

Predator effects link ecological communities: kelp created by sea otters provides an unexpected subsidy to bald eagles

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Abstract. Ecological communities are best studied at the landscape level, where linkages among communities are considered. Such linkages are often driven by increases in primary production caused by apex predators limiting herbivores. In this note, we describe a novel linkage among sea otters (*Enhydra lutris*), the long-lived woody kelp (*Pterygophora californica*), and bald eagles (*Haliaeetus leucocephalus*). While counting sea otters in an isolated group of rocky islets on the Central Coast of British Columbia, we found an eagle nest composed of mostly *Pterygophora* stalks. *Pterygophora* recruits rapidly after sea otters arrive in an area and limit sea urchins; the subsequent pulsed *Pterygophora* recruitment results in narrow age-class cohorts that senesce *en masse* after about 20 yr. When the woody stipes wash ashore, they degrade slowly and persist as beach wrack for years. These windrows of woody kelp are common on the BC coast where sea otters have re-established. We demonstrate how this subsidy can be used by bald eagles, and predict that as sea otters recover across their range in BC, further effects of *Pterygophora* to intertidal, supralittoral, and terrestrial communities will be observed.

Key words: bald eagle; habitat subsidy; kelp forest succession; landscape ecology; predator effects; *Pterygophora*; sea otter.

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Ecological communities are increasingly being studied at a landscape level, where the transport of primary production among communities is integral to the understanding of food web structure (Polis et al. 1997, Darimont et al. 2008, Jelinski 2014, Duggins et al. 2016). Nutrient subsidies between aquatic and terrestrial communities occur in myriad ecosystems (Polis and Hurd 1996, Hocking and Reimchen 2002, Maron et al. 2006). Subsidies linking adjacent communities can also include habitat subsidies, such as trees swept from land to sea that facilitate colonization of islands by small mammals, and provide

ongoing shelter once washed ashore (McCabe and McTaggart-Cowan 1945, Colombini and Chelazzi 2003). It is often apex predators that connect these ecological communities, especially when they affect primary production (Estes et al. 2011, 2016, Atwood et al. 2015).

The trophic cascade by which sea otters (*Enhydra lutris*) indirectly enhance kelp by consuming herbivorous sea urchins (Estes and Palmisano 1974) is well known and widely demonstrated (Estes and Duggins 1995, Watson and Estes 2011). Kelps (seaweeds in the order Laminariales) in turn have diverse influences on coastal

ecosystems, including increased production (Duggins et al. 1989) and habitat complexity (Mann 1973), altered water flow (Duggins 1988), and numerous knock-on effects on other species and processes (see Estes et al. 2016 for a review). The influences of this kelp extend from coastal environments into the deep sea (Harrold et al. 1998), the atmosphere (Wilmsers et al. 2012, Krause-Jensen and Duarte 2016), and onto land. When washed ashore, kelp can provide nutrient and habitat subsidies to nearshore and terrestrial communities (Dugan et al. 2003, Jelinski 2014). Known kelp effects on land derive from nutrient enhancement, which in turn fuels detritivores, omnivores, and eventually birds and small mammals (Polis and Hurd 1996, Rose and Polis 1998). Kelp wrack also provides habitat for organisms living in the intertidal, supralittoral, and adjacent terrestrial zones (Colombini et al. 2000).

In addition to the indirect effects that sea otters have on ecological communities via the provision of kelp, sea otters can affect other species directly (Estes et al. 2016). One such example occurs between sea otters and bald eagles (*Haliaeetus leucocephalus*). In the Aleutian Islands, when sea otters are abundant, bald eagle diets are composed of about 15% sea otter pups and are approximately 10% higher in kelp-associated fish species compared with the diet of eagles in areas without sea otters, where eagles consumed about 25% more sea birds (Anthony et al. 2008). In this note, we describe another effect of sea otters on bald eagles, one that links them indirectly.

While conducting sea otter surveys in 2015 and 2016 along the central coast of British Columbia, Canada, we stopped in the Gosling Rocks to check a bald eagle nest for sea otter pup remains, which were noted in this same nest during surveys conducted in the 1990s. Over a two-year period, we collected 13 bald eagle pellets composed mostly of sea otter pup fur, from the nest area. Much to our surprise, the eagle nest, which had been constructed entirely of tree branches in the 1990s, was now predominantly made from woody stipes of the kelp *Pterygophora californica* (Fig. 1).

Sea otters, which were extirpated from BC in a coast-wide fur trade that ended in the early 1900s, were reintroduced to BC waters from 1969 to 1972 and have since reoccupied much of their historic range (Nichol et al. 2015). As this growing sea otter population expanded its range, it



Fig. 1. *Pterygophora californica* stipes used in an eagle nest.

quickly reduced sea urchin abundance, thereby allowing kelp to recruit into the newly created urchin-free space (Watson and Estes 2011). *Pterygophora californica*, a long-lived woody kelp that grows to a height of about 2 m, is one such kelp species. This rapid pulse of recruitment often creates forests of perennial kelp that are dominated by a few age classes (Watson and Estes 2011). The resulting kelp stands can persist for up to 20 yr, before senescing, which, because of their narrow age range, occurs en masse (Watson and Estes 2011). These mass senescence events create episodic windrows of *Pterygophora* wrack on shore, and are frequently observed along the BC coast in areas where sea otters have occurred for more than 20 yr. These mass recruitment, extended persistence, and abrupt mass senescence events create a pulsed kelp subsidy that likely explains why *Pterygophora* suddenly appeared in the bald eagle nest in the Gosling Rocks.

The woody stipe of *Pterygophora* can be aged from its annual growth rings (De Wreede 1984),



Fig. 2. Windrows of *Pterygophora californica* stipes.

and the modal age of cohorts has been used to approximate when sea otters arrived at sites along the west coast of Vancouver Island (Watson and Estes 2011). In 1991, the modal age of *Pterygophora* at Gosling Rocks was 8 yr, which places the arrival of sea otters to this site at the early 1980s (Prizing et al. 2016). *Pterygophora* stipes, which can persist on the beach for years (Fig. 2), would have begun to appear in large numbers on the beaches adjoining the Gosling Rocks in the early 2000s, at which point eagles likely began using them for nest building.

In areas where trees are scarce or absent, raptors can be remarkably opportunistic and plastic in their use of nesting materials (Ellis et al. 2009). Golden eagles (*Aquila chrysaetos*) build nests with deer antlers, Ferruginous hawks (*Buteo regalis*) constructed nests from bison (*Bison bison*) ribs on the Great Plains in the early 1900s, and steppe eagles (*Aquila nipalensis*) have been observed using desiccated mammal skins in their nests (see review in Ellis et al. 2009). On the western shores of North America, where bald eagles nest from the Aleutian Islands to Baja,

Mexico, most nests are built with sticks and branches, and are perched in old-growth trees adjacent to the shoreline (Robards and King 1966). However, in Alaska ground nests are common at exposed, treeless islands in the Aleutians (Robards and King 1966) where nesting materials can include grasses (Robards and King 1966) and occasionally seaweed (Watts et al. 2015). *Pterygophora* does not occur in the Aleutian archipelago (Lindeberg and Lindstrom 2010) and the stipes of the kelps that do occur there are less woody and degrade more rapidly than those of *Pterygophora* which can persist on the beach for years (J. C. Watson, *personal observation*).

Along the BC coast, bald eagles also nest on the ground, constructing nests from grasses when trees (and kelp) are absent (authors, *personal observation*). The Gosling Rocks are an isolated group of about 70 rocky islets with only one treed islet (six trees >3 m tall). The nearest forested area is over 3 km away; therefore, kelp may provide a new resource for eagles nesting in this area that is easier to use than tree branches from more distant habitats. In the nearby McMullin Islands where trees are abundant, *Pterygophora* senesced and washed up along beaches in 2014, about 18 yr after sea otters were first seen in the islands (Nichol et al. 2015). Some 3 yr later, windrows of *Pterygophora* wrack still persist along the shore. Surveys of wrack biomass conducted on 101 islands in nine archipelagos in the same region revealed that the McMullin Islands had a mean of 48 g/m² of dry *Pterygophora* biomass accumulated along their shorelines. This was significantly more (ANOVA; $F_{8, 4103} = 4.861$, $P < 0.05$) than any of the other eight archipelagos which ranged in mean values from 0 to 10 g/m² (in Tukey's multiple comparisons of means the McMullin Islands archipelago differed from all of the eight other archipelagos, $P < 0.05$; Wickham 2017). Despite this, we did not detect *Pterygophora* in any of the four eagle nests we examined (by binoculars) in the McMullin Islands, although we found a collection of *Pterygophora* stipes ($n = 5$) scattered at the base of one nest. We suspect that *Pterygophora* is most useful as nesting material when trees are scarce.

The onshore deposition of seaweed wrack provides an important connection between marine and terrestrial communities. The importance of sea otters in driving kelp forest biomass and

influencing community structure is well known. Our observations illustrate another way in which sea otters can affect adjoining ecological communities; when suitable kelp, created indirectly by foraging sea otters, washes ashore, it can provide bald eagles with nesting materials. As a source of wrack, *Pterygophora* differs from most other algae in that its woody stipes degrade slowly allowing it to persist on the beach for years. Furthermore, most seaweed subsidies occur seasonally whereas the mass senescence of *Pterygophora* is demographically driven and occurs on a decadal scale; one set by the colonization history of the expanding sea otter population (Watson and Estes 2011). As the BC sea otter population continues to expand and kelp forest succession processes are re-set across the coastal landscape, further mass senescence events in *Pterygophora* will occur. Given the expanding range of sea otters along the BC coast, we predict that the windrows of senesced *Pterygophora* may have other unexpected effects on intertidal, supralittoral, and terrestrial communities.

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