

Introduced rats indirectly change marine rocky intertidal communities from algae- to invertebrate-dominated

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It is widely recognized that trophic interactions structure ecological communities, but their effects are usually only demonstrated on a small scale. As a result, landscape-level documentations of trophic cascades that alter entire communities are scarce. Islands invaded by animals provide natural experiment opportunities both to measure general trophic effects across large spatial scales and to determine the trophic roles of invasive species within native ecosystems. Studies addressing the trophic interactions of invasive species most often focus on their direct effects. To investigate both the presence of a landscape-level trophic cascade and the direct and indirect effects of an invasive species, we examined the impacts of Norway rats (*Rattus norvegicus*) introduced to the Aleutian Islands on marine bird densities and marine rocky intertidal community structures through surveys conducted on invaded and rat-free islands throughout the entire 1,900-km archipelago. Densities of birds that forage in the intertidal were higher on islands without rats. Marine intertidal invertebrates were more abundant on islands with rats, whereas fleshy algal cover was reduced. Our results demonstrate that invasive rats directly reduce bird densities through predation and significantly affect invertebrate and marine algal abundance in the rocky intertidal indirectly via a cross-community trophic cascade, unexpectedly changing the intertidal community structure from an algae- to an invertebrate-dominated system.

community structure | invasive species | *Rattus norvegicus* | trophic cascade | marine birds

Hairton *et al.* (1) laid the theoretical framework for the role of trophic interactions in structuring ecological communities, whereby carnivores keep herbivores in check via predation that releases plants from heavy grazing pressure, thus resulting in a “green world.” As a result of their article and other seminal publications on the topic, much attention in community ecology has focused on the role of predators in structuring communities. Thus, the direct and indirect effects of top-level predators on community composition have repeatedly been demonstrated at the population or community level, but landscape-level illustrations of communities transformed by top predators via trophic cascades are still scarce (but see refs. 2–4). Vertebrate predators introduced to oceanic islands throughout an archipelago provide ecologists with opportunities to investigate the presence and extent of such cascades over larger spatial scales. Studies of invasive species on islands often demonstrate direct reductions in native species abundances (5–7), but it has proven more difficult to determine the indirect trophic effects mediated by invaders and the extent to which these trophic interactions alter native community composition. The presence of invaded and noninvaded islands within a single archipelago allows for the quantification of both direct and indirect impacts on native communities imposed by introduced species and provides an opportunity to test for the persistence of community-level structuring induced by trophic interactions over landscape-level scales. We designed a natural comparison to examine the direct and indirect effects of invasive Norway rats (*Rattus norvegicus*) on marine communities in the Aleutian Islands, Alaska, and to

test the hypothesis that rats are driving a landscape-level trophic cascade that alters the marine rocky intertidal community structure.

Worldwide, rats (*Rattus spp.*) are known to extirpate marine birds on islands primarily through direct predation on their eggs, chicks, and sometimes adults (6–14). Available data indicate that predation by *R. norvegicus* on gull species on islands can reduce breeding populations by 19–47% depending on the species and location (7). In addition, gulls are known to leave islands that become infested with rats, moving their breeding grounds elsewhere (15). In the Aleutian Islands, Norway rats significantly reduce densities of both burrow- and ground-nesting marine birds, including intertidal foraging birds such as Glaucous-winged gulls (*Larus glaucescens*) and Black Oystercatchers (*Haematopus bachmani*), primarily through predation on chicks (16–19). However, the indirect impacts of rats on other communities are unknown. Gulls and oystercatchers are ground-nesting, year-round residents of the Aleutian Islands, with gulls occurring throughout the archipelago and oystercatchers occurring east of $\approx 176^\circ$ E (20). They forage extensively in the intertidal, significantly decreasing densities of intertidal invertebrates through predation and indirectly influencing the presence of fleshy algae (21–24). In the summer, oystercatchers establish combined nesting and feeding territories, thereby foraging in the intertidal near their nesting sites (20), whereas gulls feed almost exclusively in the intertidal starting in mid-July after their young begin to fledge (25). We hypothesized that islands with rats would have considerably lower bird densities and therefore reduced predation by birds on certain intertidal invertebrates. This would be reflected in substantial differences in the community structure of the rocky intertidal on islands with rats.

We measured the marine rocky intertidal community structure in July and August 2002–2004 on 8 islands with rats and 15 islands without rats (see *Materials and Methods*) at a landscape level spanning nearly the entire Aleutian archipelago (Fig. 1). We assessed gull and oystercatcher abundances by using counts conducted by the U.S. Fish and Wildlife Service (USFWS) (26). Gulls were counted on 8 islands with rats and 89 islands without rats, and oystercatchers were counted on 8 islands with rats and 85 islands without rats (excluding islands west of 176° E, where oystercatchers do not occur). Our results provide clear and compelling evidence of a landscape-level trophic cascade, whereby rats indirectly determine the marine rocky intertidal community structure on invaded Aleutian Islands through predation on birds that forage in the intertidal.

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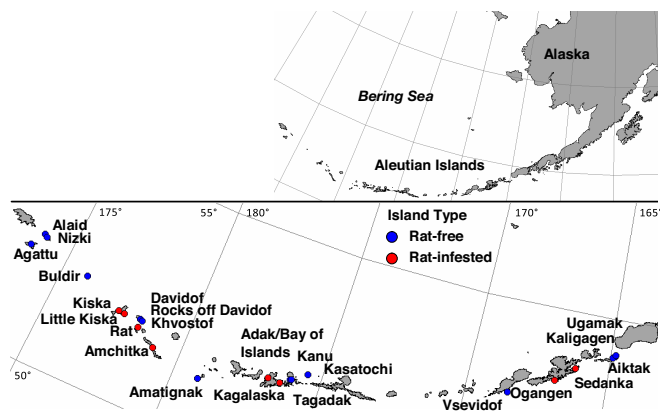


Fig. 1. The Aleutian archipelago with sample islands indicated in red (rat-infested, $n = 8$) and blue (rat-free, $n = 15$).

Results

Rats significantly reduced the densities of two important intertidal invertebrate predators. Glaucous-winged gulls and Black Oystercatchers km^{-1} of shoreline were an order of magnitude higher on rat-free islands than rat-infested islands (Fig. 2A and B) (separate variance t tests: $t = 2.4$, $\text{df} = 92.2$, $P = 0.017$; $t = 4.6$, $\text{df} = 91.0$, $P < 0.001$, respectively).

The species composition in the marine rocky intertidal communities were significantly different between islands with and without rats (MANOVAs; counts m^{-2} of individual invertebrates: Pillai Trace value = 0.850, $F_{6,16} = 15.152$, $P < 0.001$; percent cover of algae and aggregating invertebrates: Pillai Trace value = 0.593, $F_{6,16} = 3.878$, $P = 0.014$). The jackknifed classification matrices from the discriminant analyses using the classification factors derived from the percent cover data and from the count m^{-2} data assigned 83% and 96% of islands, respectively, to the correct category of rat or rat-free.

Densities of herbivorous snails and limpets were several times greater ($1319.0 \text{ m}^{-2} \pm \text{SE } 541.1$ vs. $223.7 \text{ m}^{-2} \pm \text{SE } 89.8$ and $182.4 \text{ m}^{-2} \pm \text{SE } 79.0$ vs. $30.2 \text{ m}^{-2} \pm \text{SE } 9.3$, respectively) on islands with rats than without ($t = -2.70$, $\text{df} = 21$, $P = 0.014$; $t = -2.63$, $\text{df} = 21$, $P = 0.016$, respectively) (Fig. 2C). The percentage of rocky intertidal area covered by fleshy algae on islands with rats was nearly half ($31.2\% \pm \text{SE } 4.2$ vs. $52.4\% \pm \text{SE } 4.2$) that observed on islands without rats ($t = 3.24$, $\text{df} = 21$, $P = 0.004$) (Fig. 2D).

Densities of nongrazing invertebrates eaten by gulls and oystercatchers also varied between island types. On islands with rats, densities of mussels and sea stars were >30 ($434.7 \text{ m}^{-2} \pm \text{SE } 277.0$ vs. $13.2 \text{ m}^{-2} \pm \text{SE } 5.5$) and 50 times greater ($4.0 \text{ m}^{-2} \pm \text{SE } 2.5$ vs. $0.1 \text{ m}^{-2} \pm \text{SE } 0.1$), respectively, as on islands without rats ($t = -2.13$, $\text{df} = 21$, $P = 0.045$; $t = 2.16$, $\text{df} = 21$, $P = 0.043$) (Fig. 2E), whereas barnacles covered nearly six times as much area ($17.5\% \pm \text{SE } 5.4$ vs. $3.3\% \pm \text{SE } 1.2$) in the rocky intertidal on islands with rats ($t = -3.41$, $\text{df} = 21$, $P = 0.003$) (Fig. 2F).

Densities of sessile invertebrates not eaten by gulls and oystercatchers also were significantly higher on islands with rats. Sea anemones were over three times greater ($48.5 \text{ m}^{-2} \pm \text{SE } 19.9$ vs. $14.6 \text{ m}^{-2} \pm \text{SE } 6.0$) on rat-infested islands ($t = -2.06$, $\text{df} = 21$, $P = 0.052$) (Fig. 2G), whereas the percent cover of tunicates and sponges was 340 ($3.4\% \pm \text{SE } 1.8$ vs. $0.01\% \pm \text{SE } 0.01$) and three times greater ($5.6\% \pm \text{SE } 2.2$ vs. $1.7\% \pm \text{SE } 0.8$), respectively, on rat-infested islands ($t = -2.62$, $\text{df} = 21$, $P = 0.016$; $t = -2.05$, $\text{df} = 21$, $P = 0.054$, respectively) (Fig. 2H).

Discussion

Our results demonstrate that the introduction of rats to the Aleutian Islands significantly reduces the densities of intertidal

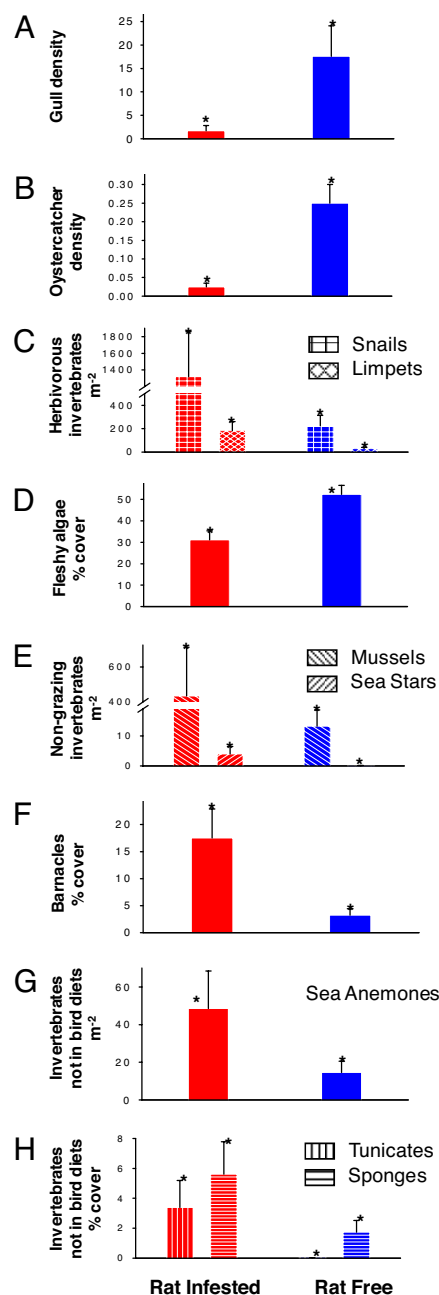


Fig. 2. Mean (\pm SE) values for parameters sampled on ($n = 8$) rat-infested (red) and ($n = 15$) rat-free (blue) islands in the Aleutian Islands. * indicates a significant difference at the $P \leq 0.05$ level. Bird densities (birds km^{-1} of shoreline) were estimated from population counts made by the U.S. Fish and Wildlife Service of rat-infested ($n = 8$) and rat-free ($n = 89$) islands. Invertebrate densities (invertebrates m^{-2}) were estimated from total counts of individuals from 480 cm^2 photo quadrats. Aggregating invertebrate and algal densities (percent cover of rocky intertidal) were estimated from point counts of species from 480 cm^2 photo quadrats. (A) Densities of Glaucous-winged gulls. (B) Densities of Black Oystercatchers. (C) Densities of algal grazing invertebrates that are known bird dietary items. (D) Percent cover of fleshy algae. (E) Densities of nongrazing invertebrates that are known bird dietary items. (F) Percent cover of barnacles, nongrazing invertebrates, and known bird dietary items. (G) Densities of sea anemones, nongrazing invertebrates that are not bird dietary items. (H) Percent cover of nongrazing aggregating invertebrates that are not bird dietary items.

foraging gulls and oystercatchers. Behavioral observations, stomach contents, and stable isotope analyses (C.M.K., D.A.C., and B.R.T., unpublished data) confirmed that marine birds,

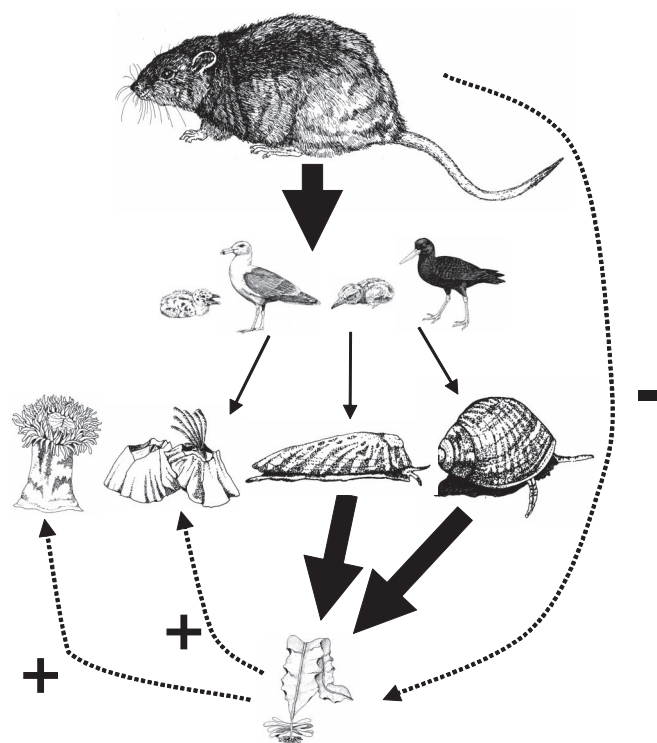


Fig. 3. Introduced Norway rats indirectly alter the intertidal community in the Aleutian Islands through direct predation on birds that forage in the intertidal. Dotted arrows indicate indirect effects, whereas solid arrows indicate direct effects. Rats keep Glaucous-winged gull and Black Oystercatcher numbers low, which releases intertidal invertebrates such as barnacles and herbivorous snails and limpets from foraging pressure. Greater numbers of grazing invertebrates leads to a significant decrease in algal cover, which allows more settling space for sessile invertebrates. The marine rocky intertidal is altered from an algae- to an invertebrate-dominated system.

along with terrestrial vegetation and marine amphipods, were rat prey. Herbivorous snails and limpets are important components of gull and oystercatcher diets (20, 21, 25, 27), and both are known to significantly reduce fleshy algal cover in the marine rocky intertidal through grazing (21, 27–31). Therefore, rat predation on the birds indirectly changes the rocky intertidal community from an algal- to an invertebrate-dominated system by releasing intertidal herbivores from predation pressure, which reduces fleshy algal cover via increased herbivory. The greater percentage of area covered by nongrazing barnacles and mussels on islands with rats is likely a consequence of both decreased predation by birds and fewer algal plants because less algae increases available space for aggregating invertebrates (32). Finally, the increase in settling space created by fewer algal plants likely contributed to the significantly higher densities of sessile invertebrates not eaten by birds on islands with rats, such as anemones, tunicates, and sponges (Fig. 3) (20, 25). Sea otters (*Enhydra lutris*) are known to have a top-down effect on subtidal kelp forests and low intertidal algal cover in the Aleutian Islands via their predation on sea urchins (3), important algal herbivores (3, 33). We did not consider a sea otter effect on the intertidal community structure in our study because sea otters are ecologically extinct in the Aleutian Islands (4, 34) and are uniformly absent from all islands. Despite their important role in intertidal kelp abundance, sea urchins were not counted in this study because urchins in the Aleutian Islands move with the tides and are thus largely subtidal (B. Konar, personal communication) and impossible to accurately count during low-tide intertidal surveys.

Bottom-up processes such as increased exposure to nutrients from seabird guano on islands without rats may be a small, but insignificant, contributing factor to the differential algal cover observed between island types. Evidence of enhanced algal growth due to increased seabird guano in South Africa (35) was confounded by differential bird predation on herbivores between sites. Wootton (36) demonstrated that nutrients supplied to intertidal marine algae via seabird guano positively influenced fleshy algal growth in only 1 of 18 species.

There are several broad implications to our findings. We provide an example of a landscape-level trophic cascade with significant large-scale ecological impacts on plant abundance and community structure in the tradition of Hairston *et al.* (1), whereby a top predator indirectly influences the abundance of vegetation through predation on an intermediate organism. This cascade is especially remarkable in that it is induced via introduced rats that are among the most successful nonindigenous animal pests on islands (8). The extirpation of native species through predation by introduced rats is well known, but we illustrate that invasive species can also have far-reaching and surprising indirect consequences that extend beyond their more obvious direct effects.

We also demonstrate an unexpected mechanism by which the terrestrial and marine communities in the Aleutian Islands are strongly linked. Marine birds nest on land while continuing to forage in the marine environment, thus connecting marine and terrestrial communities. Such connections are frequently presented as nutrient transfer from marine to terrestrial systems in the form of seabird guano (2), but we establish a link between terrestrial and marine environments, whereby an invasive terrestrial omnivore reduces populations of marine predators leading to significant changes in a marine community.

Materials and Methods

Study Sites. The Aleutian archipelago is a remote series of islands extending 1,900 km west from the Alaska Peninsula (Fig. 1). These islands are ideal for large-scale natural experiments to study the effects of introduced species (2) for several reasons, including their homogenous floral, faunal, and weather patterns; the lack of people; the large number of small islands for sampling; and the random introduction of rats throughout the chain starting as early as the late 1700s via shipwrecks, military, and other human activities (18). Rat-free islands sampled were Agattu, Aikta, Alaid, Amatignak, Buldir, Davidof, Kaligagen, Kanu, Kasatochi, Kvostof, Nizki, Rocks off Davidof, Tagadak, Ugama, and Vsevidof. Rat-infested islands sampled were Amchitka, Bay of Islands, Kagalaska, Kiska, Little Kiska, Ogangon, Rat, and Sedanka. The islands sampled within the Bay of Islands were Black, Cormorant, Green, Sea Parrot, and South Islands. These islands were grouped into one sample due to their close proximity for prevention of pseudoreplication. Islands were classified as rat-free if rats were never introduced to the island. We classified islands as rat-infested if self-sustaining populations of rats were present on the islands at the time of the surveys. Four of our rat-free islands lie west of 176° E out of the range of oystercatchers (Agattu, Alaid, Buldir, and Nizki); thus, gulls would be the only birds affecting the intertidal on these islands. Islands were chosen for accessibility, presence or absence of rats, and absence of effects by introduced foxes. Croll *et al.* (2) classified islands as fox-infested even if foxes had been removed in previous years and they determined that these islands may still be experiencing the lingering effect of fewer birds due to past fox predation. We included nine of those islands in our study, seven of which were classified as rat-free and two of which were classified as having rats; all islands had foxes removed within the past 10 or more years. Several studies demonstrate strong gull and oystercatcher recoveries within several years after fox removal (18, 19, 37, 38). To determine whether there were residual effects of fox occupation influencing our results, we performed two-factor ANOVAs on all of our intertidal-dependent variables by using rat status and previous occupation of the island by foxes as independent variables. If previous occupation by foxes had an effect on a dependent variable, there would be a significant effect of fox occupation or a significant interaction between fox occupation and rat status. All such effects were nonsignificant ($P = 0.10$ – 0.87), indicating that there were no effects resulting from the previous occupation of the islands by foxes. Therefore, we feel confident that we have avoided any potential complications from introduced foxes.

Sampling of Rocky Intertidal Communities. Study sites were chosen based on the expanse of available rocky intertidal accessible by skiff. Surveys were conducted in July and August 2002–2004. Surveys consisted of taking systematic digital photos of 480-cm² quadrats in the rocky intertidal in the low, middle, and high intertidal (corresponding to zones 4–2, respectively, in ref. 39). Photos were taken every 5 m along a 30- to 50-m transect. If the area to be sampled at 5 m was unable to be photographed due to excessive water or other natural factors that would render the photograph illegible, the next available site along the transect was chosen instead. Where large kelp or algal fronds obscured the underlying intertidal bench, we clipped the plants to <1 cm and took additional photographs, removing subsequent layers of algal cover with each photograph. These additional photos allowed us to estimate the percent cover of algal species revealed with each layer and to estimate densities of invertebrates hidden by overlying algae.

All digital photos were analyzed by using Adobe Photoshop version 6.0 (Adobe Systems). A digital grid was overlaid on each photo with grid line preferences set to 2.5 inches. Aggregating invertebrate and smaller algal species were counted as percent cover by counting their occurrence if they fell below an intersection of the grid lines and then dividing that number by the total number of intersections (60). The percentage of area covered by larger kelps was estimated by counting the percent cover of holdfasts that remained after the removal of the kelp blades. Once all kelp and algae were removed, we counted individual invertebrates and estimated percent cover of aggregating invertebrates. Invertebrates counted as percent cover were barnacles, sponges, and tunicates; all fleshy algae and kelp were counted as percent cover and included *Alaria* sp., *Cladophora* sp., *Endocladia* sp., *Fucus* sp., *Halosaccion* sp., *Laminaria* sp., *Leathesia* sp., *Mazzaella* sp., *Odonthalia* sp., *Palmaria* sp., *Porphyra* sp., and *Ulva* sp. Not all numbers from the percent cover estimates added to 100% because some areas contained rock, sand, or invertebrate species that were not counted as percent cover.

To estimate actual numbers of species, the occurrence of each individual within the photo was counted, and that number was divided by 0.048 to estimate the number of invertebrates per square meter. Species counted as individuals per square meter were anemones, chitons, herbivorous snails, limpets, mussels, and sea stars. The use of digital photographs is widely accepted as an appropriate technique to estimate the abundance of marine subtidal and intertidal organisms (40, 41).

Statistical Testing. To test for differences in the species composition of the rocky intertidal between islands with and without rats and to determine how well the intertidal data predicted whether an island had rats, we used multivariate ANOVAs (MANOVAs), followed by discriminant function analyses (DFAs). One MANOVA and a DFA were conducted with the invertebrates counted as number per m⁻² that were herbivorous snails, limpets, mussels, sea

anemones, and sea stars. The second MANOVA and DFA were conducted with the species counted as percent cover that were the fleshy algae and the aggregating invertebrates (barnacles, sponges, and tunicates). To test for differences between islands with and without rats in invertebrate numbers and percent cover of algae and aggregating invertebrates, we used *t* tests. To test for possible residual effects of introduced foxes on intertidal variables, we performed two-factor ANOVAs on all of our intertidal dependent variables using rat status and previous occupation of the island by foxes as independent variables. To test for differences in bird densities between islands with and without rats, mean numbers of birds km⁻¹ of shoreline were compared on islands that were controlled for foxes and that were surveyed between 1970 and 2007 for the USFWS database [89 without rats, 8 with rats for gulls, 85 without rats, 8 with rats for oystercatchers (excluding islands west of 176° E, where oystercatchers do not occur)]. This provided the most robust test of the hypothesis that rats affect bird abundances at the landscape level. Further, not all islands that we sampled were surveyed by the USFWS, and logistic constraints (i.e., mismatches in the timing of our intertidal surveys and USFWS bird surveys conducted during peak bird abundance) precluded us from adding additional bird survey data to the USFWS dataset. We used separate variance *t* tests because variance terms and sample sizes were different for each island type. The high proportion of islands with zero birds counted on shorelines prevented normalizing the data through transformation. However, because the high proportion of zeroes inflates the variance terms, we considered our statistics to be overly conservative and, thus, indicative of a true difference in bird densities among islands. All tests were conducted with Systat version 10.2 (Systat), and significance was tested at the $\alpha = 0.05$ level.

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