



Recolonizing sea otters spatially segregate from pinnipeds on the Canadian Pacific coastline: The implications of segregation for species conservation



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ABSTRACT

The reintroduction and recolonization of species extirpated from former ranges are key components of species conservation. Resource availability affects recolonization success and resulting distribution patterns, but top-down processes may also play a role through density-mediated or trait-mediated indirect effects that may exclude a species from otherwise suitable habitat. We predicted that the spatial distribution of recolonizing sea otters, *Enhydra lutris*, on the Canadian Pacific coastline was explained by resources as well as interspecific interactions – spatial segregation from pinnipeds, the preferred prey of killer whales *Orcinus orca*. We surveyed the summer occurrence of sea otters and pinnipeds on Vancouver Island, Canada. We quantified coastline density and bathymetry at multiple spatial scales as indices of habitat complexity and foraging habitat availability. We used generalized linear model selection to test hypotheses about sea otters' spatial relationship to resources and heterospecifics. Pinniped presence negatively predicted sea otter presence, even after accounting for complexity and foraging habitat. Sea otters may segregate from pinnipeds due to trait-mediated indirect effects of predation, leading us to hypothesize apparent competition between sea otters and pinnipeds. Research is needed to test this hypothesis; if true, refuge from apparent competitors may be a key component of recolonization habitat for sea otters. Species distribution models should quantify resource landscapes but also species-scapes: the spatial plane of species interactions that combines with resources to drive species distributions. Conservation plans based on recolonization models that include only resources may overestimate available habitat, carrying capacity, and recolonization success.

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1. Introduction

North American mammals have been extirpated from much of their range in the last century (Laliberte and Ripple, 2004). Reintroducing species to former ranges can be a key component of conservation programs (Hayward and Somers, 2009; Morrison, 2009). As species are extirpated from, or recolonize, former ranges they can markedly affect community composition and ecosystem function (Pace et al., 1999; Terborgh and Estes, 2010). To predict the success of species reintroductions and the magnitude of subsequent ecosystem change, we must understand how the biotic and

abiotic components of the recolonized landscape affect recolonization patterns. Resources are obviously important, but biotic interactions in particular may be important in shaping a species' distribution on the landscape (Wisiz et al., 2013).

Landscapes are typically quantified as mosaics of discontinuously distributed resources that affect species distributions through several mechanisms (Dunning et al., 1992; Wiens et al., 1993). However, landscapes also integrate an individual's lifetime interactions with competitors, predators, parasites, and mates (e.g. Wiens et al., 1993; Morris, 2003; Morrison, 2009). Landscapes are therefore also species-scapes, with sympatric species influencing each other's distributions through interspecific interactions such as predation and competition. Although conceptually fundamental to ecology, interspecific interactions are rarely included in models of species distributions (Godsoe and Harmon, 2012),

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with few exceptions (e.g. Aunapuu and Oksanen, 2003; Harrington and Macdonald, 2008; Vanak and Gompper, 2010).

Interspecific interactions can influence a species' distribution among habitat patches via predation, predation risk, resource or interference competition, or apparent competition among prey species that share a predator (*sensu* Holt, 1977, 1984). Landscape spatial heterogeneity can mediate these interactions – varying the outcome of predation and competition across space – thus facilitating species coexistence (Chesson, 2000). Spatially mediated interactions can manifest as patterns of spatial segregation among sympatric species, wherein one is more likely to occur in the absence of the other at local spatial scales (Amarasekare, 2003; Murrell and Law, 2003). Predation in particular is a potent selection pressure for prey species to adopt or evolve strategies that reduce predation risk (Lima, 1998; Sih et al., 1998, 2000). Predation obviously impacts prey populations through density-dependent direct or indirect effects (Abrams, 1995). However, predation can also generate trait-mediated indirect interactions (Abrams, 1995; Schmitz et al., 2004) wherein perceived predation risk influences a prey species' behaviour, such as habitat selection (Lima and Dill, 1990). Scaling up from local habitat choices to landscapes, indirect interactions can structure species distributions (Ripple and Beschta, 2004; Hebblewhite and Merrill, 2009). We suspected that indirect interactions may be affecting sea otter (*Enhydra lutris* Linnaeus) recolonization of the Canadian Pacific coastline. As a first test, we hypothesized that sea otters spatially segregate from pinnipeds, the preferred prey of their shared predator, the killer whale *Orcinus orca*.

Sea otters once numbered in the hundreds of thousands across the northeast Pacific Rim (Kenyon, 1969), but were extirpated from Canadian Pacific shores by the 1920s. In the 1970s sea otters were reintroduced to Checleseth Bay on northern Vancouver Island, British Columbia (B.C.), Canada. Sea otter populations have increased since reintroduction, recolonizing adjacent areas of the coastline (Bigg and MacAskie, 1978; Watson et al., 1997; Nichol et al., 2009). Coastal ecosystems were restructured in response to growing sea otter abundance and distribution (Watson and Estes, 2011). Sea otters are prey generalists, eating bivalves, fishes, and crabs, but preferring sea urchins (*Strongylocentrotus* spp.) (Kenyon, 1969; Reid and Estes, 1990). In the absence of sea otters, herbivorous sea urchins dominate and extirpate kelp forests, creating low-productivity “urchin barrens” (Estes and Palmisano, 1974; Estes et al., 1978; Estes and Duggins, 1995). Sea otters suppress urchin populations, allowing kelp regrowth. Regrowth initiates a trophic cascade that alters organic carbon flows (Duggins et al., 1989), carbon sequestration (Wilmer et al., 2012), fish communities (Watt et al., 2000), and predator–prey interactions among invertebrates and sea birds (see Estes et al., 2004, 2009a for reviews). Though sea otters' effects on coastal communities have been well researched, the effects of coastal communities on sea otters have not.

Sea otters are preyed upon by *transient*-ecotype (mammal-eating) killer whales (Hatfield et al., 1998; Williams et al., 2004; Vos, 2006). Killer whales in western Alaska may have sequentially switched from diminishing great whale prey populations to seals, Steller sea lions, and then sea otters, driving precipitous declines (Springer et al., 2003; Williams et al., 2004). In recent decades western Alaskan sea otter populations experienced the most precipitous decline of a mammalian carnivore in recorded history (Doroff et al., 2003), and substantial evidence supports predation by killer whales as the mechanism (Springer et al., 2008; Williams et al., 2004; Estes et al., 1998, 2009a,b). Orca predation on sea otters is only anecdotally reported in Canada, but little to no time has been dedicated to researching such events. Even in long-studied Alaskan waters, orca attacks on otters are rarely observed, yet orca predation has had marked effects (Estes et al., 1998). Sea otters have evolved with killer whales, and if killer

whales pose a predation risk – or even a perceived risk – then there may exist strong selection pressure for sea otters to minimise this risk through habitat selection.

1.1. Hypothesized drivers of sea otter occurrence

We weighed the evidence for three hypotheses.

- (i) Sea otters consume a quarter of their biomass in prey daily to meet high metabolic demands (Kenyon, 1969) and so forage frequently (Bodkin et al., 2004). Thus we hypothesized that sea otter distribution is strongly linked to prey distribution (e.g. Gregr et al., 2008). However, as the western Canadian coastline has been without sea otter predation for over five decades, prey abundance and diversity are high in newly recolonized areas (Watson and Estes, 2011), and this was true of the study area (seafloor camera surveys, unpublished data). As most sea otter foraging occurs with 30 m of water (Bodkin et al., 2004; Laidre et al., 2009), we assumed that the percent of seafloor area between 0 and 30 m deep was a reasonable proxy for forage availability.
- (ii) Winter storms are common on this coastline. Winter storms were a major source of mortality of dependent California sea otter pups (Jameson and Johnson, 1993); if storms on this coast represent a significant source of mortality, then otters may then be selecting for coastline shelter, which we indexed with coastline complexity.
- (iii) If nearby pinnipeds represent a predation risk by opportunistically foraging orcas, then sea otters may avoid areas with pinnipeds. We tested whether sea otter occurrence on Vancouver Island could be explained by the presence of harbour seals (*Phoca vitulina richardsii*) and Steller sea lions (*Eumetopias jubatus* Schreber), killer whales' preferred prey.

2. Material and methods

2.1. Study area

We surveyed the number and locations of sea otters and pinnipeds on the west coast of Vancouver Island, British Columbia, Canada (Fig. 1). We sampled the coastline from the southern extent of Clayoquot Sound in the southeast, the limit of local reports of sea otter occurrence on the recolonization gradient; to Nootka Sound in the northwest, where sea otters have been established for almost two decades (Watson and Estes, 2011). This was the northernmost point we could feasibly survey, though the ranges of all three species extend beyond this sampling frame.

The study area experiences temperate summers and mild winters with copious rain and frequent intense storms. The rugged coastline is composed of curvilinear sandy beaches and complex rocky cliffs with outlying rocky reefs. It is bordered by a subsurface shelf reaching depths over 100 m, and is cut by fjords over 300-m deep. Numerous small islands and several larger islands (circa 150 km²) dot the coastline. Sea urchins are common in rocky reefs, and bivalves (*Saxidomas*, *Macoma*, *Panopea*, *Tresus* spp.) occur in sandy sediments. Kelp forests (*Laminaria saccharina*, *Macrocystis integrifolia*, *Nereocystis luetkeana*) are clustered sporadically along the coastline, supporting a high diversity of fish, crabs and other sea otter prey. *Transient*-ecotype (mammal-eating) killer whales frequent these waters (Ford et al., 1998).

2.2. Species sampling

We surveyed the number and location of sea otters, seals, and sea lion individuals from May to October 2006 via boat-based linear transect surveys totalling over 300-km in length (Fig. 1). Survey

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