

Mammalian mesopredators on islands directly impact both terrestrial and marine communities

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Received: 6 December 2013 / Accepted: 4 September 2014 / Published online: 19 September 2014
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Abstract Medium-sized mammalian predators (i.e. mesopredators) on islands are known to have devastating effects on the abundance and diversity of terrestrial vertebrates. Mesopredators are often highly omnivorous, and on islands, may have access not only to terrestrial prey, but to marine prey as well, though impacts of mammalian mesopredators on marine communities have rarely been considered. Large apex predators are likely to be extirpated or absent on islands, implying a lack of top-down control of mesopredators that, in combination with high food availability from terrestrial and marine sources, likely exacerbates their impacts on island prey. We exploited a natural experiment—the presence or absence of raccoons (*Procyon lotor*) on islands in the Gulf Islands, British Columbia, Canada—to investigate the impacts that this key mesopredator has on both terrestrial and marine prey in an island system from which all native apex predators have been extirpated. Long-term monitoring of song sparrow (*Melospiza melodia*)

nests showed raccoons to be the predominant nest predator in the Gulf Islands. To identify their community-level impacts, we surveyed the distribution of raccoons across 44 Gulf Islands, and then compared terrestrial and marine prey abundances on six raccoon-present and six raccoon-absent islands. Our results demonstrate significant negative effects of raccoons on terrestrial, intertidal, and shallow subtidal prey abundance, and point to additional community-level effects through indirect interactions. Our findings show that mammalian mesopredators not only affect terrestrial prey, but that, on islands, their direct impacts extend to the surrounding marine community.

Keywords Predator–prey interactions · Marine food webs · Mesopredator release · Nest predation · Trophic cascades

Introduction

Medium-sized mammalian predators have been implicated in declines in the abundance and diversity of prey in habitats across the globe (Atkinson 2001; Courchamp et al. 2003; Blackburn et al. 2004; Schmidt 2003; Johnson et al. 2007; Prugh et al. 2009; Ripple et al. 2013). These mammalian predators are generally species that would be subject to top-down regulation by apex predators in intact ecological communities, and are thus defined here as ‘mesopredators’ (Crooks and Soulé 1999; Prugh et al. 2009). Their impacts have in many cases been attributed to: (1) widespread omnivory among mesopredators (Carbone et al. 2007; Prugh et al. 2009), allowing them to impact a broad range of prey species (Brashares et al. 2010); and (2) the extirpation or absence of apex predators, which may free mesopredators from top-down control (Crooks and Soulé 1999;

Communicated by Christopher N. Johnson.

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Johnson et al. 2007; Ritchie and Johnson 2009). Mammalian mesopredator impacts may be expected to be particularly severe on islands, where their expected omnivory may provide access to abundant food in the form of both terrestrial and marine prey, and where the limited land area means that larger apex predators are more likely to be extirpated or absent (Brown 1971; Marquet and Taper 1998; Terborgh et al. 2001). Indeed, dramatic impacts of mammalian mesopredators (including cats *Felis catus*, red foxes *Vulpes vulpes*, mink *Neovison vison* and raccoons *Procyon lotor*) on terrestrial biodiversity have been found in many island systems, including impacts on land birds (Atkinson 2001; Blackburn et al. 2004; Galetti et al. 2009), nesting seabirds, (Hartman and Eastman 1999), mammals (Burbidge and Manly 2002; Banks et al. 2008), reptiles (Iverson 1978) and amphibians (Banks et al. 2008; Salo et al. 2008). Given their omnivory, it stands to reason that mammalian mesopredators on islands may additionally impact the surrounding nearshore marine community. However, few studies have yet considered the potential impacts of mammalian mesopredators on intertidal and shallow subtidal prey.

Islands provide ample opportunity for omnivorous mammalian mesopredators to exploit marine prey (Carlton and Hodder 2003), and mesopredators may benefit substantially from such marine subsidies (Rose and Polis 1998). Consumption of marine prey has been suggested to exacerbate mesopredator impacts on terrestrial communities, although there is a paucity of data demonstrating that mammalian mesopredators whose diet is substantially subsidized by marine prey do indeed significantly impact terrestrial prey (Polis and Strong 1996; Polis et al. 1997; Rose and Polis 1998). Moreover, whereas it is clear that mesopredators may benefit from marine subsidies, to our knowledge no study to date has shown that mesopredator consumption of marine prey has a measurable impact on the abundance of the marine species consumed, i.e. that the impacts of terrestrial mammalian predators extend from terrestrial prey across the terrestrial-marine boundary to affect populations and communities of intertidal and subtidal organisms. Indeed research concerning the effects of terrestrial mammals on the diversity, abundance and distribution of marine prey has been identified as a conspicuous gap in the ecological literature (Carlton and Hodder 2003).

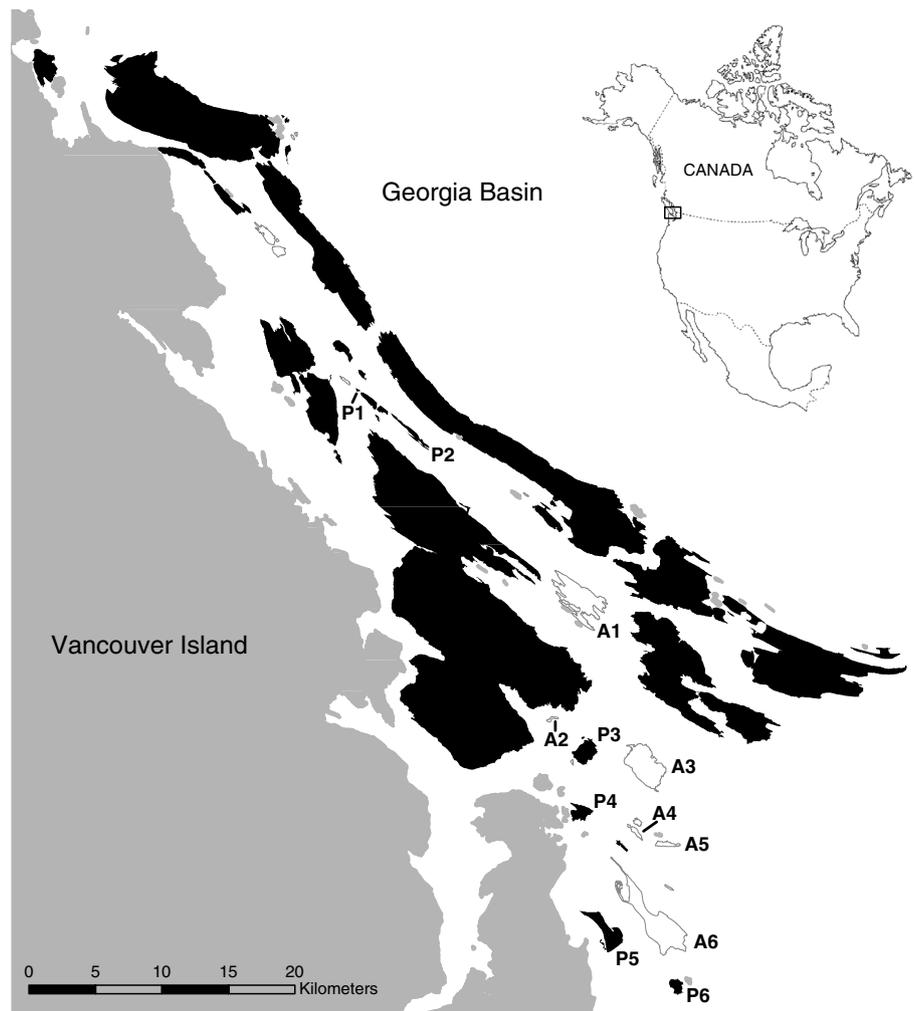
The likely extirpation or absence of large apex predators from islands, as a consequence of limited land area (Brown 1971; Marquet and Taper 1998; Terborgh et al. 2001), may further exacerbate mesopredator impacts on their prey through effects on both mesopredator abundance and behaviour. One of the most well-established principles in behavioural ecology is that animals spend more time foraging in the absence of predators (Lima and Dill 1990; Lima 1998; Zanette et al. 2013). This increase in foraging may result from either decreased time allocation to antipredator

behaviour, or increased use of profitable but risky habitats (Schmitz et al. 2004), which, in the case of mesopredators on islands, may include increased use of exposed shoreline habitats when apex predators are absent. When combined with high food availability (a likely scenario for mesopredators on islands with access to both terrestrial and marine prey), this increased foraging where predators are absent has been shown to have greater than additive effects on demography in both birds (Zanette et al. 2003, 2006) and mammals (Krebs et al. 1995; Karels et al. 2000). This may lead to very high abundances of mesopredators on islands, likely playing a major role in mediating the impacts of mammalian predators on terrestrial island prey (Atkinson 2001; Burbidge and Manly 2002; Blackburn et al. 2004, 2005; Towns et al. 2006), and potentially driving direct impacts on the intertidal and shallow subtidal communities surrounding these islands.

In this study, we investigated the impacts of raccoons (*Procyon lotor*) on terrestrial, intertidal, and shallow subtidal prey in an island system. Raccoons are archetypical mesopredators with highly omnivorous diets (Gehrt 2003), and are known to exert strong impacts on terrestrial prey in continental systems where their apex predators are absent (Soulé et al. 1988; Rogers and Caro 1998; Crooks and Soulé 1999; Schmidt 2003). Raccoons are also among the most common terrestrial mammals observed foraging in intertidal habitats (Carlton and Hodder 2003), and are thus an ideal model species with which to investigate the impacts of insular mammalian mesopredators at the terrestrial-marine interface. Raccoons occur on a subset of islands in the Gulf Islands of British Columbia, Canada, providing the opportunity to isolate their impacts on prey communities through the direct comparison of islands with and without raccoons. Moreover, all native mammalian predators of raccoons—cougars (*Puma concolor*), wolves (*Canis lupus*), and black bears (*Ursus americanus*)—have been extirpated from the Gulf Islands over the last century (Golumbia 2006), and Gulf Islands raccoons likely experience effectively no predation. In contrast, raccoons are heavily preyed upon by large carnivores on nearby Vancouver Island, occurring in up to a quarter of both cougar and wolf scats (Hansen et al. 2010). Here we report the findings of:

1. An 8-year study of raccoon predation on the nests of native songbirds (i.e. song sparrow *Melospiza melodia*).
2. A survey of 44 Gulf Islands to determine raccoon distribution.
3. A mensurative experiment comparing raccoon-present and raccoon-absent islands, which revealed significant impacts of raccoons on both terrestrial and marine prey.

Fig. 1 Distribution of raccoons on the Gulf Islands, British Columbia, Canada. Islands shown in *black* indicate those on which the presence of raccoons was established, whereas no raccoons or raccoon latrines were observed on islands shown in *white*. Islands shown in *grey* were not surveyed. Six raccoon-present (*P1–P6*) and six raccoon-absent (*A1–A6*) study islands were compared in the 2012 mensurative experiment



Materials and methods

Overview, study species, and area

We studied the impacts of raccoons on the Gulf Islands, British Columbia, Canada (Fig. 1), from 2004 to 2012. During that time, raccoon predation on songbird nests was quantified on four small Gulf Islands, as part of a long-term study on the effects of predation risk on the demography of song sparrow prey (Zanette et al. 2006, 2011; Travers et al. 2010). The high levels of raccoon predation on song sparrow nests (detailed here) implicate raccoons as the dominant nest predator in this system, and led us to undertake a survey of 44 Gulf Islands in 2011 to determine whether raccoons were present or absent, as a first step in identifying their community-level impacts. In 2012, we conducted a mensurative experiment to determine if the presence of raccoons affects the abundance of both terrestrial and marine prey, by selecting six raccoon-present and six raccoon-absent islands from among the 44 surveyed in 2011, and quantifying the abundance of selected species of birds,

intertidal fish, and both intertidal and shallow subtidal invertebrates. In 2013 we conducted a methodologically comparable but less extensive survey of the relative abundance of raccoons along shorelines in Clayoquot Sound, British Columbia, on adjacent Vancouver Island where large carnivores (cougars, wolves and black bears) remain common and are known to regularly eat raccoons.

The apex mammalian predators (cougars, wolves and black bears) that were formerly present throughout the Gulf Islands have largely been extirpated from all islands by humans over the last century (Golumbia 2006). Their former presence is indicated by: (1) museum specimens of wolves, and (2) the fact that cougars and black bears occasionally reappear on some Gulf Islands. All of these large carnivores are capable of swimming between islands (Lindzey and Meslow 1977; Darimont and Paquet 2002; Elbroch et al. 2010) and annual sightings throughout the archipelago number between six and 20 for cougars and zero to 34 for black bears (records from 2009 on; BC Ministry of Environment, unpublished data). There are no resident animals or viable populations of large carnivores on

Table 1 Island area and occurrence of raccoons and raccoon sign on the 12 Gulf Islands study islands

Island name (Fig. 1)	Area (ha)	Raccoons (km ⁻¹) nocturnal ^a	Raccoons (km ⁻¹) diurnal ^a	Maximum no. adults seen	Maximum no. adults and juveniles seen	Latrines per tree
Mowgli (P1)	4	2.5	0	4	10	0.18
D'Arcy (P6)	83	0.5	0	3	4	0.07
Wallace (P2)	87	3.5	0.4	36	51	0.10
Coal (P4)	140	3.7	3.7	25	25	0.36
Portland (P3)	225	5.0	2.0	46	46	0.28
James (P5)	335	0.2	0	2	4	0.11
Russell (A2)	12	0	0	0	0	0
Domville (A4)	31	0	0	0	0	0
Rum-Gooch (A5)	49	0	0	0	0	0
Moresby (A3)	594	0	0	0	0	0
Prevost (A1)	674	0	0	0	0	0
Sidney (A6)	854	0	0	0	0	0

^a Number of raccoons observed per kilometre during boat-based transects. Two nocturnal transects were run for each island, and values presented here are from the transect on which the most raccoons were observed

these islands, and the individuals sighted are almost certainly all migrants from adjacent Vancouver Island. These contemporary sightings are generally restricted to the larger Gulf Islands (i.e. >2,000 ha), and are responded to by attempted removal by provincial conservation officers.

The Gulf Islands constitute a network of ecologically similar islands located in the north Pacific between Vancouver Island and the North American mainland (Fig. 1), lying between 48°33'59"N, 123°16'33"W and 49°09'17"N, 123°47'31"W. Vegetation falls mainly into the coastal Douglas fir (*Pseudotsuga menziesii*) biogeoclimatic zone, and elevation ranges from 0 to 360 m above sea level. The islands as a whole are classified as approximately 70 % forested, 13 % rural, 6 % agricultural, 2 % suburban, and 9 % other (Jewell et al. 2007). A quarter of the islands surveyed in 2011 lie within the Gulf Islands National Park Reserve, and on the other three-quarters there are a further 21 provincial parks and ecological reserves.

Quantifying raccoon predation on song sparrow nests

We monitored predation on song sparrow nests by continuously videorecording nests on four small islands (including Portland Island, used in the mensurative experiment described below) each year from 2004 to 2012. We previously reported that the average nest predation rate in the Gulf Islands is 53 % (Zanette et al. 2006) and that raccoons are the principal nest predator in this system (Travers et al. 2010). Here we quantify the percentage of nest predation events attributable to raccoons and other predators, including corvids, the second most important nest predator (see “Results”). In addition to attacks on song sparrow nests, raccoons were filmed attacking the nests of fox sparrows

(*Passerella iliaca*), white-crowned sparrows (*Zonotrichia leucophrys*), and spotted towhees (*Pipilo maculatus*). Details concerning the video recording procedures can be found in Zanette et al. (2011) (Supplementary Online Material).

Surveying for raccoon presence or absence in the Gulf Islands

Two independent methods were used to assess raccoon presence and estimate relative abundance among the Gulf Islands; we counted the number of: (1) raccoons directly observed in or near the intertidal zone both day and night, and (2) raccoon scat piles (i.e. latrines) at the bases of trees along the shoreline (Hartman and Eastman 1999). Direct counts provide unambiguous evidence of the presence of raccoons, but are essentially a snapshot of the moment the count is conducted. Latrine transects provide information on raccoon presence over a longer time frame and thus augment the ‘snapshot’ provided by direct counts. Nocturnal and diurnal direct count surveys were conducted by searching along the shoreline of all islands from an outboard-powered boat (Zodiac Pro 12) approximately 20 m off shore, and covered a minimum of 8 km of shoreline or the entire circumference of the island. Nocturnal surveys were conducted with the aid of spotlights (Hartman and Eastman 1999), and species identifications were confirmed by at least two observers. Two-kilometre latrine transects (Hartman and Eastman 1999) were walked along the tree line within ~15 m of the high tide line and observers recorded the total number of latrines and the total number of trees checked for scat piles (Table 1). Direct counts of raccoons were conducted on a total of 44 Gulf Islands between 10

May and 11 Aug 2011, and latrine transects were conducted on 37 of these islands.

The 12 Gulf Islands compared in our mensurative experiment in 2012 were chosen based on 2011 surveys, with further latrine transects and diurnal (one per island) and nocturnal (two per island) boat-based surveys conducted for each island (between 10 May and 21 Aug 2012) to verify the pattern of raccoon presence or absence observed in 2011 (Table 1). On the six islands designated raccoon-present, raccoons were invariably detected during both nocturnal surveys. No raccoons were detected during any survey of the six islands designated raccoon-absent. The absence of raccoons on these six islands is further supported by our own long-term observations, as well as those of island residents and ecologists working for the Gulf Islands National Park Reserve.

Design of the mensurative experiment

To quantify the impacts of raccoons on both terrestrial and marine prey, we selected six raccoon-present and six raccoon-absent Gulf Islands (hereafter, ‘study islands’) from those surveyed in 2011, with present and absent islands matched for: (1) size (Table 1), (2) geographic distribution (Fig. 1), (3) human land use, and (4) land tenure. All 12 study islands are predominantly wilderness. Land use consisted of public campgrounds [three raccoon-present islands (P), three raccoon-absent islands (A)], sparsely distributed private cottages (four P, five A), and small hobby farms (one per island on two P and two A). Six of the 12 islands (two P, four A) are wholly or partially part of the Gulf Islands National Park Reserve, and a seventh (P) is partly a provincial park. Islands were balanced for land tenure, with wholly public (two P, one A), wholly private (three P, two A), or partly public-partly private islands (one P, three A). We alternated sampling of raccoon-present and raccoon-absent islands, and there was consequently no difference in median sampling date (median date for both raccoon-present and raccoon-absent islands = 3 July 2012; $n = 132$, Mann–Whitney $U = 2269$, $P = 0.672$).

On all 12 study islands we quantified the abundance of selected species of birds, intertidal fish, and both intertidal and shallow subtidal invertebrates. The bird species selected were those whose nests we had directly observed (from video) being attacked by raccoons, along with those whose nests were likely equally vulnerable based on location. During our survey of the presence of raccoons, we directly observed raccoons foraging on intertidal fish (e.g. pricklebacks, family Stichaeidae), shore crabs (*Hemigrapsus nudus* and *Hemigrapsus oregonensis*), and red rock crabs (*Cancer productus*), and accordingly focused on these species in our assessment of the impacts of raccoons on marine prey abundance.

Quantifying raccoon impacts on bird abundance

To quantify the effects of the presence of raccoons on bird abundance, we focused on small passerines that, like song sparrows (Zanette et al. 2011), nest <1 m from the ground. We included those species that were directly observed to be victims of raccoon nest predation (song sparrows, fox sparrows, white-crowned sparrows, and spotted towhees), as well as orange-crowned warblers (*Oreothlypis celata*), and dark-eyed juncos (*Junco hyemalis*), which nest on the ground and may therefore be expected to be at least as vulnerable to raccoon attack as those listed above. We additionally quantified the abundance of corvids (northwestern crows, *Corvus caurinus*, and common ravens, *Corvus corax*) because, as the second most important nest predator (as determined from video data), their abundance might be expected to affect songbird abundance (Weidinger 2002). Moreover, corvid abundance could be affected by the presence of raccoons because corvids themselves are potential victims of raccoon nest predation (Chamberlain-Auger et al. 1990).

We quantified raccoon impacts on bird abundance using point counts (Hutto et al. 1986; Morley and Winder 2013). Each point count lasted 10 min and surveyed a circular area of 50-m radius (i.e. 0.79 ha); all point-count data are presented as the number of birds detected per unit area surveyed. All point counts ($n = 16$ per island) were performed between 1 and 2 h after sunrise, and each island was surveyed on two dates between 19 May and 29 June 2012. Point counts were conducted within 50 m of the high-tide line and were spaced approximately 200 m apart (mean \pm SD distance between points = 203.3 ± 11.9 m). The same two observers performed all counts. The observers performed the first point count on an island together, and an audio recording of this first point count was made using a portable audio recorder (H2 Handy Recorder; Zoom, Tokyo) to permit verification of accuracy. Abundance estimates from both observers were significantly correlated with those from audio recordings (Spearman rank correlation; observer 1, $r_s = 0.69$, $P = 0.002$; observer 2, $r_s = 0.50$, $P = 0.036$; $n = 18$).

For each point count location, the observer estimated percent cloud cover, rain intensity, wind speed, forest cover, and shrub cover (Zanette and Jenkins 2000). There were no systematic differences between raccoon-present and raccoon-absent islands in any of these variables (Mann–Whitney U -tests, all $P \geq 0.2$).

Quantifying raccoon impacts on intertidal fish

As noted, foraging raccoons were directly observed feeding on intertidal fish, and we therefore quantified the abundances of pricklebacks and northern clingfish (*Gobiesox*

maeandricus) in both the mid and high intertidal zones using standard intertidal quadrat methods (Scrosati and Heaven 2007). The mid intertidal zone is characterized by macroalgal cover (predominantly *Ulva* sp. and *Fucus gardneri*), whereas the drier high intertidal zone is dominated by barnacles (predominantly *Balanus glandula* and *Semibalanus cariosus*). In each zone, we chose a random starting point in boulder-cobble habitat and laid a 50-m transect line parallel to the water line. Ten 0.25-m² quadrats were then sampled at 5-m intervals along this transect by searching under rocks down to the substrate (either sand or bedrock).

Quantifying raccoon impacts on intertidal shore crabs

Also as noted, we directly observed raccoon predation on shore crabs (both *Hemigrapsus nudus* and *Hemigrapsus oregonensis*) and therefore quantified intertidal shore crab abundance using the same methods as described for intertidal fish. Shore crabs were grouped into three size classes based on carapace width: small ≤ 1.3 cm, medium = 1.31–2.0 cm, large >2.0 cm. We focused our sampling effort on medium and large shore crabs, as these were the size classes that raccoons were observed to consume. All quadrat sampling was conducted between 20 May and 17 August 2012.

Quantifying raccoon impacts on red rock crabs

Based on direct observations of raccoons consuming red rock crabs in the intertidal and large amounts of red rock crab shell observed in raccoon scat, it is evident that red rock crabs are frequently preyed upon by Gulf Islands raccoons. Because red rock crabs are not adapted to tolerate air exposure (deFur and McMahon 1984), raccoons must wade into the ocean to capture them. Red rock crabs occur in large subtidal populations and, during each tide cycle, they migrate from the shallow subtidal into the intertidal as the tide rises, and migrate out again as the tide falls (Robles et al. 1989). Out-migrating individuals that linger too long in shallow water as the tide recedes are vulnerable to predation by wading raccoons. Data on the size and sex of red rock crabs killed by raccoons (below) are consistent with smaller individuals, and females (being smaller), being more vulnerable to raccoon predation because they are physically able to remain submerged and so linger longer at shallower depths. Though the loss of individuals to raccoon predation may significantly reduce the abundance of red rock crabs in the intertidal in a given tide cycle, this may not constitute a large loss when considering the shallow subtidal red rock crab population as a whole (Ellis et al. 2005).

We assessed the effects of the presence of raccoons on the abundance of red rock crabs in four ways: we quantified

raccoon predation on red rock crabs in a given tide cycle by counting the number of freshly preyed-upon carapaces and measuring and sexing those carapaces that were sufficiently intact, we gauged the abundance of red rock crabs accessible to raccoons in the intertidal by wading in and hand-capturing crabs ourselves, we assessed the effect of raccoons on the abundance of red rock crabs in the shallow subtidal by setting crab traps in the shallow subtidal over a 24-h period (i.e. over two full tide cycles), and we measured the carapace size of all red rock crabs captured to determine if there was a size bias consistent with raccoons being more likely to prey upon smaller individuals, as suggested by the size of freshly preyed-upon carapaces. If smaller crabs are more likely to be preyed upon and larger crabs are more likely to escape raccoon predation, then one would expect the average size of live-caught crabs to be smaller on raccoon-absent islands, where smaller crabs have a better chance of survival.

Remains of red rock crabs killed by raccoons are readily distinguished by their location and the condition of the carapace. Raccoons leave red rock crab remains in situ in the intertidal. Gulls are the only other predator in this area that do this and gull kills are easily distinguished by characteristic square-shaped holes left in the carapace from beak punctures (Ellis et al. 2005). Freshly preyed-upon carapaces are readily differentiated from older remains and molts because bits of flesh remain attached to the inside of the carapace, which is often associated with a pile of appendages (Ellis et al. 2005). To estimate the number of red rock crabs killed by raccoons during a given tide cycle, we followed procedures developed by Ellis et al. (2005), walking 2-km transects along the shoreline 10 min after daily low tide and counting the number of freshly preyed-upon red rock crab carapaces encountered. All transects were conducted by the same two observers between 17 June and 4 August 2012. In 78 cases, carapaces were sufficiently intact that we could measure the carapace width, and in 39 cases the abdomen remained attached, allowing us to identify the sex of the victim. As described in “Results”, the small average carapace size in this sample of 78 red rock crabs killed by raccoons (relative to the average size of live-trapped red rock crabs) is consistent with smaller crabs being more vulnerable to raccoon predation.

To gauge the abundance of red rock crabs in the intertidal that are accessible to raccoons, the same observer each time waded into the water to a depth of 15–20 cm and searched 5 × 2-m line transects. All crabs encountered were caught with the aid of a small dip net, and then measured (carapace width), sexed, and individually marked with a paint pen, before being returned to the water. Twenty transects were searched over 1 km of shoreline with each separated by 50 m. Each transect was searched twice between 15 June and 17 August 2012, with at least 24 h separating searches.

For each transect, we recorded percent algal cover and the predominant substrate type (four-point scale based on particle size, 1 = bedrock, 2 = boulder, 3 = cobble, 4 = sand), since these variables could affect the observer's ability to locate crabs. However, correlations between the number of crabs detected on a given transect and both algal cover and substrate type were very low [Spearman rank correlation; algal cover, $r_s = 0.12$, $P = 0.01$; substrate type, $r_s = -0.01$, $P = 0.80$; $n = 467$ (all transects surveyed)], indicating that these variables did not affect counts. Moreover, neither variable differed significantly between raccoon-present and raccoon-absent islands (Mann–Whitney U -test; algal cover, $U = 27$, $P = 0.116$; substrate type, $U = 23$, $P = 0.388$).

To assess the effect of the presence of raccoons on the abundance of red rock crabs in the shallow subtidal we set collapsible mesh crab traps (2-cm mesh) baited with ~200 g frozen herring just below the low tide line for a period of 24 h, thus capturing two full tide cycles and the corresponding in and out migrations from the shallow subtidal to the intertidal and back. Ten traps were deployed over at least 1 km of shoreline, with 100 m separating each trap. All crabs captured were measured (carapace width), sexed, and individually marked with a paint pen, before being returned to the water. Trapping was conducted between 18 June and 2 August 2012.

Quantifying raccoon shoreline use where apex predators persist (Clayoquot Sound)

To begin exploring the potential role of apex predators in mediating raccoon impacts on intertidal and shallow subtidal communities, in 2013 we conducted a methodologically comparable but less extensive survey of the relative abundance of raccoons along shorelines in Clayoquot Sound, British Columbia, on the central west coast of Vancouver Island (between 49°23'10"N, 126°13'42"W and 49°04'50"N, 125°45'02"W; approximately 140 km from our Gulf Islands study sites). Large carnivores (cougars, wolves and black bears) remain common in Clayoquot Sound, and here raccoons are heavily preyed upon by these predators, occurring in a quarter of both cougar and wolf scats (Hansen et al. 2010). Vegetation in Clayoquot Sound falls mainly into the coastal western hemlock (*Tsuga heterophylla*) biogeoclimatic zone, and areas surveyed in 2013 largely lie within the Clayoquot Sound Biosphere, a UNESCO Biosphere Reserve. Our 2013 survey was conducted on uninhabited islands and coastal areas in sheltered waters to the east of Tofino, British Columbia, where the intertidal and shallow subtidal communities are generally comparable to those in the Gulf Islands. Between 10 and 13 August 2013, we conducted boat-based nocturnal and diurnal direct count surveys in Clayoquot Sound using methods identical to those used in the Gulf Islands, and covering a total of

33 km of shoreline. We also walked 2 km of latrine transects in Clayoquot Sound in areas where we had observed raccoons to be present.

Statistical analyses

Bird abundance data were analysed using mixed-effects ANOVAs with a Poisson error distribution (i.e. Poisson GLMM) (Zuur et al. 2009). Data from each point count were used as the dependent variable in these analyses to test for a fixed effect of raccoon presence on bird abundance. Island was included as a random effect in all analyses to account for multiple observations taken on each island ($n = 12$). We conducted separate analyses testing the effect of the presence of raccoons on the abundance of: (1) small shrub- and ground-nesting songbirds, and (2) corvids. We also estimated a main effect of observer in each analysis, and tested for an interaction between observer and raccoon presence. To ensure that our results were robust, we further conducted a much more simplified model, using data calculated at the level of the island (i.e. island-level mean values of bird abundance). In this two-way ANOVA, we tested for island-level effects of raccoon presence, observer, and their interaction on bird abundance, and obtained identical results (not shown).

All intertidal and shallow subtidal prey abundance data were analysed using island-level means per quadrat (intertidal fish and shore crabs) or total individuals counted per island (red rock crabs) ($n = 12$ in all cases) and Mann–Whitney U -tests. Because the mid and high intertidal zones constitute distinct environments (as described above) with a different community composition (Irons et al. 1986), data from these zones were analysed separately when considering fish and shore crab abundance. To test if there was a difference in the size of red rock crabs between raccoon-present and raccoon-absent islands, consistent with raccoons being more likely to prey upon smaller individuals, we used transect-level (crabs hand captured in the intertidal) or trap-level (crabs trapped in the shallow subtidal) size values for each sex and conducted mixed-effects ANOVAs, with island as a random effect to account for multiple samples taken on each island ($n = 12$). We conducted separate analyses of the data on: (1) crabs hand captured in the intertidal, and (2) crabs trapped in the shallow subtidal. If the mixed-effects ANOVA revealed a significant interaction between sex and raccoon presence, we then tested for a difference in crab size within each sex using separate mixed-effects ANOVAs, again including island as a random effect. As with the bird abundance data described above, simple two-way ANOVAs using island-level mean crab size values tested for the effects of raccoon presence, crab sex, and their interaction on crab size, which again yielded identical results.

Results

Raccoon predation on song sparrow nests

As noted in the “Materials and methods”, our long-term data showed that the average nest predation rate in the Gulf Islands is 53 % (Zanette et al. 2006), and thus approximately half of all nests monitored suffered nest predation. We directly observed 48 attacks by predators on song sparrow nests, and raccoons accounted for 47.9 % of these attacks. Thus, approximately one quarter of all song sparrow nests initiated fell victim to raccoon predation. Corvids accounted for a further 27.1 % and mink (*Neovison vison*, 12.5 %), brown-headed cowbirds (*Molothrus ater*, 6.3 %), owls (4.2 %), and garter snakes (*Thamnophis elegans*, 2.1 %) accounted for the remaining nest predation events.

Raccoon presence and abundance in the Gulf Islands and Clayoquot Sound

Figure 1 presents the results of our 2011 survey, showing Gulf Islands on which raccoons were deemed to be present based on either direct observation or the presence of latrines. There was a highly significant association between these two methods (two-tailed Fisher’s exact test, $P < 0.001$). There were 22 islands on which raccoons were directly observed and latrines were found, and ten on which neither was observed. Consistent with latrines providing additional, independent information, there were five islands where latrines were found but no raccoons were seen, and no islands where the opposite was the case. For the 22 islands on which both raccoons and latrines were observed, estimates of relative raccoon abundance based on both methods (raccoons per km; latrines per tree) were significantly correlated (Spearman rank correlation, $r_s = 0.70$, $P < 0.001$).

Our 12 Gulf Islands study islands were resurveyed in 2012, and the results are reported in Table 1. We surveyed 77 km of shoreline across the 12 study islands, with the total distance being roughly equally divided between raccoon-present and raccoon-absent islands. The 33 km of shoreline surveyed in apex predator-present Clayoquot Sound in 2013 is thus comparable to the length of shoreline surveyed on the six raccoon-present Gulf Islands. Taking the total number of raccoons seen divided by the total length of shoreline surveyed (77 km in the Gulf Islands and 33 km in Clayoquot Sound), there were nine times as many raccoons seen per kilometre at night and 18 times as many seen per kilometre during the day in the Gulf Islands (1.77 km^{-1} night, 0.54 km^{-1} day) compared to Clayoquot Sound (0.20 km^{-1} night, 0.03 km^{-1} day). Our latrine transects on our 12 Gulf Islands study islands resurveyed in 2012 corroborate our direct count results, there being

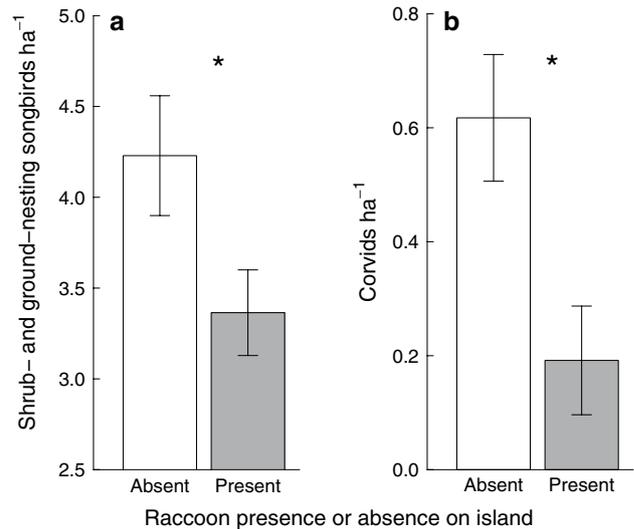


Fig. 2 Shrub- and ground-nesting songbird (a) and corvid (b) abundance per hectare on raccoon-present (grey bars) and raccoon-absent (white bars) islands. Values are mean \pm SE. * $P < 0.05$

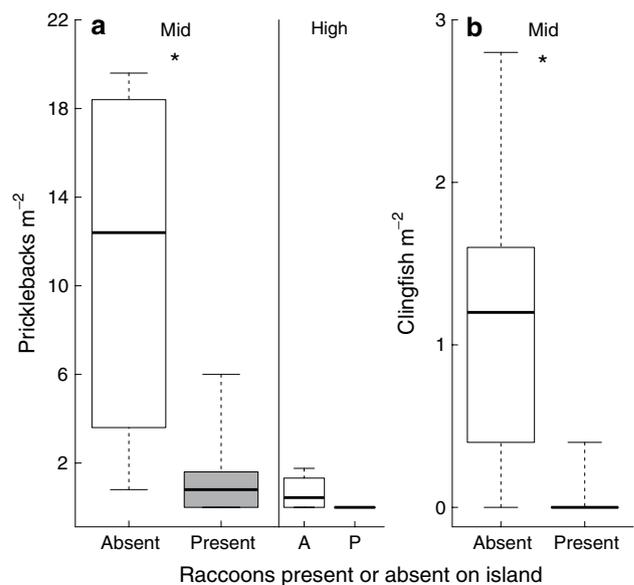


Fig. 3 a Prickleback and b northern clingfish abundance (m^{-2}) in the mid (mid) and high (high) intertidal zones on raccoon-present (grey bars) and raccoon-absent (white bars) islands. No clingfish were observed in the high intertidal zone on any island. Data are presented as standard box plots; the bold horizontal black lines indicate median values, the box edges represent the 25 and 75 % quartiles, and the whiskers signify the range. * $P < 0.05$

no latrines found on raccoon-absent islands (Table 1). We walked a total of 24 km conducting latrine transects on our 12 study islands, half of which (12 km) were on raccoon-present islands. As described in the “Materials and methods”, we also walked 2 km of latrine transects in Clayoquot Sound. The average number of latrines per tree found

on raccoon-present Gulf Islands (0.18) was six times the number found in Clayoquot Sound (0.03), consistent with the shoreline abundance of raccoons being much reduced where apex predators persist.

Effects of raccoon presence on bird abundance

Considering our 12 Gulf Islands study islands, there were significantly (21 %) fewer shrub- and ground-nesting songbirds counted (raccoon presence, $F_{1,10} = 6.4, P = 0.012$; presence \times observer interaction, $F_{1,10} = 0.03, P = 0.860$; Fig. 2a), as well as significantly (69 %) fewer corvids counted (raccoon presence, $F_{1,10} = 5.4, P = 0.020$; presence \times observer interaction, $F_{1,10} = 3.7, P = 0.083$; Fig. 2b), on raccoon-present, as compared to raccoon-absent islands.

Effects of raccoon presence on intertidal fish

There were significantly (94 %) fewer pricklebacks (Mann–Whitney $U = 32, P = 0.025$; Fig. 3a) on raccoon-present islands in the mid intertidal zone. Northern clingfish were also significantly less abundant on raccoon-present islands in the mid intertidal zone (Mann–Whitney $U = 32, P = 0.016$), being virtually absent where raccoons were present (Fig. 3b). In the high intertidal zone, clingfish were absent, while pricklebacks were rare, and tended to be rarer on raccoon-present islands, though not significantly so (Mann–Whitney $U = 27, P = 0.059$; Fig. 3a).

Effects of raccoon presence on shore crabs

There were significantly fewer shore crabs (*Hemigrapsus* spp.) in the large (90 % fewer; Mann–Whitney $U = 36, P = 0.004$; Fig. 4a) and medium (89 % fewer; Mann–Whitney $U = 35, P = 0.006$; Fig. 4b) size classes on raccoon-present islands in the high intertidal. Both large and medium shore crabs tended to be rare in the mid intertidal and both tended to be rarer on raccoon-present islands (Fig. 4), but not significantly so (large, Mann–Whitney $U = 27.5, P = 0.114$; medium, Mann–Whitney $U = 27, P = 0.180$).

Effects of raccoon presence on red rock crabs

On raccoon-present islands, we counted a median of 7.4 red rock crab carapaces per kilometre (range 0.5–16.0) diagnosed as having been freshly killed by raccoons during that tide cycle. As expected, we found no carapaces of red rock crabs freshly killed by raccoons on raccoon-absent islands. The average carapace size of red rock crabs freshly

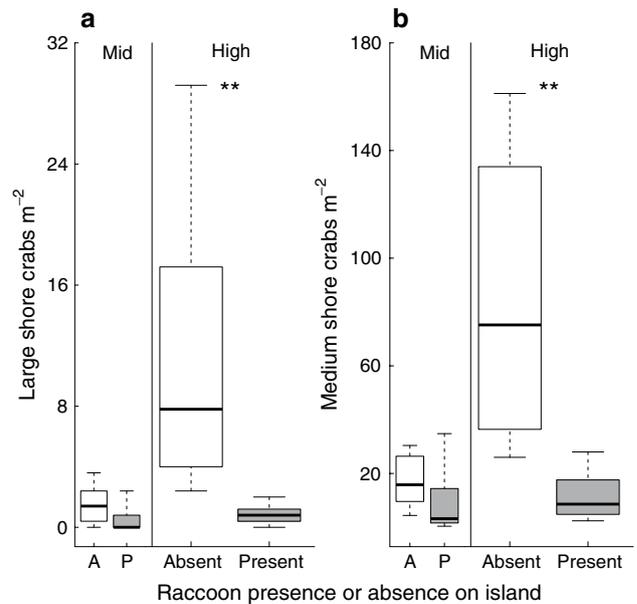


Fig. 4 a Large (>2.0-cm carapace width) and b medium-sized (1.31- to 2.0-cm carapace width) shore crab abundance (m^{-2}) in the mid (mid) and high (high) intertidal zones on raccoon-present (grey bars) and raccoon-absent (white bars) islands. Data are presented as standard box plots; the bold horizontal black lines indicate median values, the box edges represent the 25 and 75 % quartiles, and the whiskers signify the range. $**P < 0.01$

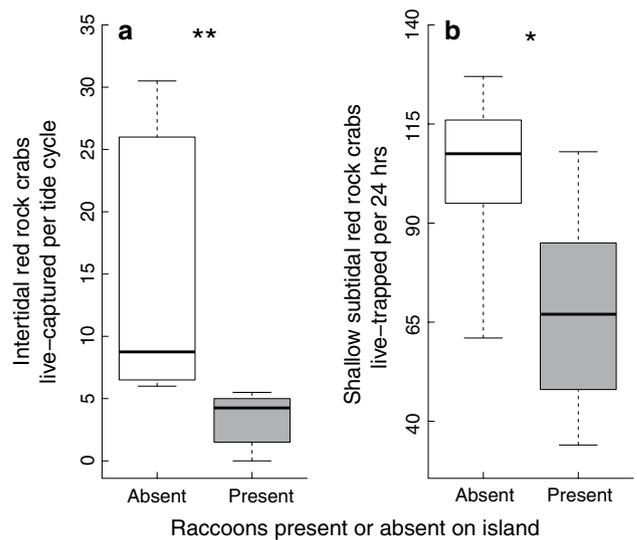


Fig. 5 a Intertidal and b shallow subtidal red rock crab abundance, considering red rock crabs live-captured per tide cycle, and live-trapped per 24 h (two full tide cycles), respectively, on raccoon-present (grey bars) and raccoon-absent (white bars) islands. Data are presented as standard box plots; the bold horizontal black lines indicate median values, the box edges represent the 25 and 75 % quartiles, and the whiskers signify the range. $*P < 0.05, **P < 0.01$

killed by raccoons was $8.3 (\pm 2.16 \text{ SD})$ cm, and most victims were female (82.1 %), consistent with smaller crabs being more vulnerable to raccoon predation (details below).

There were significantly (51 %) fewer red rock crabs in the intertidal on raccoon-present islands (Mann–Whitney $U = 36$, $P = 0.004$; Fig. 5a) in any given tide cycle. There were also significantly (38 %) fewer red rock crabs in the shallow subtidal on raccoon-present islands (Mann–Whitney $U = 31$, $P = 0.037$; Fig. 5b) during any given 24-h period (i.e. over any two full tide cycles).

The average size of live-caught red rock crabs tended to be smaller on raccoon-absent islands, consistent with the freshly preyed-upon red rock crab carapace data indicating that raccoons are more likely to prey upon smaller individuals (horizontal solid and dashed lines, Fig. 6), and that smaller red rock crabs are thus likely to have a better chance of survival on islands without raccoons. Data on the sizes of red rock crabs hand-captured in the intertidal and those live-trapped in the shallow subtidal were analysed separately. Considering red rock crabs accessible to raccoons in the intertidal, there was a significant raccoon presence by crab sex interaction ($F_{1,10} = 9.7$, $P = 0.014$), wherein males were indeed significantly smaller on raccoon-absent islands ($F_{1,10} = 4.09$, $P = 0.043$; raccoon-present = 12.69 ± 0.35 cm, raccoon-absent = 10.02 ± 0.60 ; mean \pm SE), but females were not ($F_{1,10} = 1.75$, $P = 0.186$; raccoon-present = 7.76 ± 0.45 cm, raccoon-absent = 8.15 ± 0.37). Considering red rock crabs live-trapped in the shallow subtidal (Fig. 6), there was a significant main effect of the presence of raccoons ($F_{1,10} = 4.47$, $P = 0.034$), wherein both males and females were smaller on raccoon-absent islands (presence by sex interaction, $F_{1,10} = 0.07$, $P = 0.795$), consistent with smaller red rock crabs having a better chance of survival on raccoon-absent islands.

Discussion

Our results show that mammalian mesopredators on islands may not only affect terrestrial communities, but can directly impact marine communities as well. We found significant effects of raccoon presence on terrestrial birds (Fig. 2), intertidal vertebrates (Fig. 3) and invertebrates (Fig. 4), and both intertidal and shallow subtidal red rock crab populations (Figs. 5, 6). These findings corroborate the broad breadth of the impacts mammalian mesopredators are anticipated to have on island communities.

Raccoon impacts on terrestrial bird communities

Raccoons are known to negatively affect songbird populations in continental systems (Wilcove 1985; Small and

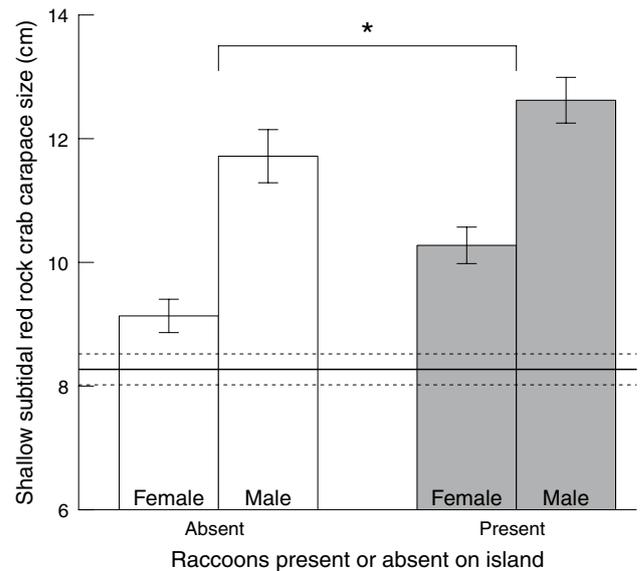


Fig. 6 Shallow subtidal red rock crab carapace size (cm) comparing males and females live-trapped on raccoon-present (grey bars) and raccoon-absent (white bars) islands. Values are mean \pm SE. For comparison, the carapace size of red rock crabs freshly preyed upon by raccoons is indicated by the horizontal solid (mean) and dashed (\pm SE) lines. * $P < 0.05$

Hunter 1988; Schmidt and Whelan 1999), particularly in areas where apex predators are absent (Soulé et al. 1988; Rogers and Caro 1998; Crooks and Soulé 1999; Schmidt 2003). Our video data demonstrate a clear impact of raccoon predation on song sparrow nests in the Gulf Islands, and our finding that both shrub- and ground-nesting songbirds and corvids are less abundant on raccoon-present islands (Fig. 2) is consistent with the hypothesis that mammalian mesopredators on islands negatively affect bird abundance. Taken together with our findings concerning intertidal and shallow subtidal prey, these negative effects on bird abundance corroborate that mammalian mesopredators whose diet is substantially subsidized by marine prey may significantly impact terrestrial prey (Rose and Polis 1998).

As outlined above, our video data indicate that, after raccoons, corvids are the second most important predator on song sparrow nests, accounting for more than a quarter of all nest predation events, and this was the principal reason for quantifying corvid abundance. Though we knew from the literature that corvids could also be affected by raccoon nest predation (Chamberlain-Augur et al. 1990), it was nonetheless surprising to find a strong effect of the presence of raccoons on corvid abundance (Fig. 2b). This discovery raises interesting questions about trophic interactions among the terrestrial predators on these islands, as the presence of raccoons is evidently reducing the abundance of a competitor for other songbird nests. Conceivably, this

putative interaction between the predators may have attenuated the difference in abundance of shrub- and ground-nesting songbirds between raccoon-present and raccoon-absent islands.

Direct killing as a primary cause of reduced bird abundance on raccoon-present islands is supported by our observations of high levels of raccoon predation on song sparrow nests, as well as an extensive literature implicating raccoons in songbird declines (Wilcove 1985; Small and Hunter 1988; Schmidt and Whelan 1999). However, it is possible that the lower number of birds detected on raccoon-present islands partially results from changes in bird behaviour. Passerines are able to assess landscape-level predation risk and adjust breeding territory selection (among other reproductive strategies) accordingly (Fontaine and Martin 2006; Lima 2009; Forsman et al. 2013). Both shrub- and ground-nesting songbirds and corvids may be able to assess raccoon presence [potentially through the detection of excrement (Forsman et al. 2013)] and preferentially nest on islands where raccoons are absent. As discussed in the previous paragraph, the presence of raccoons affects corvid abundance, and shrub- and ground-nesting songbirds may also conceivably use auditory cues (Zanette et al. 2011) from corvids to assess the likely abundance of raccoons.

Raccoon impacts on nearshore marine communities

Our results indicate that terrestrial mammalian mesopredators on islands may directly impact both the intertidal and shallow subtidal marine communities. Input from marine sources may strongly influence terrestrial populations and communities (e.g. Polis and Hurd 1996; Rose and Polis 1998; Stapp and Polis 2003; Field and Reynolds 2011). However, such marine subsidies are generally viewed as one-way interactions [i.e. donor controlled (Polis and Strong 1996)] in which the terrestrial receivers benefit, but have no effect on the marine populations and communities that support them. Here we show that raccoon populations with access to marine resources impact the local abundance of their marine prey. Furthermore, the role of terrestrial predators in structuring intertidal communities has received surprisingly little attention (Carlton and Hodder 2003), with most studies of intertidal communities focusing exclusively on marine organisms (Ellis et al. 2007). In a rare counter-example, Kurlle et al. (2008) found that Norway rat (*Rattus norvegicus*) predation on nesting seabirds on Alaska's Aleutian Islands indirectly affects the intertidal community through a trophic cascade, demonstrating the breadth of the impact of small mammals on island ecosystems. In our system, raccoons have been promoted to the top of both the terrestrial and nearshore marine food chains and thereby have a direct impact on both nesting birds and

intertidal and subtidal species. This direct effect may in turn initiate trophic cascades both within the terrestrial (as discussed above) and intertidal communities. Trophic cascades within the intertidal community may be anticipated because large crab species, such as the red rock crab, are themselves major intertidal predators (Behrens Yamada and Boulding 1996; Ellis et al. 2007).

Our results suggest that the level of predation exerted by raccoons on red rock crabs present in the intertidal at low tide leads to significant reductions in the size of the shallow subtidal source populations (Fig. 5b). We found: (1) substantial numbers of freshly preyed-upon carapaces in any given tide cycle on raccoon-present islands, (2) lower numbers of live-trapped red rock crabs in the shallow subtidal on raccoon-present islands, and (3) a smaller average size of subtidal red rock crabs on raccoon-absent islands (consistent with the anticipated higher survival of smaller individuals on these islands). Taken together, these results indicate that direct killing of red rock crabs (particularly small individuals) by raccoons leads to measurable changes in shallow subtidal red rock crab abundance. Nonetheless, our results do not rule out the possibility that the lower number of red rock crabs trapped on raccoon-present islands is partially due to changes in red rock crab habitat use (e.g. fewer individuals may migrate into the intertidal on raccoon-present islands) (Dill et al. 2003).

Mesopredator release in an island system

Several factors likely drive the strong impacts of raccoons observed in this study, including the current absence of native apex predators that were formerly widespread throughout the Gulf Islands, which has likely resulted in the relaxation of both direct predation and behavioural suppression of raccoons. Our results may therefore be partially attributable to the effects of mesopredator release, broadly defined as the ecological phenomena that occur when a mesopredator is 'released' from top-down control (Prugh et al. 2009; Elmhagen et al. 2010). Several studies from continental systems have documented mesopredator-driven declines in the abundance and diversity of terrestrial species at lower trophic levels following reductions in apex predator numbers (Prugh et al. 2009; Ritchie and Johnson 2009; Brashares et al. 2010). Our study demonstrates strong impacts on terrestrial prey in an island system that additionally extend to the surrounding marine community, impacting intertidal and shallow subtidal prey. Our comparison of the relative abundance of raccoons along shorelines in the Gulf Islands with that in apex predator-present Clayoquot Sound indeed suggests that apex-predator presence could potentially mitigate raccoon impacts on intertidal and shallow subtidal prey, either by locally reducing raccoon numbers or by reducing their use of risky shoreline

habitats (or both). This is not a direct test of the effect of apex-predator presence on raccoon impacts, but strongly indicates that such a test may provide a promising avenue for future research.

The impacts of mesopredator release may be particularly severe on islands precisely because island mesopredators can exploit both terrestrial and marine prey. Dramatic increases in abundance are known to result from the combination of high food availability, and increased time spent foraging in the absence of predators (Krebs et al. 1995; Karels et al. 2000; Zarette et al. 2003, 2006). Such dramatic increases in abundance may be expected to be common in the case of mesopredator release because mesopredators are typically omnivores and so likely always have access to abundant food of some sort (Brashares et al. 2010), which they can spend virtually all their time eating in the absence of apex predators. Given the opportunity to exploit both terrestrial and marine prey, island mesopredators may be particularly likely to increase in abundance when enabled to spend more time foraging in the absence of apex predators. We suggest that our results provide some support for this scenario. Gulf Islands raccoons are definitely exploiting both terrestrial (Fig. 2) and marine (Figs. 3, 4, 5, 6) prey, providing them access to abundant food; and our evidence suggests that they may be spending more time foraging given that we observed considerable diurnal activity (Table 1) in this generally nocturnal species (Gehrt 2003), and that the level of diurnal activity was 18 times higher than in apex predator-present Clayoquot Sound. This combination of factors could lead to substantial increases in raccoon abundance, potentially contributing to the markedly (at least nine times) greater number of raccoons observed along shorelines in the Gulf Islands compared to apex predator-present Clayoquot Sound.

Conservation implications

Globally, island bird and mammal communities have been severely impacted by mammalian mesopredators (Burbidge and Manly 2002; Blackburn et al. 2004), and our results suggest that marine communities may be similarly affected. The loss of native apex predators is considered by some to be ‘humankind’s most pervasive influence on the natural world’ (Estes et al. 2011, p 301), and we stress that a focus on the loss or absence of native apex predators in island systems may help elucidate why the impacts of mammalian mesopredators on islands have been so dramatic. Our results highlight two important objectives for the conservation of island ecosystems. Firstly, preventing the spread of mammalian mesopredators to currently unoccupied islands should be a major conservation priority (Morley and Winder 2013), and implementation of eradication programs, which have shown marked success

on islands (Zavaleta et al. 2001), may be warranted when new introductions occur. This is of immediate relevance to our study system since our results clearly indicate that preventing the spread of raccoons to currently unoccupied Gulf Islands (Fig. 1) is crucial to maintaining the ecological integrity of the Gulf Islands National Park Reserve, and should be prioritized by park managers. Secondly, as we have outlined, the role apex predators play in suppressing the foraging behaviour of mesopredators (Ritchie and Johnson 2009; Brashares et al. 2010; Wilson et al. 2010; Hudgens and Garcelon 2011) may be particularly critical in island systems, meaning that where mesopredator eradication is inappropriate (e.g. because the mesopredator is native), maintaining or restoring native apex predators in islands systems may be even more essential than elsewhere (Prugh et al. 2009; Ritchie and Johnson 2009; Brashares et al. 2010).

Acknowledgments We thank the numerous field crews that assisted in collecting the camera data concerning raccoon predation on song sparrow nests, and in particular M. C. Allen, M. Travers and A. F. White. A. Currie, T. Diesch and D. Hope provided field assistance in the Gulf Islands, and we thank J. Sibbald for assistance in Clayoquot Sound. Thanks to Parks Canada, BC Parks and the owners of Coal, Domville, James, Moresby and Mowgli islands for access to the sites; and T. Golumbia and B. Clinchy for their support. Two anonymous reviewers provided helpful comments on the manuscript. Funding was provided by Natural Sciences and Engineering Research Council of Canada Discovery grants to M. C., L. Y. Z. and L. M. D., in addition to a Premier’s Research Excellence Award and Canada Foundation for Innovation grant to L. Y. Z. This work was approved by the Animal Care Committees of the University of Western Ontario and University of Victoria and conforms to the legal requirements of Canada.

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