers of invertebrates on islands with rats (see Figures 6-8). The numbers and types of species present in the rocky intertidal on Rat Island fit with this pattern. Rat Island had large numbers of sea urchins, herbivorous snails, and limpets along with a high percentage of area covered by sponges and encrusting coralline algae.

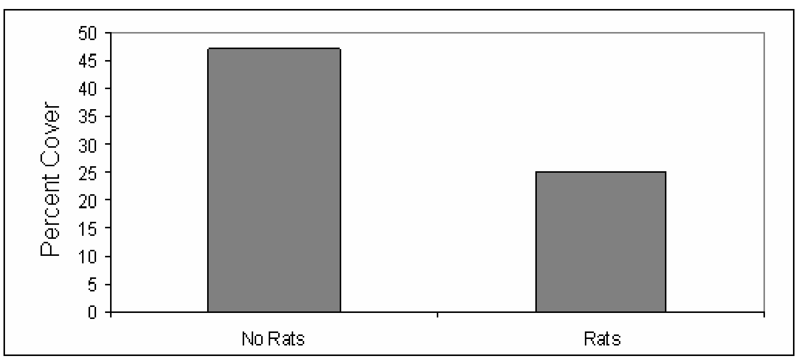

Figure 6. The percent cover of all fleshy algal species from all tidal heights from all Aleutian Islands surveyed with and without rats (n=15 and 17, respectively). There is significantly more algal cover on islands without rats ($t = 8.74$, $df = 360$, $P = 0.00$).

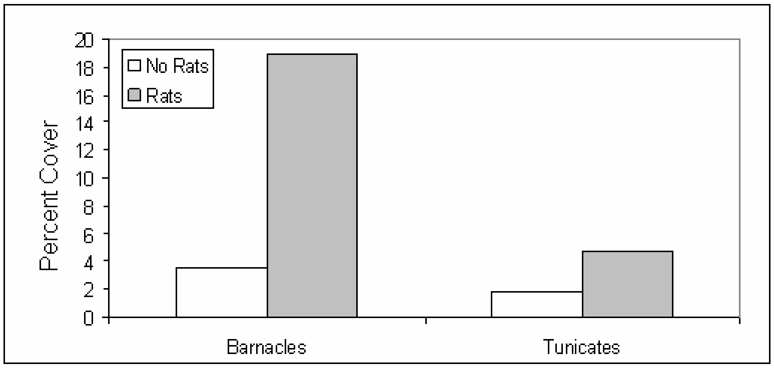

Figure 7. The percent cover of particular invertebrate species from all tidal heights from all Aleutian Islands surveyed with and without rats (n=15 and 17, respectively). There are significantly more of each species on islands with rats (Barnacles: $t = 9.24$, $df = 343$, $P < 0.01$; Tunicates: $t = 3.30$, $df = 387$, $P < 0.01$).

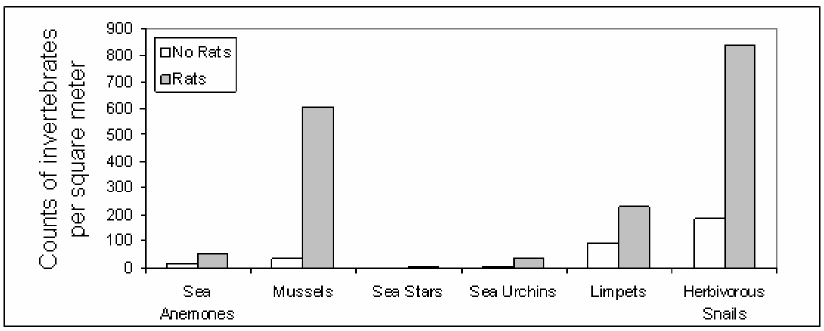

Figure 8. The number of invertebrates per square meter from all tidal heights from all Aleutian Islands surveyed with and without rats (n=15 and 17, respectively). There are significantly more invertebrates on islands with rats (Anemones: $t = 2.31$, $df = 236.9$, $P = 0.02$; Mussels: $t = 4.33$, $df = 259.8$, $P = 0.00$; Sea stars: $t = 3.59$, $df = 260.9$, $P = 0.00$; Sea urchins: $t = 3.36$, $df = 267.8$, $P = 0.00$; Limpets: $t = 3.04$, $df = 327.6$, $P = 0.00$; Herbivorous snails: $t = 4.21$, $df = 296.9$, $P = 0.00$).

These data fit well with my hypothesis that rats keep populations of marine birds that forage on intertidal invertebrates low, thereby releasing those invertebrates from foraging pressure and allowing for an increase in their numbers.

Unfortunately, there were too few data points for adequate statistical analyses to compare the intertidal communities on the north and south sides of the islands. However, trends are apparent. For example, it appears there are more limpets in the middle and low intertidal zones on the south side of the island than the north and there were more sea urchins in the low and middle intertidal on the north side. In addition, in the low intertidal zone, the north side is nearly 100% covered with fleshy algae, while the south side coverage is just under 45%. There may be variations in disturbance, predation, and/or settlement and/or reproductive patterns between the north and the south sides of the island that contribute to these species differences. The south side of Rat Island is exposed to the North Pacific Ocean with no additional land masses present for over two thousand miles, while there are several islands within twenty miles of the north side facing the Bering Sea. This discrepancy in exposure could contribute significantly to differences in disturbance levels via wave action and debris coming ashore which could lead to variation in numbers of limpets and algal cover between the two island sides. Higher levels of disturbance could provide more area for settlement of limpet larvae while precluding their invertebrate predators (i.e. sea stars) and preventing extensive algal cover. In addition, in areas of high surf exposure, limpet habitat is increased due to more water availability higher in the intertidal which allows for greater numbers of individuals (Ricketts et al. 1985) and certain species of algae are less able to maintain a presence on wave battered intertidal benches. Finally, limpet numbers can vary significantly year to year, and these data may be reflecting a pattern that is specific to 2003. There appears to be more sea urchins on the north side of the island. Urchins are known to be more prevalent on the Bering Sea side than the Pacific Ocean side of the Aleutian Islands due to the greater expanse of available sub-tidal habitat provided by the larger undersea shelf. In addition, sea otters (*Enhydra lutris*) are the primary predators of sea urchins and severe reduction in their numbers in the Aleutian Islands has lead to a significant increase in sea urchin abundance since the mid-1990's, especially in the Bering Sea (Estes and Palmisano 1974, Estes et al. 1978, Estes et al. 1998, Estes pers. comm.).

I am also investigating rat foraging ecology on several of the Aleutian Islands. The rat observation data indicate that, at night, rats are not feeding on large intertidal invertebrates, but instead are foraging primarily on amphipods in the beach wrack and either *Fucus* sp. and/or small invertebrates harbored on the Fucoid algae. This contrasts with data reported by Navarette and Castilla (1993) wherein they observed shell remains of intertidal organisms such as limpets and crabs in the burrows of Norway rats and surmised that rats were foraging on these invertebrates. Further elucidation of rat diet will be obtained upon analysis of the stable carbon and nitrogen isotope data from rat tissues and their supposed prey. In addition to the tissues from 15 rats and many possible prey items collected on Rat Island, I collected tissues from 26 rats and possible prey items from 6 other islands for additional stable isotope analysis (Kurle, unpublished data). These analyses will further allow me to estimate Norway rat foraging ecology in the Aleutian Islands.

Conclusions

1. The intertidal species composition on Rat Island appears to display the pattern observed on 14 additional Aleutian Islands with rats. That is, Rat Island contains high numbers of herbivorous invertebrates that would commonly serve as primary prey items for Glaucous-winged gulls and Black Oystercatchers.

2. Statistical comparison of the rocky intertidal communities on the north and south sides of Rat Island were not possible, but trends in species composition were observed. Limpets appeared to be more abundant on the south side of the island whereas sea urchins appeared to be in higher numbers on the north side. In addition, fleshy algal species appeared to cover a larger amount of area in the low intertidal zones on the north side of the island.

3. I saw no evidence of rats foraging on large intertidal invertebrates during behavioral observations conducted at night.

Recommendations

1. The intertidal species composition on Rat Island fits the patterns observed on islands with rats throughout the Aleutian Archipelago. For this reason, rat eradication should be considered on the basis that their presence appears to be indirectly altering marine intertidal communities. The larger study comparing islands throughout the Aleutian Chain is currently being analyzed and will likely add further support to this recommendation.

2. Following eradication of rats from Rat Island and after a suitable amount of time has passed to allow for marine bird recolonization, further surveys of the intertidal communities on Rat Island could be conducted for recovery measurements.

LITERATURE CITED

Andres, B. A., and G. A. Falxa. 1995. Black Oystercatcher: *Haematopus bachmani*. The Birds of North America **155**:1-20.

Atkinson, I. A. E. 1985. The spread of commensal species of *Rattus* to oceanic islands and their effects on island avifaunas. ICBP Technical Report No. 3, International Council for Bird Preservation, Washington D.C.

Bailey, E. P. 1993. Introduction of foxes to Alaskan Islands - history, effects on avifauna, and eradication. Resource Publication 193, United States Department of the Interior, Fish and Wildlife Service, Washington D.C.

Bertram, D. F., and D. W. Nagorsen. 1995. Introduced rats, Rattus spp., on the Queen Charlotte Islands: Implications for seabird conservation. Canadian Field-Naturalist **109**:6-10.

Brook, F. J. 1999. Changes in the landsnail fauna of Lady Alice Island, northeastern New Zealand. Journal of the Royal Society of New Zealand **29**:135-157.

Brown, K. P., H. Moller, J. Innes, and P. Jansen. 1998. Identifying predators at nests of small birds in a New Zealand forest. Ibis **140**:274-279.

Chapin III, F. S., E. S. Zavaleta, V. T. Eviner, R. L. Naylor, P. M. Vitousek, H. L. Reynolds, D. U. Hooper, S. Lavorel, O. E. Sala, S. E. Hobbie, M. C. Mack, and S. Diaz. 2000. Consequences of changing biodiversity. Nature **405**:234-242.

Coblentz, B. E. 1990. Exotic organisms: a dilemma for conservation biology. Conservation Biology **4**:261-265.

di Castri, F. 1989. History of biological invasions with special emphasis on the Old World. Pages 1-30 *in* J. A. Drake, editor. Biological Invasions: a Global Perspective. John Wiley & Sons, New York.

Drummond, D. C. 1960. The food of *Rattus norvegicus* Berk. in an area of sea wall, saltmarsh and mudflat. Journal of Animal Ecology **29**:341-347.

Elton, C. S. 1958. The Ecology of Invasions by Animals and Plants. Methuen, London.

Estes, J. A., and J. F. Palmisano. 1974. Sea otters: their role in structuring nearshore communities. Science **185**:1058-1060.

Estes, J. A., N. S. Smith, and J. F. Palmisano. 1978. Sea otter predation and community organization in the western Aleutian Islands, Alaska. Ecology (Tempe) **59**:822-833.

Estes, J. A., M. T. Tinker, T. M. Williams, and D. F. Doak. 1998. Killer whale predation on sea otters linking oceanic and nearshore ecosystems. Science **282**:473-475.

Gaston, A. J. 1994. Status of the Ancient Murrelet, Synthliboramphus antiquus, in Canada and the effects of introduced predators. Canadian Field-Naturalist **108**:211-222.

Innes, J., R. Hay, I. Flux, P. Bradfield, H. Speed, and P. Jansen. 1999. Successful recovery of North Island kokako Callaeas cinerea wilsoni populations, by adaptive management. Biological Conservation **87**:201-214.

Irons, D. B., R. G. Anthony, and J. A. Estes. 1986. Foraging strategies of glaucous-winged gulls [Larus glaucescens] in a rocky intertidal community. Ecology (Tempe) **67**:1460-1474.

Jones, I. L., C. M. Gray, J. Dusureault, and A. L. Sowls. 2001. Auklet demography and Norway Rat abundance and distribution at Sirius Point, Kiska Island, Alaska in 2001. Unpublished Report United States Fish and Wildlife Service.

Kozloff, E. N. 1983. Seashore Life of the Northern Pacific Coast: An illustrated guide to Northern California, Oregon, Washington, and British Columbia., 2nd edition. University of Washington Press, Seattle.

Lovegrove, T. G. 1996. A comparison of the effects of predation by Norway (Rattus norvegicus) and Polynesian rats (R. exulans) on the saddleback (Philesturnus carunculatus). Notornis **43**:91-112.

Major, H. L., and I. L. Jones. 2002. Impacts of the Norway rat on the auklet breeding colony at Sirius Point, Kiska Island, Alaska in 2002. Unpublished Report United States Fish and Wildlife Service.

Major, H. L., and I. L. Jones. 2005. Distribution, biology and prey selection of the introduced Norway Rat *Rattus norvegicus* at Kiska Island, Aleutian Islands, Alaska. Pacific Conservation Biology **11**:105-113.

Martin, J.-L., J.-C. Thibault, and V. Bretagnolle. 2000. Black rats, island characteristics, and colonial nesting birds in the Mediterranean: Consequences of an ancient introduction. Conservation Biology **14**:1452-1466.

Moors, P. J., I. A. E. Atkinson, and G. H. Sherley. 1989. Prohibited Immigrants: The Rat Threat to Island Conservation. World Wildlife Fund for Nature, Wellington, New Zealand.

Navarrete, S. A., and J. C. Castilla. 1993. Predation by Norway rats in the intertidal zone of central Chile. Marine Ecology Progress Series **92**:187-199.

Parker, I. M., D. Simberloff, W. M. Lonsdale, K. Goodell, M. Wonham, P. M. Kareiva, M. H. Williamson, B. V. Holle, P. B. Moyle, J. E. Byers, and L. Goldwasser. 1999. Impact: toward a framework for understanding the ecological effects of invaders. Biological Invasions **1**.

Pickering, J., and C. A. Norris. 1996. New evidence concerning the extinction of the endemic murid Rattus macleari from Christmas Island, Indian Ocean. Australian Mammalogy **19**:19-25.

Pye, T., R. Swain, and R. D. Seppelt. 1999. Distribution and habitat use of the feral black rat (Rattus rattus) on subantarctic Macquarie Island. Journal of Zoology (London) **247**:429-438.

Ricketts, E. F., J. Calvin, J. W. Hedgpeth, and D. W. Phillips. 1985. Between Pacific Tides, Fifth edition. Stanford University Press, Stanford, California.

Robinet, O., J. L. Craig, and L. Chardonnet. 1998. Impact of rat species in Ouvea and Lifou (Loyalty Islands) and their consequences for conserving the endangered Ouvea Parakeet. Biological Conservation **86**:222-232.

Simberloff, D. 2000. Extinction-proneness of island species: causes and management implications. Raffles Bulletin of Zoology **48**:1-9.

Soule, M. E. 1990. The onslaught of alien species, and other challenges in the coming decades. Conservation Biology **4**:233-239.

Taylor, R. H., G. W. Kaiser, and M. C. Drever. 2000. Eradication of Norway rats for recovery of seabird habitat on Langara Island, British Columbia. Restoration Ecology **8**:151-160.

Towns, D. R. 1996. Changes in habitat use by lizards on a New Zealand island following removal of the introduced Pacific Rat Rattus exulans. Pacific Conservation Biology **2**:286-292.

Vitousek, P. M. 1988. Diversity and biological invasions of oceanic islands. Pages 181-189 *in* E. O. Wilson and F. M. Peter, editors. Biodiversity. The National Academy of Sciences, Washington, D.C.

Vitousek, P. M., C. M. D'Antonio, L. L. Loope, and R. Westbrooks. 1996. Biological invasions as global environmental change. American Scientist **84**:468-479.

Vitousek, P. M., H. A. Mooney, J. Lubchenco, and J. M. Melillo. 1997. Human Domination of Earth's Ecosystems. Science **277**:494-499.

Wootton, J. T. 1992. Indirect effects, prey susceptibility, and habitat selection: impacts of birds on limpets and algae. Ecology **73**:981-991.

Wootton, J. T. 1995. Effects of birds on sea urchins and algae: a lower-intertidal trohic cascade. Ecoscience **2**:321-328.

Wootton, J. T. 1997. Estimates and tests of per capita interaction strength: Diet, abundance, and impact of intertidally foraging birds. Ecological Monographs **67**:45-64.

Appendix I. Tissue samples taken for stable carbon and nitrogen isotope analysis. Rat tissues are kidney (K), liver (L), muscle (M), fur (F), and bone (B). For rat observation sites, see Figure 2.

Location	Date	Species	Number	Tissues Collected
Rat Observation Site A	8.07.03	*Rattus norvegicus*	8	K, L, M, F, B
Rat Observation Site B	8.08.03	*Rattus norvegicus*	2	K, L, M, F, B
Rat Observation Site C	8.08.03	*Rattus norvegicus*	5	K, L, M, F, B
Rat Observation Site A	8.08.03	*Alaria* sp.	3	Whole Plant
Rat Observation Site A	8.08.03	Amphipod	5	Whole animal
Rat Observation Site A	8.08.03	Beach Wrack	4	Whole Plant
Rat Observation Site A	8.08.03	Bivalve	3	Whole animal
Rat Observation Site A	8.08.03	Crabs, Hermit	2	All animal tissue, no shell
Rat Observation Site A	8.08.03	Fly	3	Whole animal
Rat Observation Site A	8.08.03	*Fucus* sp.	3	Whole Plant
Rat Observation Site A	8.08.03	*Halosaccion* sp.	3	Whole Plant
Rat Observation Site A	8.08.03	*Honkenya* sp.	3	Stalks and leaves separated
Rat Observation Site A	8.08.03	Isopod	5	Whole animal
Rat Observation Site A	8.08.03	Limpet	5	All animal tissue, no shell
Rat Observation Site A	8.08.03	*Mazzaella* sp.	3	Whole Plant
Rat Observation Site A	8.08.03	Pill Bug	1	Whole animal
Rat Observation Site A	8.08.03	*Porphyra* sp.	3	Whole Plant
Rat Observation Site A	8.08.03	Snail	10	All animal tissue, no shell
Rat Observation Site A	8.08.03	*Ulva*	3	Whole Plant
Rat Observation Site B	8.08.03	Amphipod	5	Whole animal
Rat Observation Site B	8.08.03	Crabs, Hermit	1	All animal tissue, no shell
Rat Observation Site B	8.08.03	Fly	2	Whole animal
Rat Observation Site B	8.08.03	*Fucus* sp.	3	Whole Plant
Rat Observation Site B	8.08.03	*Halosaccion* sp.	3	Whole Plant
Rat Observation Site B	8.08.03	Isopod	5	Whole animal
Rat Observation Site B	8.08.03	Limpet	3	All animal tissue, no shell
Rat Observation Site B	8.08.03	*Mastocarpus* sp.	3	Whole Plant
Rat Observation Site B	8.08.03	*Mazzaella* sp.	3	Whole Plant
Rat Observation Site B	8.08.03	*Porphyra* sp.	3	Whole Plant
Rat Observation Site B	8.08.03	Snail	10	All animal tissue, no shell
Rat Observation Site B	8.08.03	*Ulva*	3	Whole Plant

Appendix II. List of Aleutian Islands surveyed from 2002-2004 for my larger project designed to determine if introduced rats affect rocky intertidal and marine bird species assemblages.

Islands Surveyed With Rats (n = 15)	Islands Surveyed Without Rats (n = 17)
Adak	Agattu
Amchitka	Aiktak
Attu	Alaid
Black	Amatignak
Cormorant	Buldir
Great Sitkin	Davidof
Green	Kaligagen
Kagalaska	Kanu
Kiska	Kasatochi
Little Kiska	Khvostof
Ogangen	Little Sitkin
Rat	Nitzki
Sea Parrot	Rocks off Davidof
Sedanka	Semisopochnoi
South	Tagadak
	Ugamak
	Vsevidof