Context-Dependence of a Cross-System Trophic Cascade in Gwaii Haanas, British Columbia.

by

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Abstract

Increasing evidence suggests that the occurrence and magnitude of trophic cascades are highly context-dependent, yet the mechanisms mediating these indirect effects remain difficult to detect and predict. We examined the strength of evidence for a cross-system trophic cascade whereby invasive terrestrial predators (Norway rats, *Rattus norvegicus*) were hypothesized to directly reduce avian shoreline predators and indirectly magnify intertidal macroinvertebrates, thereby reducing macroalgal biomass. Simultaneously, we quantified the extent to which wave intensity mediated these indirect effects. We found that densities of successful American Black Oystercatcher (*Haematopus bachmani*) breeding pairs were, on average, 50% lower on rat-invaded than rat-free islands. Furthermore, we detected evidence for an effect of rats on grazer biomass (*Wi*=0.996) and this effect was reduced on wave exposed islands. We found no consistent pattern however, in grazer density between rat-free and rat-infested islands, regardless of wave exposure intensity or quantification method. Sheltered islands with rats had 74% less macroalgal biomass than those without, whereas exposed rat-invaded islands had 39% less macroalgal biomass than their rat free counterparts. Consequently, we found strong evidence that the mediating effect of wave exposure on invasion status appears to drive intertidal macroalgal biomass (*Wi*=0.998). Identifying the conditions that promote or inhibit the cascading effects of introduced and/or recovering natural predators will allow managers to better anticipate where these indirect effects might occur and tailor their conservation and management actions.

Keywords: Context dependence; intertidal; Gwaii Haanas; trophic cascade; mixed effects models; marine management

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Introduction

Emerging evidence suggests that the cascading effects of predator depletion and recovery can be highly context-dependent (Micheli et al. 2005, Frank et al. 2006, Salomon et al. 2008). Yet, little is known about the mechanisms that alter the occurrence and magnitude of these indirect effects (Borer et al. 2005). Identifying the abiotic and biotic factors that alter the strength of top-down, consumer-driven forces will improve our ability to forecast where, when, and under what conditions trophic cascades are likely to occur (Agrawal et al. 2007, Salomon et al. 2010). Here, we examine the strength of evidence for a cross-system trophic cascade, hypothesized to have been triggered by an introduced terrestrial predator in a coastal marine ecosystem, and the factors that mediate its occurrence and magnitude.

Factors that Alter Trophic Cascade Occurrence and Magnitude

Multiple factors have been shown to either facilitate or inhibit trophic cascades at both primary and secondary trophic links (Polis et al. 2000, Shears et al. 2008, Grosholz & Ruiz 2009). In marine ecosystems, high food-web diversity and functional redundancy can dissipate trophic effects (Frank et al. 2006), as can habitat diversity and complexity by providing refuge for prey (Micheli et al. 2005). Changes in the presence of some species can also indirectly alter feeding, hiding, aggregating, or other behaviours in downstream species (Dill et al. 2003), potentially masking or promoting other trophic cascades. High nutrient availability can override increased herbivory pressure, thereby dampening consumer-driven impacts (Korpinen et al. 2007, Sieben et al. 2010), as can abiotic effects that constrain grazing rates. For example, grazing rates of various fish and invertebrates can be inhibited by high wave force (Gaines & Denny 1993, Kawamata 1998, Duggins et al. 2001, Shears et al. 2008, Taylor & Schiel 2010). Lastly, novel consumers can trigger novel cascades, some of which have been shown to cross ecosystem boundaries.

Species Invasions Can Trigger Cross-System Trophic Cascades

Invasive species can elicit far-reaching indirect effects on food webs by altering habitat characteristics, modifying animal behaviour and triggering trophic cascades (Kurle et al. 2008, Grosholz & Ruiz 2009, Simberloff 2009). In the Aleutian Island archipelago, invasive Norway rats (*Rattus norvegicus*) directly reduce densities of intertidally foraging birds (Glaucous-winged gulls, *Larus glaucescens* and Black Oystercatchers, *Haematopus bachmani*) through direct predation on eggs and chicks in terrestrial nests (Kurle et al. 2008). Loss of these birds releases predation pressure on intertidal molluscan grazers (snails, limpets and chitons) which become more numerous. This dynamic has led to declines of macroalgae, providing a striking example of a cross-system trophic cascade where a novel terrestrial predator induces cascading effects on intertidal island ecosystems.

History of rat invasion on Haida Gwaii and Gwaii Haanas

Norway Rats were introduced to the archipelago of Haida Gwaii (formerly known as the Queen Charlotte Islands), located off the northwest coast of British Columbia, Canada, as early as 1900, though they did not become common until the 1980s (Golumbia et al. 2008). Supply ships and forestry float camps were the vector that transported the predators to and among Haida Gwaii’s islands. Since then, rats have been implicated in the decline or extirpation of many mammalian and avian species including Dusky shrews (*Sorex monticolus elassodon* and *S. monticolus prevostensis*), Keen’s mice (*Peromyscus keeni keeni* and *P. keeni prevostensis*), Northern goshawk (*Accipiter gentilis*), Northern saw-whet owl (*Aegolius acadicus*), and Haida ermine (*Mustela erminea haidarum*). Most notable are the declining populations of ground-nesting seabirds, who make relatively easy prey for rats (Golumbia 1999). These include Cassin’s Auklet (*Ptychoramphus aleutica*), Rhinocerous Auklet (*Cerorhinca* *monocerata*), Fork-tailed and Leach's Storm-petrel (*Oceanodroma furcate* and *O. leucorhoa*), Ancient Murrelet (*Synthliboramphus antiquus*), and Black Oystercatcher (*Haematopus bachmani*). Given the known impacts of rats on the islands, a rat eradication strategy has been devised for Gwaii Haanas which includes the eventual eradication of rats from the islands. This system provides a timely arena for; 1) investigating the factors that drive the occurrence and magnitude of cross-system trophic cascades and 2) establishing a pre rat-eradication baseline upon which future ecosystem-level effects of these targeted management policies can be evaluated.

Research Questions and Hypotheses

Here, we quantify the direct and indirect effects of invasive rats on an intertidal species assemblage and the extent to which wave exposure mediates these effects. Based on previous work (Kurle et al. 2008) and local natural history, we predicted that rat-invaded islands would have lower densities of Black Oystercatchers, greater invertebrate grazer densities and size, and reduced macroalgal biomass. We further predicted that wave exposure would alter the feeding rates of macroinvertebrate grazers, such that islands with high exposures were expected to have lower grazing rates which would thereby dissipate the cascading effects of predator introduction.

Methods

Study Area

We surveyed rocky intertidal benches on rat and rat-free islands in southern Haida Gwaii (formerly the Queen Charlotte Islands), a remote archipelago located on the northwest coast of British Columbia, Canada (52°26’N, 131°22’W) (Fig. 1A). The Gwaii Haanas National Park Reserve, National Marine Conservation Area Reserve and Haida Heritage Site (henceforth Gwaii Haanas), affords some degree of protection (prohibition of logging and offshore drilling) to the southern half of this island chain where our sites where located (Fig. 1B). The marine and terrestrial environments of Gwaii Haanas once supported settlements of Haida people dating back 12,650 cal BP (Fedje et al. 2011). The Haida continue to have a presence in Gwaii Haanas today, in part through the Haida Gwaii Watchmen Program that staffs seasonal Haida guardian and interpreters at 5 cultural sites. Gwaii Haanas also receives approximately 2000 visitors per year (Parks Canada 2010) mainly summer travelers and area managers and scientists, with relatively little impact to these remote island ecosystems.

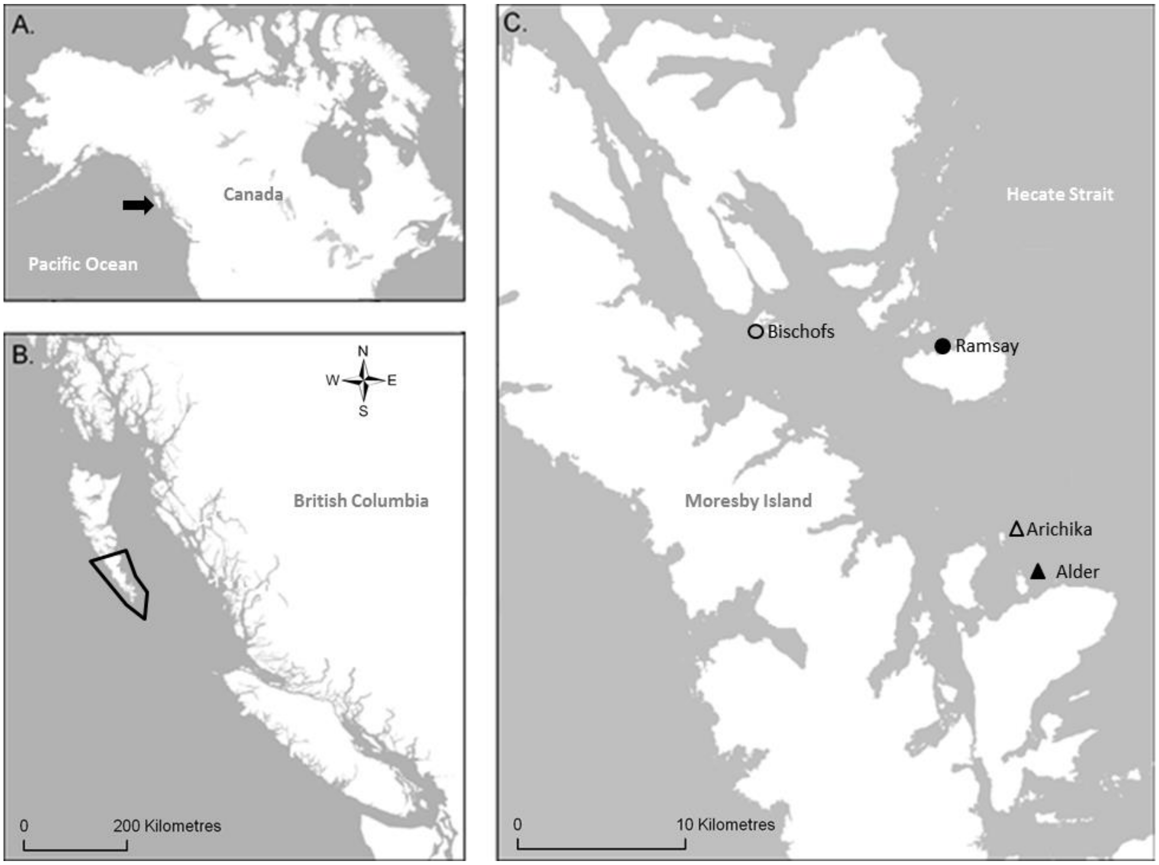

Figure 1. ***This research was conducted A) on the northwest coast of British Columbia, Canada, on the island archipelago of Haida Gwaii, within B) Gwaii Haanas National Marine Conservation Area Reserve and Haida Heritage Site. C) A total of 12 sites were nested within 4 islands (3 sites per island) varying in invasion status (rat invaded = open symbols, rat-free = filled symbols) and wave exposure (high = circles, low = triangles).***

Survey Design

To test the direct and indirect effects of rats on intertidal assemblages and the degree to which wave exposure may mediate these effects, we established 3 replicate sites nested within two island pairs of rat-invaded and rat-free islands (n= 4 islands), that varied in wave exposure (exposed and sheltered) (n= 12 sites total). Alder and Arichika served as high wave exposure, rat-free and rat-invaded islands respectively whereas Ramsay and Bischofs served as low wave exposure, rat-free and rat-invaded islands respectively (Fig. 1C).

At each site, we sampled ten randomly stratified $0.25m^2$ quadrats along a 50m transect running parallel to shore in the mid-low intertidal. We avoided sampling locations containing large tidepools to reduce habitat heterogeneity. In each quadrat, we estimated percent cover of dominant macroalgal species and sessile invertebrates, measured the maximum length of all macroinvertebrate grazers (Appendix A), and counted the number of laminarian algae stipes or holdfasts. To estimate macroalgal biomass, we removed and weighed all laminarians and other macroalgae within a randomly chosen 25 x 25 cm corner of each quadrat. We estimated biomass of invertebrate grazers using length-weight regressions (Appendix B) by measuring animals collected near, but not in, our survey sites.

Invasion Status

The islands we selected were assigned a status of rat-invaded or rat-free based on previously collected small mammal trapping results (Burles 2009). To reduce confounding effects of other introduced predators, we avoided islands that had evidence of introduced black rats (*Rattus rattus*) and raccoons (*Procyon lotor vancouverensis*). Rat-invaded islands were known to exclusively host populations of Norway rats (*Rattus norvegicus*), while rat-free islands hosted no invasive mammals. The two rat-invaded islands were also selected because they were first in line for rat eradication, which took place after our 2011 sampling season, their importance as former seabird colonies, the low-cost of eradication efforts due to their relatively small size, and the high feasibility of long-term success owing to their distance from other invaded islands (Burles 2009). In addition to assessing impacted (rat-invaded) and control (rat-free) sites, our data will later serve as pre-eradication data to test the effects of this large-scale management experiment on coastal ecosystems and its ability to restore them in a Before-After-Control-Impact (BACI) research design.

Wave Force

We quantified wave exposure in two ways. First, islands were grouped into two wave exposure categories (high and low) based on differences in observed intertidal species assemblage and differences in fetch. To better estimate the magnitude of variation in wave exposure among sites, we estimated maximum wave force with a wave exposure model (WEMo) that generates estimates of representative wave energy (RWE) resulting from wind-generated waves reaching the shore (Fonseca & Malhotra 2010). In brief, RWE is computed based on linear wave theory and ray tracing technique and represents the total wave energy in one wavelength per unit wave crest width reported in J/m. Inputs to the model include local bathymetry, and the top 5% hourly wind speed and wind occurrence frequency from eight compass headings over the preceding years.

Black Oystercatcher Densities

On each island (n=2 sheltered, n=2 exposed), the abundance of successful Black Oystercatcher breeding pairs, standardized to the total length of each island's shoreline was estimated annually over two years (2010 & 2011). Specifically, nests were surveyed for activity twice per season by boat and on foot (for full survey details see Parks Canada 2011).

Statistical Analysis

Model Structure

Differences in Black Oystercatcher densities between rat and rat-free islands were compared using generalized linear models where the density of successful Black Oystercatcher breeding pairs per kilometer was modeled first as a function of invasion status and then compared to an intercept-only model. To test for the indirect effects of rats and mediating effects of wave exposure (herein denoted as *status* and *exposure*) on intertidal communities, we constructed linear mixed effects (LME) models for natural log transformed macroinvertebrate grazer, *Katharina tunicata,* and macroalgal biomass using a Gaussian error distribution and identity link function. Generalized linear mixed effects models (GLMM) were constructed for total grazer density and *Katharina tunicata* density using a Poisson error distribution and a log link function. The latter was tested due to *Katharina tunicata's* experimentally documented high per capita interaction strength (Paine 1992) and strong influence on macroalgal productivity (Paine 2002). Grazers included the collection all herbivorous chitons, snails and limpets found in the quadrats (Supplementary Table 1). In each model, site and year were treated as random effects and fixed effects included various combinations of Norway rat invasion status and either categorical wave exposure or model derived estimates of representative wave energy. Analyses were conducted in R (R Development Core Team 2012) with the lmer function from the lme4 package (Bates & Maechler 2012).

Model Selection

We used an information-theoretic approach (Burnham & Anderson 2002) to quantify and compare the relative strength of evidence for alternative candidate models of intertidal invertebrate and macroalgal density and biomass, and the direct and indirect effects of Norway rat invasion (*status*) and wave exposure (*exposure*). We used small-sample bias-corrected Akaike's Information Criterion (AIC_c) standardized to the best fit model to produce ΔAIC_c values (Burnham & Anderson 2002). The lower the AIC_c score for a given model, the better the trade-off between complexity (number of parameters) and fit (Log likelihood) for that model. ΔAIC_c values ≤ 2 signal that a model has substantial empirical support. We determined the relative strength of evidence for each model by normalizing the model likelihoods to a set of positive Akaike weights (W_i). Given that ecological models are always only an approximation of reality and that models ranked below the best fit model contain useful information, we used all models in our multi-model averaging (Anderson 2008). From our candidate model set, we calculated multi-model averaged parameter estimates and relative variable importance (RVI) using the MuMIn package in R (Bartoń 2012). RVI for a given factor is determined by summing the Akaike weights across all models in the candidate set in which the factor occurs (Burnham & Anderson 2002). To further interpret the relative importance of each factor and the interaction terms in our candidate model set, we standardized our predictors to a common scale by subtracting their mean and dividing by 2 standard deviations (Gelman 2008).

Results

Black Oystercatcher Density

Surveys revealed that densities of successful breeding oystercatcher pairs were, on average, approximately 50% lower on rat-invaded than rat-free islands in 2010 (0.32 vs. 0.86 pairs/km) and 2011 (0.54 vs. 1.2 pairs/km, Appendix C). Strong evidence suggests that the number of successful breeding pairs of oystercatchers is strongly influenced by the absence of rats i.e. *status* (W_i=0.998, Table 1).

Table 1. ***Strength of evidence for status and intercept only generalized linear models of density of successful breeding pairs of Black Oystercatchers.***

Model	***n***	***K***	**Log likelihood**	**AICc**	**Δ AIC_c**	***AICc W_i***
Status	**4**	**3**	**-40.65**	**93.3**	**0.0**	**0.998**
Intercept only	4	2	-105.46	217.3	124.0	<0.001

Grazer Density and Biomass

We found no consistent pattern in grazer density between rat-free and rat-invaded islands, regardless of wave exposure (Fig. 2A). Both quantitative models of grazer density, with exposure quantified as either a categorical or continuous variable, revealed little relative support for an effect of rats (W_i=0.443, 0.385), wave exposure (W_i=0.338, 0.396), or these factors in combination (W_i=0.160, 0.161) (Table 2 & 3, Fig. 5CH). We did however detect evidence for an effect of rats on grazer biomass (W_i=0.996, RVI=0.8) when wave exposure was modeled as a continuous variable, given that the next best model, which included wave exposure as a factor, fell over 12.5 ΔAICc units away (Fig. 5C, Table 3). On average, sheltered islands with rats had 58% more invertebrate grazer biomass than their rat-free counterparts (82% more in 2010, 34% in

2011). This effect was reduced on wave exposed islands where islands with rats had, on average, only 14% more grazer biomass than rat-free islands, furthermore, this effect was only really apparent in 2011. Furthermore, because the confidence intervals of these variables cross 0, there is uncertainty in their parameter estimate (Fig. 5I).

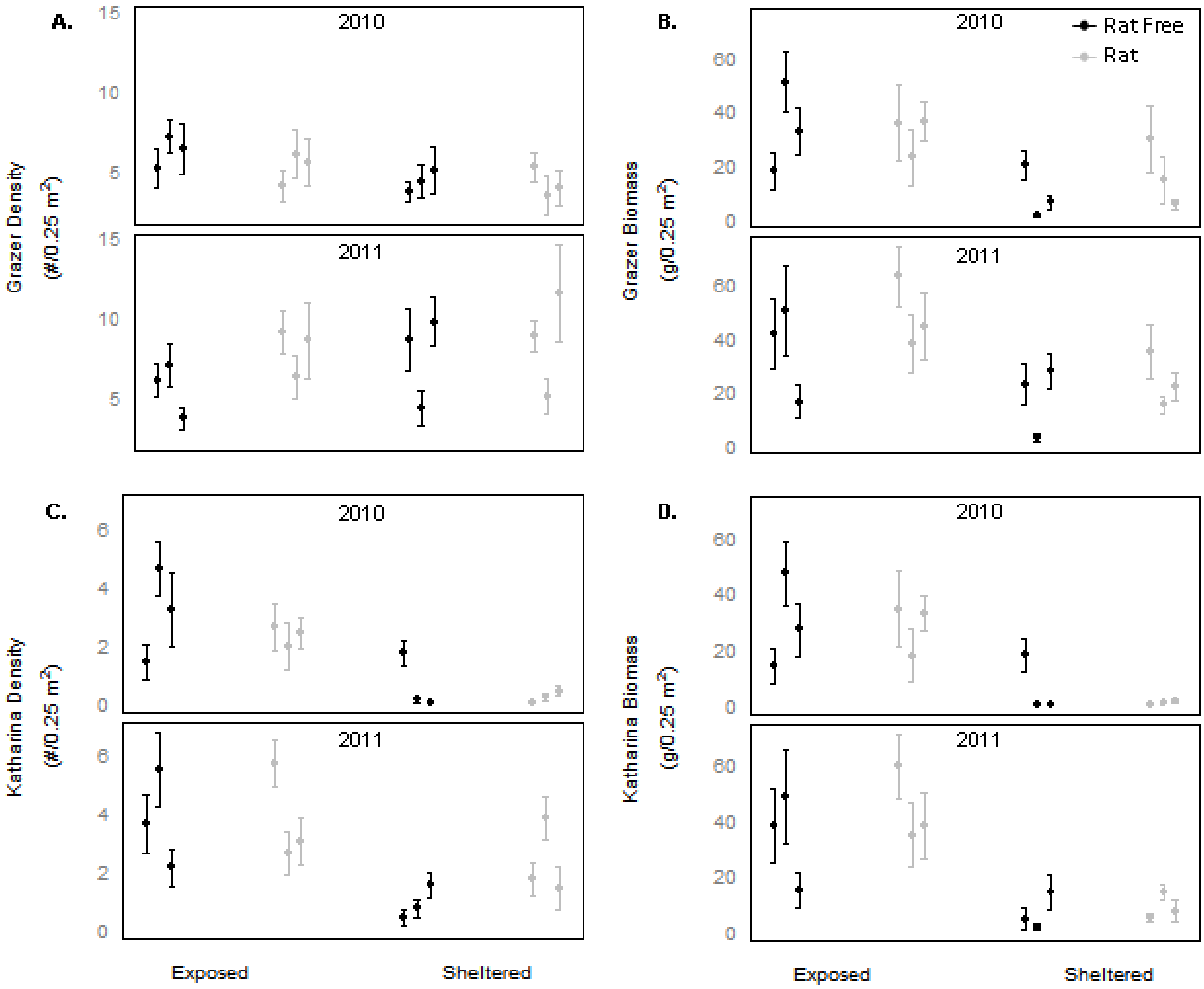

Figure 2. ***Biomass and density (+/- SE) of invertebrate grazers (limpets, snails and chitons) and Katharina tunicata at 12 replicate sites on two rat and two rat-free islands varying in wave exposure.***

Katharina tunicata Density, Size and Biomass

We observed higher densities, larger size classes and thus greater biomass of *Katharina tunicata* on wave exposed compared to wave sheltered islands, regardless of their invasion status (Fig. 2CD, Fig. 3). Yet, exposed islands with rats had on average only 12% fewer *Katharina tunicata* than rat-free islands (25% less in 2010, 1% more in 2011), whereas sheltered islands with rats had 49% more *Katharina tunicata* than their rat-free counterparts (67% less in 2010, 165% more in 2011). Among our set of candidate models of *Katharina tunicata* density, we found relatively strong empirical support for all of those models that included wave exposure as a factor, whether wave exposure was treated as a categorical factor (RVI=1) or a continuous factor, derived from bathymetry and wind data (RVI=0.93) (Table 2 & 3, Fig. 2DI). Furthermore, when wave exposure intensity values were estimated for each site, we found reasonable evidence for wave intensity mediating the indirect effect of rats on *Katharina tunicata* density (W_i=0.766) relative to the next best model that only included site-specific estimates of wave intensity (ΔAIC_c=3.8, W_i=0.114). We also detected stronger evidence for the indirect effect of rats on *Katharina tunicata* biomass (W_i=0.996) than that of wave exposure alone (ΔAIC_c=13.5, W_i=0.001) when wave exposure intensity values were estimated for each site (Table 3). The relative effect of rats versus wave exposure however was less clear when wave exposure was treated as a categorical factor (Table 2) because the top 3 models had ΔAIC_c values ≤ 2. Among these models of *Katharina tunicata* biomass, wave exposure had the greatest relative importance (RVI=1), while the effect of rats was slightly less important (RVI=0.73) and this parameter estimate was imprecise.

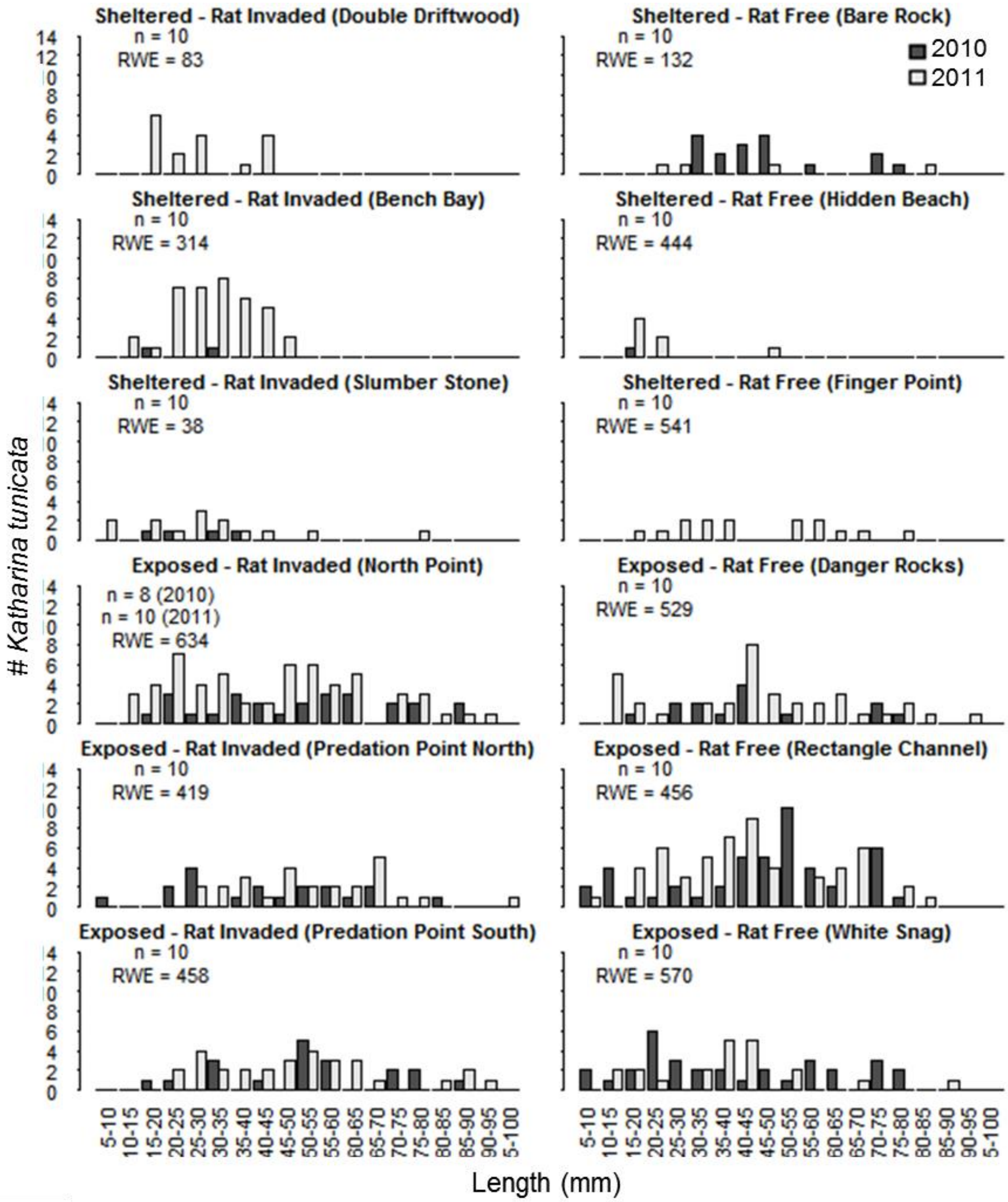

Figure 3. Size frequency histograms of Katharina tunicata.

Macroalgal Biomass

As predicted, islands with rats had consistently less macroalgal biomass than rat-free islands and the magnitude of this effect varied as a function of wave exposure (Fig. 4). On average, sheltered islands with rats had 74% less macroalgal biomass than those without rats, whereas exposed islands with rats had 39% less macroalgal biomass than those without the invading terrestrial predator. Furthermore, this effect was consistent across years. According to our model comparison, we found strong evidence that the presence of rats (*Invasion Status*), wave exposure category (*Exposure*), and the mediating effect of wave exposure on invasion status (*Invasion Status * Exposure*) drives intertidal macroalgal biomass (W_i=0.998, Table 2), particularly given that the next best model which included invasion *status* and *exposure* but excluded the mediating effect of waves (interaction term) was 12.3 ΔAIC_c units greater that the wave mediating model. Furthermore, all 3 factors had the same high relative variable importance (RVI=1, Fig. 5B). However, when wave exposure was estimated from a bathymetric, wind driven model, we detected support for the indirect effect of rats (*Invasion Status*) on intertidal macroalgal biomass (W_i=0.996, RVI=0.84, Fig. 5G), and little support for the direct (W_i=0.002) or mediating (W_i=<0.001, RVI=0.3) effect of wave exposure (Table 3). Note that the scaled coefficients for all three variables in this model cross 0 (Fig. 5G) suggesting that the parameter estimates are imprecise.

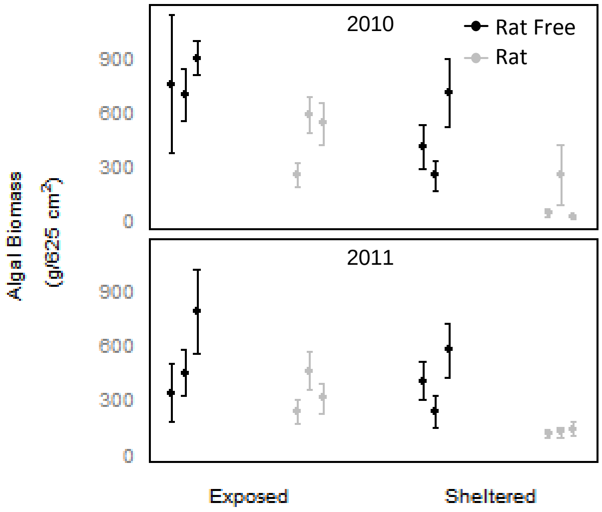

Figure 4. ***Biomass of macroalgae algae at 12 replicate sites on two rat and two rat-free islands varying in wave exposure.***

Table 2. Strength of evidence for alternative candidate models of the density and biomass of invertebrate grazers and Katharina tunicata and of macroalgal biomass across islands that vary in rat-invasion status and wave exposure measured as a category. (Note: full model is denoted as Invasion Status * Exposure)

Response and Model	***n***	***K***	**Log likelihood**	**AIC_c**	**ΔAIC_c**	**AIC_c W_i**
Grazer Density - Poisson						
Invasion Status	12	4	-383.76	775.7	0.0	0.443
Exposure	12	4	-384.03	776.2	0.5	0.338
Invasion Status +	12	5	-383.74	777.7	2.0	0.160
Invasion Status *	12	6	-383.70	779.8	4.1	0.058
Grazer Biomass - Logged						
Exposure	12	5	-530.39	1071.0	0.0	0.3658
Invasion Status +	12	6	-529.59	1071.6	0.5	0.2822
Invasion Status *	12	7	-528.55	1071.6	0.5	0.2786
Invasion Status	12	5	-531.99	1074.2	3.2	0.0735
Katharina tunicata Density – Poisson						
Exposure	12	4	-278.23	564.6	0.0	0.521
Invasion Status +	12	5	-277.95	566.2	1.5	0.242
Invasion Status *	12	6	-276.92	566.2	1.6	0.237
Invasion Status	12	4	-285.36	578.9	14.3	<0.001
Katharina tunicata Biomass – Logged						
Invasion Status *	12	7	-679.28	1373.0	0.0	0.416
Invasion Status +	12	6	-680.63	1373.6	0.6	0.311
Exposure	12	5	-681.82	1373.9	0.8	0.272
Invasion Status	12	5	-688.90	1388.1	15.0	<0.001
Macroalgal Biomass - Logged						
Invasion Status *	**12**	**7**	**-602.51**	**1219.5**	**0.0**	**0.998**
Invasion Status +	12	6	-609.78	1231.9	12.4	0.002
Exposure	12	5	-612.77	1235.8	16.3	<0.001
Invasion Status	12	5	-613.09	1236.4	16.9	<0.001

Note. Models with varying numbers of parameters (*K*), differences in small-sample bias-corrected Akaike Information Criterion (ΔAIC_c), and normalized Akaike weights (W_i). All models with interaction terms include Invasion and Exposure as factors. Bold typeface indicates instances of one clear best model.

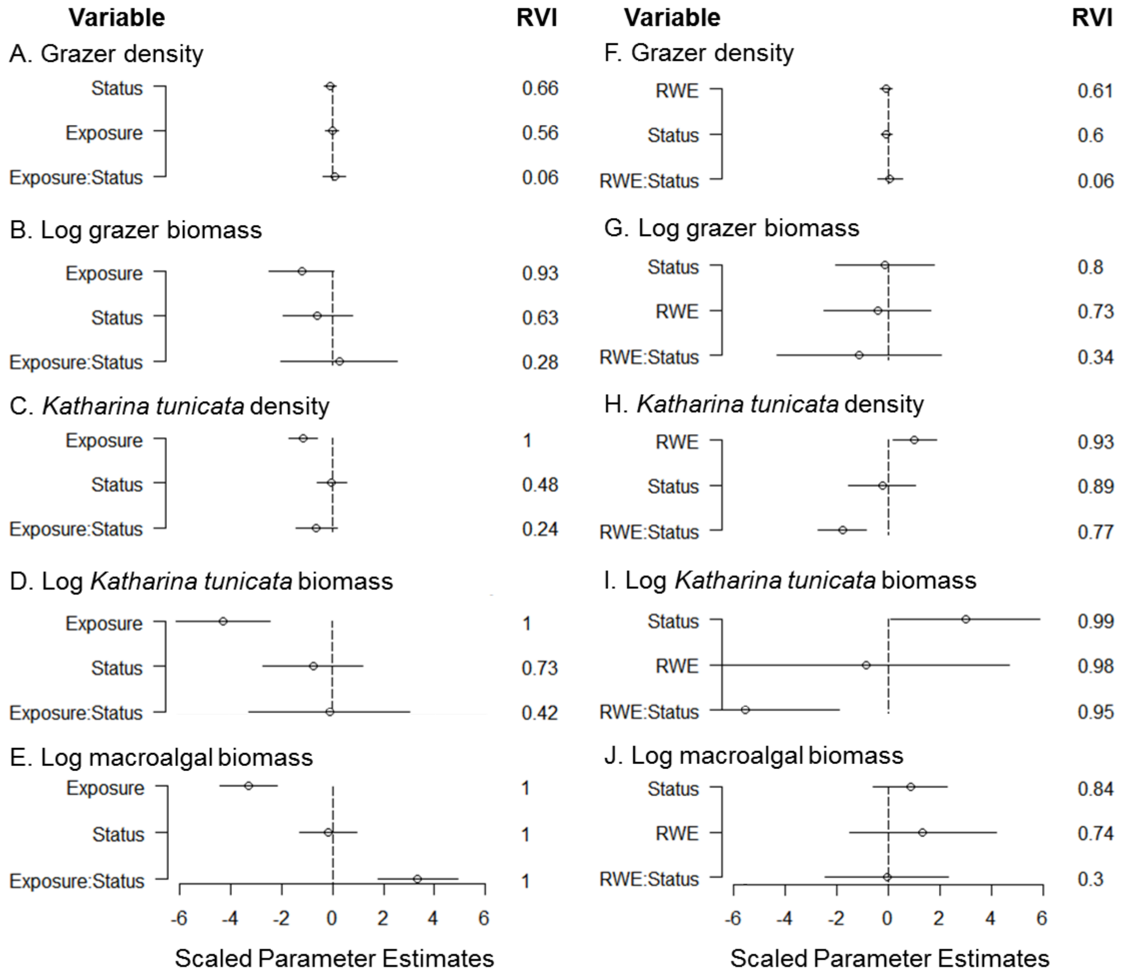

Figure 5. ***Scaled parameter estimates (circles) with 95% confidence intervals (lines) for each factor in our averaged mixed effects models. Predictor variables and their associated parameters are ranked in decreasing order of relative importance on a scale of 0 to 1. Relative variable importance values (RVI), were calculated by summing the Akaike weights (W_i) over the subset of models for in which the variable was found. Sections A-E represent models based on categorical wave exposure and sections F-J represent models based on relative wave exposure. Note that the continuous RWE values were standardized prior to model averaging to allow direct comparison with the categorical binary variable, status – therefore these relative importance variables are not the sums of W_i values found in Table 3.***

Table 3. ***Strength of evidence for alternative candidate models explaining the spatial variation in the density and biomass of invertebrate grazers and Katharina tunicata and of macroalgal biomass across islands that vary in rat-invasion status and wave exposure measured as Representative Wave Energy. (Note: full model is denoted as Invasion Status * Exposure)***

Response and Model	***n***	***K***	**Log likelihood**	**AIC$_c$**	**ΔAIC$_c$**	**AIC$_c$ W_i**
Grazer Density - Poisson						
Exposure	12	5	-383.73	777.7	0.0	0.396
Invasion Status	12	5	-383.76	777.8	0.1	0.385
Invasion Status + Exposure	12	6	-383.58	779.5	1.8	0.161
Invasion Status * Exposure	12	7	-383.56	781.6	3.9	0.057
Grazer Biomass - Logged						
Invasion Status	**12**	**6**	**-531.72**	**1075.8**	**0.0**	**0.996**
Exposure	12	6	-537.99	1088.4	12.5	0.002
Invasion Status + Exposure	12	7	-536.95	1088.4	12.6	0.002
Invasion Status * Exposure	12	8	-541.27	1099.2	23.4	<0.001
Katharina tunicata Density - Poisson						
Invasion Status * Exposure	**12**	**7**	**-278.04**	**570.6**	**0.0**	**0.766**
Exposure	12	5	-282.06	574.4	3.8	0.114
Invasion Status	12	5	-282.49	575.2	4.7	0.074
Invasion Status + Exposure	12	6	-281.90	576.2	5.6	0.046
Katharina tunicata Biomass - Logged						
Invasion Status	**12**	**6**	**-685.02**	**1382.4**	**0.0**	**0.996**
Invasion Status + Exposure	12	7	-689.81	1394.1	11.7	0.003
Exposure	12	6	-691.78	1395.9	13.5	0.001
Invasion Status * Exposure	12	8	-690.99	1398.6	16.2	<0.001
Macroalgal Biomass - Logged						
Invasion Status	**12**	**6**	**-607.03**	**1226.4**	**0.0**	**0.996**
Invasion Status + Exposure	12	7	-611.82	1238.1	11.7	0.003
Exposure	12	6	-613.46	1239.3	12.9	0.002
Invasion Status * Exposure	12	8	-616.65	1249.9	23.5	< 0.001

Note. Models with varying numbers of parameters (*K*), differences in small-sample bias-corrected Akaike Information Criterion (ΔAIC$_c$), and normalized Akaike weights (W_i). All models with interaction terms include Invasion and Exposure as factors. Bold typeface indicates instances of one clear best model.

Discussion

Overall, we detected evidence of a cross-system trophic cascade triggered by invasive rats, manifesting in the intertidal of Gwaii Haanas. The magnitude of these effects however varied across trophic levels and as a function of wave intensity. Specifically, as predicted for the top trophic level of this coastal food web, islands with rats consistently had 50% fewer breeding oystercatchers (Table 1). Although we found no consistent pattern in grazer density between rat-free and rat-infested islands (Fig. 2A), we did detect evidence for an effect of rats on macroinvertebrate grazer biomass broadly (Fig. 2B) and *Katharina tunicata* biomass in particular (Fig. 2D), such that sheltered islands with rats had 34-82% more grazer biomass than their rat-free counterparts. The indirect effect of rats on intertidal grazers appears to be altered by the physical context in which these species interact. Rat-invaded islands had between 74% and 39% less macroalgal biomass than rat-free islands (Fig. 4). Furthermore, the indirect effects of rats on macroalgal biomass were magnified at sheltered sites and dampened at wave exposed sites, suggesting that wave exposure can mediate the cascading effects of this invasive terrestrial predator.

Context-Dependence of Trophic Cascades

Context-dependency implies that hypothesized trajectories and magnitudes of species interactions are complex and depend on species composition, habitat characteristics and disturbance regimes (Polis et al. 2000, Dill et al. 2003, Micheli et al. 2005, Frank et al. 2006, Shears et al. 2008, Grosholz & Ruiz 2009). Recently, there has been increasing effort to determine how these trajectories and magnitudes of effects can be predicted from increasing information on the range of conditions under which species interactions take place (Wardle & Zackrisson 2005, Boyer et al. 2009, Crowe et al. 2011, O’Connor & Donohue 2013).

In Gwaii Haanas, wave exposure explained a high proportion of the variation in community assemblage we observed in the intertidal depending on how it was measured. Wave exposure was only consistently included among the top models when it was treated as two broad categories (high vs. low). Estimates of wave exposure (RWE) derived from a bathymetric wind-driven model offered precise, spatially-explicit values but may have been less accurate than our broad wave exposure classes based on fetch and intertidal community assemblage. Furthermore, these estimates are not designed to incorporate ocean swell.

Physical disturbance regimes are well known to mediate interactions among species, particularly in intertidal ecosystems (Dayton 1971, Sousa 1979). In many cases higher wave exposure has a negative effect on grazing rates of herbivores on macroalgae. High wave action can mediate foraging by driving grazers into refugia, thereby allowing macroalgae to flourish in adjacent exposed areas (Addy & Johnson 2001) or by inhibiting the formation and advancement of feeding fronts necessary for large-scale impacts on macroalgal stands (Kawamata 1998, Gagnon et al. 2006, Lauzon-Guay & Scheibling 2009). In other cases, grazing can be most destructive to macroalgae at intermediate but variable hydrodynamic forces due to additive impacts of water motion that is generally low enough to allow grazers to persist, but punctuated by occasional high energy events during which plants break at points on their stipes that have been compromised by grazing (Duggins et al. 2001). In addition, the spatial distribution of algae and invertebrate dispersal and recruitment also varies with wave exposure and water flow rates, which can also mediate the effects of foraging behaviour on the intertidal community (Menge et al. 1997, Gaylord et al. 2006, Sanford & Worth 2010). Though wave exposure is known to be a major driver of diversity in nearshore marine systems, other factors are also known to influence species abundances and trophic interactions in intertidal systems.

Species composition and food web complexity is another factor that has been shown to dissipate trophic effects (Frank et al. 2006) in marine systems. Cascades may only be induced when strongly interacting species are involved (Heiman 2005, Soulé et al. 2005) as the invader and at all trophic levels in the system. The magnitude of trophic cascades can also be influenced by home-range and space-use patterns of organisms at multiple trophic levels (Micheli et al. 2005, Shears et al. 2008). While rats, grazers and algae are effectively bound to islands; avian predators are highly mobile and are not confined to feeding on the shores of the islands where they nest. This could potentially decouple the population dynamics of intertidal grazers from the expected effects of invaded islands hosting lower densities of successfully breeding Black Oystercatchers nesting sites. Though our study focused on this one particularly notable primary consumer, there are also others in our focal system known to prey on intertidal invertebrates. Informal observations at and around our field sites and conversations with local knowledge holders yielded evidence of intertidal molluscan prey being taken by river otters (*Lontra canadensis*), bald eagles (*Haliaeetus leucocephalus*), northwestern crows (*Corvus caurinus*) and gulls (*Larus spp.*). Direct predation by these consumers could counter the indirect effects of decreased Black Oystercatcher predation on rat invaded islands, depending on how closely their prey choices match those included in our study – effectively masking rat-induced trophic cascades. This has been shown experimentally in a rocky intertidal system in Ireland, where intermediate consumers mediate the cascading effects of predator removal (O'Connor & Donohue 2013).

The lack of an apparent impact of invasion status on grazer density may be attributed to a compensatory mechanism where the removal of some grazing invertebrates by Black Oystercatchers allows others to flourish. Dethier and Duggins (1988) demonstrated a similar effect where densities of small limpets increased following removal of *Katharina tunicata*. Our observed differences in invertebrate biomass in the absence of differences in density could be due to a mechanism whereby decreased predation by birds on rat-invaded islands results in larger-bodied grazers being left uneaten and leading to greater biomass measurements than on uninvaded shores where birds selectively eat large grazers but leave similar densities of smaller individuals. This is, of course, a dynamic system and the numbers and sizes of intertidal grazers change over time with avian predators expected to alter their feeding locations and preferences accordingly, as is common for many predators (Holling 1973, Estes et al. 2004).

Conservation and Management Implications

Invader-induced trophic cascades and the factors that alter their occurrence and magnitude, have direct implications for conservation and management strategies (Soulé & Estes 2003, Heiman 2005, Estes et al. 2011). First, species invasions can have broad repercussions across food webs and ecosystems, affecting both nutrient and energy flow, as well as the physical habitat structure (Simberloff 2009). Ecosystem impacts from invaders can be drastically different than those caused by loss and recovery of native species due to deficiency of predator control on novel species, synergistic effects with other invaders, and a lack of defenses of native biota to the novel organism (Simberloff & Von Holle 1999, Simberloff 2009) Exotic species control is therefore a worthwhile endeavour, especially on remote island ecosystems, which are particularly sensitive to species invasions (Whittaker & Fernández-Palacios 2007, Fridley 2011). In particular, many sea-bird species are reliant on isolated islands as safe places to breed and raise their young. Populations of such birds have been hard-hit by the introduction of predators to nesting islands (Blackburn et al. 2004, Croll et al. 2005, Jones et al. 2008). Rats are a particularly notable example of invading predators affecting seabirds on islands (Jones et al. 2008). Not all invasive species impacts are so readily apparent though, and these can require more careful monitoring to reveal.

Monitoring over appropriate temporal and spatial scales allows for detection of invasive species impacts that may vary within the population dynamics of either the introduced or native species or that may only develop after a time lag (Parker et al. 1999). Similarly, it is important to track the changes in the ecosystem after removal of invasives. In cases where ecosystems have been severely damaged, monitoring may reveal that additional active restoration actions are necessary to attain the intended improvements to ecosystem functioning (Mulder et al. 2009, Gaertner et al. 2012, Simberloff et al. 2013).

We also assert that while observational studies such as ours are useful in gaining an understanding of ecosystems, they only allow us to detect patterns. Attaining a solid understanding of system processes and enhancing our predictive power requires *in situ* experimental manipulation (Díaz et al. 2003, Paine 2010, O'Connor & Donohue 2013). In this study, for example, the most striking differences between rat- and rat-free islands were at the highest (birds) and lowest (algae) trophic levels, in contrast to the attenuation of trophic cascades that is generally expected to occur at the herbivore-plant interface (Shurin et al. 2002). We also cannot confidently discern whether differences in algal biomass are due to the rat-invaded vs. rat-free status of our islands or due to the differences in wave exposure at the sites. The greatest differences in macroalgal abundance were found between the sites we classified as sheltered. However our wave modeling showed that the rat-free sites had higher wave exposure than their sheltered rat-invaded counterparts, which could also be responsible for the abundance of macroalgae. In our example here, experimental manipulation of avian predators via exclusion cages could reveal if a cascading mechanism is indeed structuring the intertidal community, as they have on other rocky shores (Wootton 1994, Rilov & Schiel 2006, Ellis et al. 2007). We therefore encourage managers to embark on experimental approaches within monitoring programs as has been implemented and prescribed by those before us (Peterson 1990, Walters & Holling 1990, Estes & Peterson 2000, McPherson & DeStefano 2002).

Regardless of whether they are induced by species loss or non-native species introduction, the mounting evidence for the highly context-dependent nature of trophic cascades, guides us to suggest that when establishing monitoring programs, managers should ensure they encompass and account for how impacts differ with relevant environmental factors. As we have shown here, mixed effects modeling paired with an information theoretic approach serves as a powerful tool to assist managers in identifying where and under what conditions ecological impacts occur, thus improving their ability to select the most useful sites for further monitoring and management interventions. It is through careful consideration and examination of these ecosystem dynamics and the results of our efforts to protect them that we can move towards effective conservation of invaded habitats and their inhabitants.

References

Addy T, Johnson L (2001) Littorine foraging behavior and population structure on a wave-exposed shore: non-linear responses across a physical gradient. Journal of Shellfish Research 20:385–391

Agrawal AA, Ackerly DD, Adler F, Arnold AE, Cáceres C, Doak DF, Post E, Hudson PJ, Maron J, Mooney KA, Power M, Schemske D, Stachowicz J, Strauss S, Turner MG, Werne E (2007) Filling key gaps in population and community ecology. Frontiers in Ecology and the Environment 5:145–152

Anderson DR (2008) Model based inference in the life sciences: A primer on evidence. Springer New York, New York, NY

Bartoń K (2012) Multi-model inference (Package “MuMIn”).

Bates D, Maechler M (2012) Linear mixed-effects models using S4 classes (Package “lme4”).

Blackburn T, Cassey P, Duncan R (2004) Avian extinction and mammalian introductions on oceanic islands. Science 305:1955–1958

Borer ET, Seabloom EW, Shurin JB, Anderson KE, Blanchette CA, Broitman B, Cooper SD, Halpern BS (2005) What determines the strength of a trophic cascade? Ecology 86:528–537

Boyer KE, Kertesz JS, Bruno JF (2009) Biodiversity effects on productivity and stability of marine macroalgal communities: the role of environmental context. Oikos 118:1062–1072

Burles DW (2009) Rat management strategy. In: Bergman C (ed) Gwaii Haanas Resource Conservation Strategic Planning Series. Parks Canada, Skidegate, BC, p 22

Burnham KP, Anderson DR (2002)Model selection and multi-model inference - a practical information-theoretic approach, 2nd edn. Springer

Croll DA, Maron JL, Estes JA, Danner EM, Byrd G V (2005) Introduced predators transform subarctic islands from grassland to tundra. Science 307:1959–1961

Crowe TP, Frost NJ, Hawkins SJ (2011) Interactive effects of losing key grazers and ecosystem engineers vary with environmental context. Marine Ecology Progress Series 430:223–234

Dayton PK (1971) Competition, disturbance, and community organization: the provision and subsequent utilization ofspace in a rocky intertidal community. Ecological Monographs 41:351–389

Dethier MN, Duggins DO (1988) Variation in strong interactions in the intertidal zone along a geographical gradient: a Washington-Alaska comparison. Marine Ecology Progress Series 50:97–105

Díaz S, Symstad AJ, Chapin III FS, Wardle DA, Huenneke LF (2003) Functional diversity revealed by removal experiments. Trends in Ecology & Evolution 18:140–146

Dill LM, Heithaus MR, Walters CJ (2003) Behaviorally mediated indirect interactions in marine communities and their conservation implications. Ecology 84:1151–1157

Duggins D, Eckman JE, Siddon CE, Klinger T (2001) Interactive roles of mesograzers and current flow in survival of kelps. Marine Ecology Progress Series 223:143–155

Ellis JC, Shulman MJ, Wood M, Witman JD, Lozyniak S (2007) Regulation of intertidal food webs by avian predators on New England rocky shores. Ecology 88:853–863

Estes JA, Danner EM, Doak DF, Konar B, Springer AM, Steinberg PD, Tinker MT, Williams TM (2004) Complex trophic interactions in kelp forest ecosystems. Bulletin of Marine Science 74:621–638

Estes JA, Peterson CH (2000) Marine ecological research in seashore and seafloor systems: accomplishments and future directions. Marine Ecology Progress Series 195:281–289

Estes JA, Terborgh J, Brashares JS, Power ME, Berger J, Bond WJ, Carpenter SR, Essington TE, Holt RD, Jackson JBC, Marquis RJ, Oksanen L, Oksanen T, Paine RT, Pikitch EK, Ripple WJ, Sandin SA, Scheffer M, Schoener TW, Shurin JB, Sinclair ARE, Soulé ME, Virtanen R, Wardle DA (2011) Trophic downgrading of planet earth. Science 333:301–306

Fedje D, Mackie Q, Lacourse T, McLaren D (2011) Younger Dryas environments and archaeology on the Northwest Coast of North America. Quaternary International 242:452–462

Fonseca MS, Malhotra A (2010) WEMo (Wave Exposure Model) User Manual. Beaufort, North Carolina

Frank KT, Petrie B, Shackell NL, Choi JS (2006) Reconciling differences in trophic control in mid-latitude marine ecosystems. Ecology Letters 9:1096–1105

Fridley JD (2011) Invasibility of communities and ecosystems. In: Simberloff D, Rejmánek M (eds) Encyclopedia of biological invasions. University of California Press, Berkeley and Los Angeles, p 356–360

Gaertner M, Fisher JL, Sharma GP, Esler KJ (2012) Insights into invasion and restoration ecology: time to collaborate towards a holistic approach to tackle biological invasions. NeoBiota 12:57–76

Gagnon P, Himmelman JH, Johnson LE (2006) Organismal defenses versus environmentally mediated protection from herbivores: Unraveling the puzzling case of Desmarestia viridis (Phaeophyta). Journal of Experimental Marine Biology and Ecology 334:10–19

Gaines SD, Denny MW (1993) The largest, smallest, highest, lowest, longest, and shortest: extremes in ecology. Ecology 74:1677–1692

Gaylord B, Reed DC, Raimondi PT, Washburn L (2006) Macroalgal spore dispersal in coastal environments: mechanistic insights revealed by theory and experiment. Ecological Monographs 76:481–502

Gelman A (2008) Scaling regression inputs by dividing by two standard deviations. Statistics in Medicine 27:2865–2873

Golumbia TE (1999) Introduced species management in Haida Gwaii (Queen Charlotte Islands). In: Darling LM (ed) Proceedings of a conference on the biology and management of species and habitats at risk. Ministry of Environment, Lands and Parks, Victoria, BC and University College of the Cariboo, Kamloops, BC, p 15 – 19

Golumbia TE, Bland L, Moore K, Bartier P (2008) History and current status of introduced vertebrates on Haida Gwaii. In: Gaston AJ, Golumbia TE, Martin J-L, Sharpe ST (eds) Lessons from the islands: introduced species and what they tell us about how ecosystems work. Proceedings from the Research Group on Introduced Species 2002 Symposium. Canadian Wildlife Service, Environment Canada, Ottawa, p 8–31

Grosholz ED, Ruiz GM (2009) Multitrophic effects of invasions in marine and estuarine systems. In: Rilov G, Crooks JA (eds) Biological invasions in marine ecosystems. Springer-Verlag, Berlin Heidelburg, p 305–324

Heiman K (2005) Strongly interacting nonindigenous species. BioScience 55:548

Holling CS (1973) Resilience and stability of ecological systems. Annual Review of Ecology and Systematics 4:1–23

Jones HP, Tershy BR, Zavaleta ES, Croll D a, Keitt BS, Finkelstein ME, Howald GR (2008) Severity of the effects of invasive rats on seabirds: a global review. Conservation Biology 22:16–26

Kawamata S (1998) Effect of wave-induced oscillatory flow on grazing by a subtidal sea urchin Strongylocentrotus nudus (A. Agassiz). Journal of Experimental Marine Biology and Ecology 224:31–48

Korpinen S, Jormalainen V, Honkanen T (2007) Bottom–up and cascading top–down control of macroalgae along a depth gradient. Journal of Experimental Marine Biology and Ecology 343:52–63

Kurle CM, Croll DA, Tershy BR (2008) Introduced rats indirectly change marine rocky intertidal communities from algae- to invertebrate-dominated. Proceedings of the National Academy of Sciences of the United States of America 105:3800–4

Lauzon-Guay J-S, Scheibling RE (2009) Food dependent movement of periwinkles (Littorina littorea) associated with feeding fronts. Journal of Shellfish Research 28:581–587

McPherson GR, DeStefano S (2002) Applied ecology and naturalresource management. Cambridge University Press, Cambridge

Menge BA, Daley BA, Wheeler PA, Dahlhoff E, Sanford E, Strub PT (1997) Benthic-pelagic links and rocky intertidal communities: bottom-up effects on top-down control? Proceedings of the National Academy of Sciences of the United States of America 94:14530–5

Micheli F, Benedetti-Cecchi L, Gambaccini S, Bertocci I, Borsini C, Osio GC, Romano F (2005) Cascading human impacts, marine protected areas, and the structure of mediterranean reef assemblages. Ecological Monographs 75:81–102

Mulder CPH, Grant-Hoffman MN, Towns DR, Bellingham PJ, Wardle DA, Durrett MS, Fukami T, Bonner KI (2009) Direct and indirect effects of rats: does rat eradication restore ecosystem functioning of New Zealand seabird islands? Biological Invasions 11:1671–1688

O'Connor NE, Donohue I (2013) Environmental context determines multi-trophic effects of consumer species loss. Global Change Biology 19:431–440

Paine RT (1992) Food-web analysis through field measurement of per capita interaction strength. Nature 355:73–75

Paine RT (2002) Trophic control of production in a rocky intertidal community. Science 296:736–739

Paine RT (2010) Macroecology: does it ignore or can it encourage further ecological syntheses based on spatially local experimental manipulations? (American Society of Naturalists address). The American Naturalist 176:385–93

Parker IM, Simberloff D, Lonsdale WM, Goodell K, Wonham M, Kareiva PM, Williamson MH, VonHolle B, Moyle PB, Byers JE, Goldwasser L (1999) Impact: toward a framework for understanding the ecological effects of invaders. Biological Invasions 1:3–19

Parks Canada (2010) Gwaii Haanas National Marine Conservation Area Reserve and Haida Heritage Site - Interim Management Plan and Zoning Plan. Skidegate, BC

Parks Canada (2011) 2011 Black oystercatcher survey in Gwaii Haanas. Skidegate, BC

Peterson C (1990) On the role of ecological experimentation in resource management: managing fisheries through mechanistic understanding of predator feeding behaviour. In: Huges RN (ed) Behavioural Mechanisms of Food Selection. Springer, Berlin Heidelberg, p 821–846

Polis GA, Sears ALW, Huxel GR, Strong DR, Maron J (2000) When is a trophic cascade a trophic cascade? Trends in Ecology & Evolution 15:473–475

R Development Core Team (2012) R: A language and environment for statistical computing.

Rilov G, Schiel DR (2006) Seascape-dependent subtidal-intertidal trophic linkages. Ecology 87:731–744

Salomon AK, Gaichas SK, Shears NT, Smith JE, Madin EMP, Gaines SD (2010) Key features and context-dependence of fishery-induced trophic cascades. Conservation Biology 24:382–394

Salomon AK, Shears NT, Langlois TJ, Babcock RC (2008) Cascading effects of fishing can alter carbon flow through a temperate coastal ecosystem. Ecological Applications 18:1874–1887

Sanford E, Worth DJ (2010) Local adaptation along a continuous coastline: prey recruitment drives differentiation in a predatory snail. Ecology 91:891–901

Shears NT, Babcock RC, Salomon AK (2008) Context-dependent effects of fishing: variation in trophic cascades across environmental gradients. Ecological Applications 18:1860–1873

Shurin JB, Borer ET, Seabloom EW, Blanchette CA, Cooper SD, Halpern BS (2002) A cross-• ecosystem comparison of the strength of trophic cascades. Ecology Letters 5:785–791

Sieben K, Rippen AD, Klemens Eriksson B (2010) Cascading effects from predator removal depend on resource availability in a benthic food web. Marine Biology 158:391–400

Simberloff D (2009) Rats are not the only introduced rodents producing ecosystem impacts on islands. Biological Invasions 11:1735–1742

Simberloff D, Holle B Von (1999) Positive interactions of nonindigenous species: invasional meltdown? Biological Invasions 1:21–32

Simberloff D, Martin J-L, Genovesi P, Maris V, Wardle DA, Aronson J, Courchamp F, Galil B, García-Berthou E, Pascal M, Pyšek P, Sousa R, Tabacchi E, Vilà M (2013) Impacts of biological invasions: what's what and the way forward. Trends in Ecology and Evolution 28:58–66

Soulé ME, Estes JA (2003) Ecological effectiveness: conservation goals for interactive species. Conservation Biology 17:1238–1250

Soulé ME, Estes JA, Miller B, Honnold DL (2005) Strongly interacting species: conservation policy, management, and ethics. BioScience 55:168–176

Sousa WP (1979) Disturbance in marine intertidal boulder fields: the nonequilibrium maintenance of species diversity. Ecology 60:1225–1239

Taylor DI, Schiel DR (2010) Algal populations controlled by fish herbivory across a wave exposure gradient on southern temperate shores. Ecology 91:201–211

Walters CJ, Holling CS (1990) Large-scale management experiments and learning by doing. Ecology 71:2060–2068

Wardle DA, Zackrisson O (2005) Effects of species and functional group loss on island ecosystem properties. Nature 435:806–10

Whittaker RJ, Fernández-Palacios JM (2007)Island biogeography: ecology, evolution, and conservation, 2nd edn. Oxford University Press, New York

Wootton JT (1994) Predicting direct and indirect effects: an integrated approach using experiments and path analysis. Ecology 75:151–161

Appendices

Appendix A.

Species names for all grazing invertebrates included in models and animal type.

Species	**Type**
Acmaea mitra	Limpet
Astraea gibberosa	Snail
Calliostoma ligatum	Snail
Diadora aspera	Limpet
Katharina tunicata	Chiton
Lepidochitona spp.	Chiton
Lottiadae spp.	Limpet
Mopalia spp.	Chiton
Tegula funebralis	Snail
Tonicella spp.	Chiton

Appendix B.

Length weight regression equations for all invertebrates catalogued in field survey.

Species	***N***	**Equation**
Acmaea mitra	31	Mass (g) = 0.0002 x length (cm) $^{3.1499}$
Astraea gibberosa	81	Mass (g) = 6E-05 x length (cm) $^{3.4267}$
Calliostoma ligatum	29	Mass (g) = 0.0002 x length (cm) $^{3.3122}$
Ceratostoma foliatum	32	Mass (g) = 0.0036 x length (cm) $^{2.0383}$
Dermasterias imbricate	44	Mass (g) = 0.0001 x length (cm) $^{2.6914}$
Diadora aspera	23	Mass (g) = 0.0004 x length (cm) $^{2.8288}$
Henricia leviscula	23	Mass (g) = 0.0149 x length (cm) $^{1.3609}$
Katharina tunicata	36	Mass (g) = 0.0007 x length (cm) $^{2.428}$
Lepidochitona spp.	5	Mass (g) = 0.002 x length (cm) $^{1.6958}$
Lottiadae spp.	49	Mass (g) = 8E-05 x length (cm) $^{3.0296}$
Mopalia spp.	6	Mass (g) = 0.0001 x length (cm) $^{2.9137}$
Pisaster ochraceous	12	Mass (g) = 0.0153 x length (cm) $^{1.7842}$
Tegula funebralis	40	Mass (g) = 0.0006 x length (cm) $^{2.3894}$
Tonicella spp.	29	Mass (g) = 9E-05 x length (cm) $^{3.4163}$

Appendix C.

Density of successful breeding pairs standardized to shoreline length for all islands included in the study.

Exposure, Status and Island	# pairs/km 2010	# pairs/km 2011	Mean
Exposed			
Rat Free – Alder	0.84	1.48	1.16
Rat Invaded – Arichika	0.00	0.83	0.42
Sheltered			
Rat Free – Ramsay	0.88	0.92	0.90
Rat Invaded – Bischofs	0.65	0.65	0.65
Mean			
Rat Free – both islands, both years	0.86	1.20	1.03 (+/- 0.15 SE)
Rat Invaded – both islands, both years	0.32	0.54	0.53 (+/- 0.18 SE)

Appendix D.

Site Characteristics and Locations.

Island Site	Characteristics			Location	
	Invasion Status	Wave Exposure Category	Relative Wave Exposure (J/m)	Latitude (°N)	Longitude (°W)
Alder	- R	Exposed			
Danger Rocks			529.06	52.45266	-131.32045
Rectangle Channel			456.20	52.45199	-131.32013
White Snag			570.14	52.45044	-131.31774
Arichika	+ R	Exposed			
North Point			634.59	52.47371	-131.34423
Predation Point North			419.11	52.46835	-131.34035
Predation Point South			458.26	52.46769	-131.33967
Ramsay	- R	Sheltered			
Bare Rock			132.87	52.57271	-131.40413
Finger Point			541.71	52.56907	-131.42381
Hidden Beach			444.56	52.57199	-131.40456
Bischofs	+ R	Sheltered			
Bench Bay			314.08	52.56995	-131.55731
Double Driftwood Bay			83.19	52.57481	-131.57239
Slumber Stone			38.09	52.57479	-131.57289

Note. Invasion status is coded as + R if an island has invasion rats and – R if it is rat-free.