



Marine to Terrestrial Subsidies on the Gaviota Coast

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Objectives

The primary objectives of this report are 1) to understand the likely role, if any, of animals in providing energetic connectivity across ecosystems along the Gaviota coastline of California, including identifying those taxa likely most important to maintaining any connectivity, with a focus on connectivity between marine and inland terrestrial ecosystems, and 2) to synthesize existing knowledge on subsidy impacts to evaluate the likely ecological importance of connectivity in this environment, including identifying areas and times where connectivity is likely to be most important.

We first provide a general summary overview on the role of animal derived subsidies in ecosystems, highlighting their ecological importance and context dependence, and emphasizing limitations to this report. We then summarize knowledge on spatial subsidies from the region and similar Mediterranean ecosystems. Finally, we review taxa likely to be important as vectors or recipients of subsidies in the Gaviota coast, pulling data from current camera trapping studies in the region and data from the literature on these species.

Section I: Overview of spatial subsidies

Animal Subsidies

Movement of resources and energy across ecosystems is a pervasive and important ecological phenomenon and fundamentally drives patterns of productivity and biodiversity in both the '*donor*' and '*recipient*' ecosystems (see inset Terminology Box, pg 2). Disruption of these subsidies can cause whole scale transformation of ecosystems (e.g. grassland to tundra, Croll et al 2005) and of ecosystem processes (reviewed in more depth to follow). These *spatial subsidies* (resources produced in one system but moved to another, also often referred to as *allochthonous resources*) can be delivered as *passive subsidies* via abiotic forces (e.g. waves or currents washing marine wrack onto shore, wind

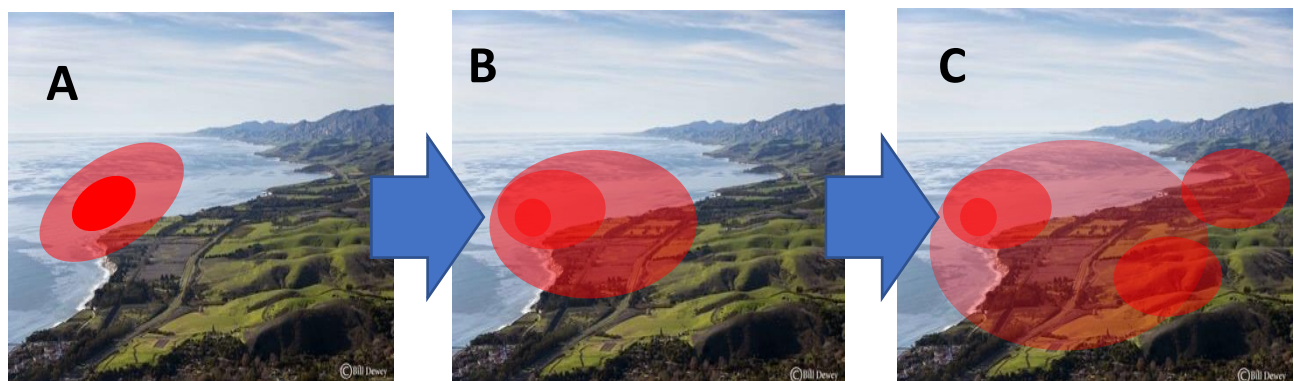


Figure 1. Physical, abiotic processes such as upwellings and waves may create an underlying nutrient gradient in a landscape (A). Animals may then transfer nutrients directionally, including against natural physical gradients (e.g. animals transferring nutrients upland into the interior (B). Secondary consumption may further distribute these nutrients, often creating spatial heterogeneity in distribution of subsidized nutrients (e.g. animals moving nutrients to dens, along riverways) (C).

moving nutrient rich dust across continents, gravity carrying falling leaves into streams) or ‘actively’ via animal *vectors*.

While animal driven *active subsidies*, the focus of this report, were once thought to be relatively unimportant to ecosystem scale processes, that dogma has been largely upended in the last 30 years. Animal subsidies are now known to often be comparable in magnitude to those derived from all passive subsidies – those moved by wind, water, erosion, currents, and wildfire (Earl and Zollner 2017). Moreover, animal vectored subsidies have several ecological characteristics that often make them more critically important to ecosystems than are abiotic subsidies (as reviewed by McInturff et al 2019). Most notably, they are capable of moving nutrients spatially back across the natural abiotic gradients – for example, salmon move nutrients upstream, seabirds systematically transfer nutrients back to islands they ranoff from, and migratory animals often move nutrients directionally against widespread wind or current patterns (Fig 1B). Furthermore, animals often react to the nutrient gradients they create – creating opportunities for feedback or synergy, ultimately altering landscapes in which they live (Fig 1C). Additionally, animals can behaviorally modify the times they use resources, for instance to coincide with times of stress or shortage in recipient ecosystems; the ability to change timing of delivery of resources can be particularly critical in reducing temporal variability and stress in recipient ecosystems. Lastly, animal resources are often of particularly high quality, as animals tend to concentrate limiting nutrients

Terminology

Active subsidies: Nutrients redistributed across and within ecosystems via biotic vectors, usually mobile animals, often against natural nutrient gradients. Examples include seabirds foraging at sea and defecating on land, rats foraging in intertidal but defecating – and dying – on land.

Allochthonous resources: A synonym for spatial subsidies.

Donor ecosystems: The ecosystem that produces the resources moved via active or passive processes to the recipient ecosystem. E.g. for seabirds foraging at sea and defecating on land, the ocean is the donor ecosystem. However, it is important to note that nutrient redistribution is often circular, such that donor ecosystems are also recipient ecosystems. For instance, oceans are recipient ecosystems for nutrients that run off from terrestrial sources.

Passive subsidies: Nutrients distributed across and within ecosystems by environmental and physical processes such as wind, current, gravity and erosion. Examples include marine algae being washed ashore, dirt and nutrients running off terrestrial habitats and into aquatic ones, leaves falling from trees into rivers and then being carried into the ocean.

Recipient ecosystems: The ecosystem that received the resources moved via active or passive processes from the donor ecosystem. E.g. for seabirds foraging at sea and defecating on land, the land is the recipient ecosystem. However, it is important to note that nutrient redistribution is often circular, such that donor ecosystems are also recipient ecosystems. For instance, land is the donor system ecosystem for nutrients that run off from terrestrial sources into the sea.

Spatial subsidies: Resources that are produced in one ecosystem but moved to another via either abiotic or biotic processes. Resources are typically macro or micronutrients that are limiting in the recipient ecosystem – with common examples being nitrogen, phosphorus, and iron – often transported in the form of some organic material (e.g. plant debris, guano, carcasses).

– such that animal derived subsidies can have disproportionately large impacts compared to their biomass.

Animal vectored subsidies can be classified into two basic types. The first case is when the animal gathers resources in one system and moves it to another system (via excretion, gametes, or egestion). Examples of this first type of subsidy include seabirds foraging at sea and returning to shore to rest and defecate (Young et al 2010, 2016); migratory grazers such as wildebeest consuming and excreting large amounts of plant material across space (Holdo et al 2007); hippopotamus feeding on land at night and defecating in rivers where they rest during the day (Stears et al 2018). The second type is when animals themselves become subsidies as carcasses. For instance great whales when they die subsidize deep water environments creating entirely novel ‘whale fall’ ecosystems (Bennet et al 1994, Roman & McCarthy 2010); salmon enrich otherwise low nutrient stream ecosystems from their carcasses at the end of their migrations (Deacy et al 2016), and emergent insects and amphibians carry the nutrients in their bodies from freshwater streams and lakes where they typically develop to the terrestrial ecosystems where they ultimately die (Capps et al 2015, Dryer et al 2015).

Animal vectored subsidies are highly vulnerable to disruption. Indeed, early humans may have disrupted upwards of 90% of nutrient transport by the systematic reductions of large animals (Doughty et al 2015). Animal subsidies depend not only on the persistence of the animal itself at robust population sizes (as nutrient redistribution is typically proportional to the abundance of the animal), but it also relies on the animal being able to persist in its natural behavior. Certainly, disruptions that alters the abundance of the animal (e.g. introduction of a non-native predator or disease) are well documented to change the subsidy movement, with cascading effects on plant and consumer communities. For instance, introduction of foxes and rats on islands has caused whole ecosystem transformation of plant and animal communities on these islands through their negative impacts on the seabirds that typically vector nutrients to these systems (Croll et al 2005, Maron et al 2006). However, ecosystem changes that affect behavior can have equally dramatic effects. For instance, introduced plants have been shown to cause birds to change nesting locations, causing a downward spiral of nutrient depletion and subsequent biodiversity loss in invaded ecosystem without any absolute change in total bird abundance (Young et al 2010, 2016). Similarly, the introduction or removal of wolves in Yellowstone appears to primarily change the landscape of nitrogen availability by changing the location in which elk feed (as elk avoid landscapes where wolves are present), not through changes in abundance of elk (Frank 2008). Barriers to movement or migration are likely to be particularly important in altering spatial subsidies.

Ecosystem Importance

The most straightforward impact of subsidies is on basic ecosystem productivity (typically quantified as the biomass of carbon produced per unit area). As subsidies often remove previous (often nutrient based) limitations to productivity, subsidized ecosystems typically show strong increases in productivity. For example, subsidized islands in Baja California have productivity levels 3 to 24 times higher than unsubsidized islands (Anderson & Polis 1999, Fig 4). This huge bottom up stimulus trickles up to

consumers, such that animal subsidies can often form between 25-100% of total carbon of consumers in an ecosystem (Baxter et al 2005). These consumer affects can be critical to survival or reproduction even of top consumers (e.g. grizzly bears, and wolves; Adams et al 2010) The loss of these subsidies thus often has major negative impacts on plants and consumers reliant on them, these impacts could be particularly challenging for at risk or endangered species. For examples endangered bats rely on emergence of aquatic insects (Kurta & Whitaker 1998), while endangered shorebirds forage on insects in intertidal marine wrack, and endangered whales feed on migratory salmon (Foster et al 2012). Disruption of these subsidies could cause decline or extirpation of these at risk species.

The changes that animals drive to their ecosystems can also often create feedbacks, often positive, but sometimes negative. For instance, anemonefish that subsidize anemones through their defecation cause those anemones to grow, creating more habitat not only for more anemonefish but also nursery habitat for other species of damselfish (McIntyre et al 2008). Similarly, grazing animals create highly productive grazing lawns by concentrating nutrients (Augustine 2003); these fertilized lawns further concentrate grazers but also support different plant and animal communities, furthering landscape level diversity.

Animals in subsidized ecosystems show a range of different responses – including increases in reproduction, increases in body condition, and changes in behavior and physiology – in addition to changes in absolute abundance. Likewise, in addition to changes in community composition and abundance, plants in subsidized ecosystems show systematic changes in leaf quality, structure, and life form (reviewed in Ellis et al 2006). Both plant and animal communities have been shown to have changes in richness and diversity as well as composition in response to addition or removal of subsidies (Fukami et al 2006, Young et al 2013).

Unsurprisingly, given the magnitude of changes observed for plant, animal, and microbial communities, there is also strong evidence for changes in complex ecosystem processes with the addition or interruption of subsidies. For instance, the loss of marine subsidies on islands in New Zealand has been shown to change rates of decomposition and mineralization (Fukami et al 2006). Additionally, both modelling and field work have also shown that the removal of subsidies can cause fundamental changes in food web structure and stability (Young et al 2013, Huxel & McCann, 1998; Nowlin et al., 2007; Leroux & Loreau, 2008).

Context Dependence

Animal subsidies occur across a diverse set of taxonomic groups (from zooplankton to whales) and ecosystems (arctic to tropics), and span a wide range spatial and temporal scales. However, despite the strong overall importance of animal derived subsidies at a global scale, it is important to highlight that animal subsidies are not universally important or positive across ecosystems and contexts. For instance, while seabird guano transforms communities in highly nutrient limited coral atolls, it often has relatively limited impact on temperate ecosystems and can even be toxic (Mulder et al 2006, Ellis et al 2006). Likewise, in arid systems, and at high densities of seabirds, the guano can actually have negative

consequences as the concentrated guano becomes toxic, triggering reduced plant or consumer diversity (Ellis et al 2006). Subsidies can also negatively impact specific consumers; for instance, seasonal subsidies to a predator can increase their populations, and allow them to have strong negative impacts to prey in seasons when the subsidy is not present. In order to understand the likely impact of subsidies (and their disruption) it is critical to consider characteristics of 1) the subsidy (and its vector), 2) the impacted ecosystems (donor and recipient ecosystems, although we will focus only on recipient ecosystems here), and 3) the specific consumer or process of interest.

The four basic characteristics of the subsidy that influence its impact are considered to be the quantity, quality, timing and duration of the subsidy. While these are well reviewed elsewhere (see Subalusky and Post 2019), a few simple rules of thumb related to each of these characteristics merit mentioning here as they influence the focal species of this report. While quantity of nutrients from excretion typically scales with body mass (suggesting large and abundant species will be important), it is also impacted by metabolic type, with endotherms having higher average rates of excretion per unity body mass than do ectotherms, making them more likely to have strong impacts on subsidy delivery. Animal carcasses and gametes, tend to be particularly high quality resources (as compared to excretion, egestion), such that any changes in their abundance will likely have large ecosystem impacts. Large animals also tend to be slightly higher quality as carcasses, and take longer to decay – creating long, high quality resources to ecosystems when they decay. Larger animals also tend to make longer distance movements, making them more likely to connect distant ecosystems than are smaller species; although flying and swimming

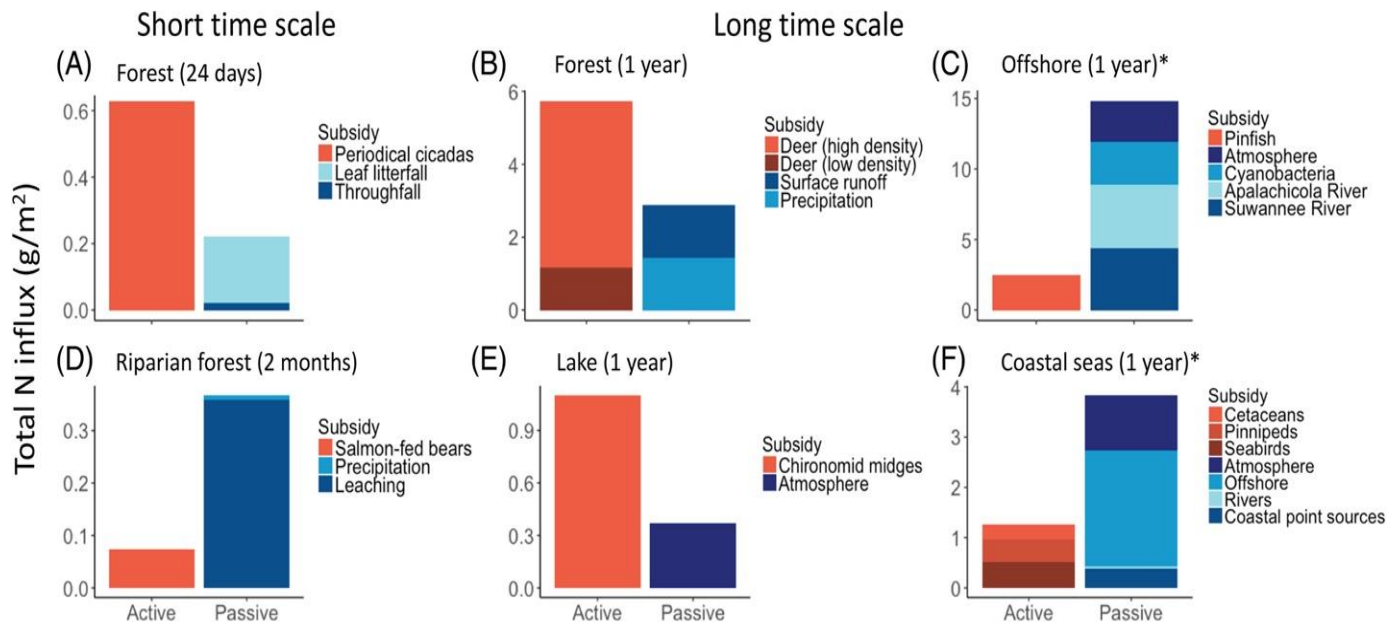


Figure 2. The amount of nutrients delivered from spatial subsidies can vary by orders of magnitude across ecosystems. Additionally the relative importance of active (red) subsidies vs passive (blue) subsidies varies dramatically by ecosystem. As of yet we lack a systematic framework to accurately estimate the relative importance of either active or passive subsidies in an ecosystem without actually measuring them. Figure adapted from McInturf et al 2019.

species cover proportionately longer distances than do terrestrial species. Migratory species are unsurprisingly particularly important in movement.

Ecosystem characteristics that influence the impact on the recipient ecosystem include the productivity or resource availability in the recipient ecosystem, the extent and scale of spatial heterogeneity of resources within the recipient ecosystem, and the extent of seasonality or other temporal variability within the recipient system. For example hippos, which forage on land during the night but defecate in rivers during the day, have dramatically divergent impacts depending both on size and productivity of river, and on seasonality. In large rivers and wet time periods, hippopotamus subsidies are known to increase primary and secondary productivity, whereas they instead drive eutrophication and fish die-offs and even disease outbreaks in small water sources in dry periods (McCauley et al 2015, Stears et al 2018, Subalusky et al 2018, Dutton et al 2018). The temporal scale at which animal subsidies are delivered vary wildly and include regular short term 'press' subsidies (e.g. constant movement of nutrients by whales from deep water to shallow water habitats) or intermittent 'pulse' subsidies over long periods (e.g. dispersal of nutrients in streams from cicadal emergence events, Meninger et al 2008) (Figure 3). Depending on the extent to which pulse subsidies are retained in a landscape, these pulse and press subsidies can have very different ecosystem impacts.

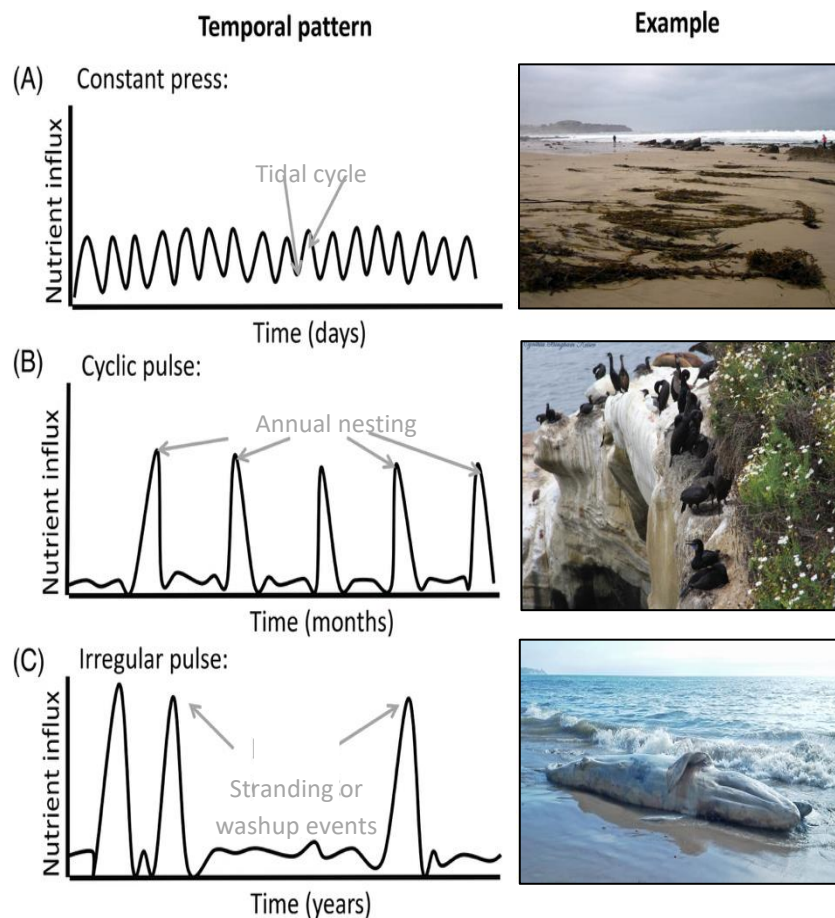


Figure 3. Nutrient subsidies can be delivered at a relatively constant (press) level, such as regular high tide delivery of marine wrack (A). They can come in cyclical pulses, such as regular nesting seasons of seabirds (B) or they can be delivered irregularly such as via intermittent carcass wash up or El-Niño storm events (C). Figure adapted from McInturf et al 2019.

Marine to Terrestrial Subsidies

As highlighted above, significant subsidy movement has been documented in nearly every type of ecosystem. However, the body of research on spatial subsidies largely emerged from studies of marine to terrestrial subsidies (notably including work by Gary Polis in Baja California; Figure 4), and this connection has remained one of the most well studied and richly documented type of spatial subsidy. Marine to terrestrial subsidies take many forms but often include marine wrack (algae and other marine organisms that wash on to shore), intertidal foraging by terrestrial animals (shorebirds, mice, lizards), subtidal foraging (and subsequent terrestrial excretion or egg laying) by seabirds, pinnipeds and turtles, and upriver migration by anadromous fish. After they are brought to land (or freshwater habitats) they may be incorporated by plants (e.g. Bilby et al 2003, Young et al 2010), directly consumed by other animals, or washed back to other habitats and subsequently have myriad effects on terrestrial ecosystems (Spiller et al 2010). While marine wrack is not itself an animal vectored subsidy, its incorporation into inland ecosystems is almost entirely driven by animals and thus, for the purpose of this report we consider it with animal driven subsidies.

Marine subsidies have been shown to play important roles in subsidizing consumers even far inland – for instance supporting inland coyotes and mice, remote caribou herds, or wolf populations > 1000 km from the ocean (Stapp and Polis 2003, Ben-David et al 2001, Adams et al 2010). However, it may take multiple steps and many animal vectors to move these allochthonous resources from coastal or riparian to inland ecosystems, so it can be difficult to trace. Additionally, it is important to recognize that marine subsidies do not necessarily remain within terrestrial ecosystems; they frequently are subsequently moved to third ecosystems (e.g. riparian

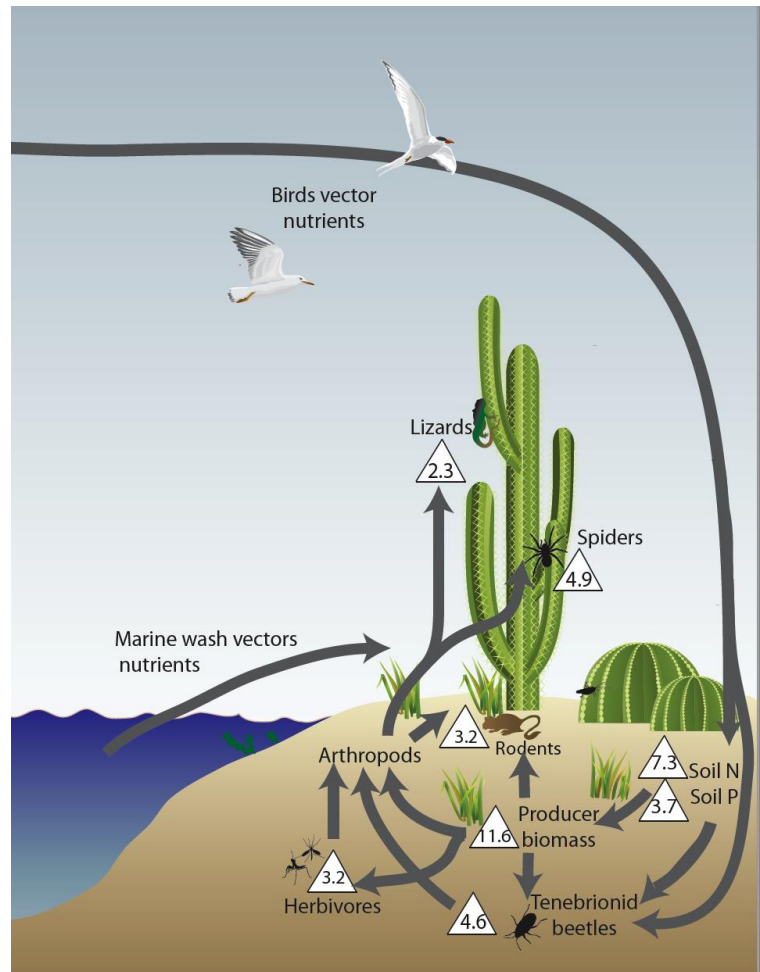


Figure 4. Work in Baja California has shown that marine nutrients transform island ecosystems, causing increases in soil nutrients, plant abundance, and abundance of higher level consumers. Numbers in triangles indicate the increase in abundance of consumers in subsidized vs unsubsidized consumers (e.g. lizards are 2.3 times more common on subsidized islands). This formative work transformed our understanding of the importance of aquatic subsidies to terrestrial communities and draws many parallels to local systems.

or lake ecosystems, or most commonly of all, are returned to the sea) creating new distributions of nutrients within the original donor system.

Missing Baselines

It is critical to recognize that while the Gaviota coast is considered an undeveloped ecosystem in the context of the transformed and developed landscape of much of California, it is by no means a pristine ecosystem. Much of the historic large fauna of California was lost, probably on early contact with humans in Plesitocene (e.g. mammoths, ground sloths; Barnosky et al 2004). Much additional fauna was lost or seriously reduced upon European settlement (e.g. grizzly bears, perhaps wolves or elk). Grassland communities were dramatically transformed through invasive grasses and grazing of domestic stock, driving dramatic changes in consumer communities. Based on research in other systems, it is likely that these losses caused dramatic changes in ecosystem connectivity. However, restoring to a pre-human baseline is infeasible and certainly out of scope of this report.

Likewise, we recognize that early humans have, in much of the world, long played an important role in

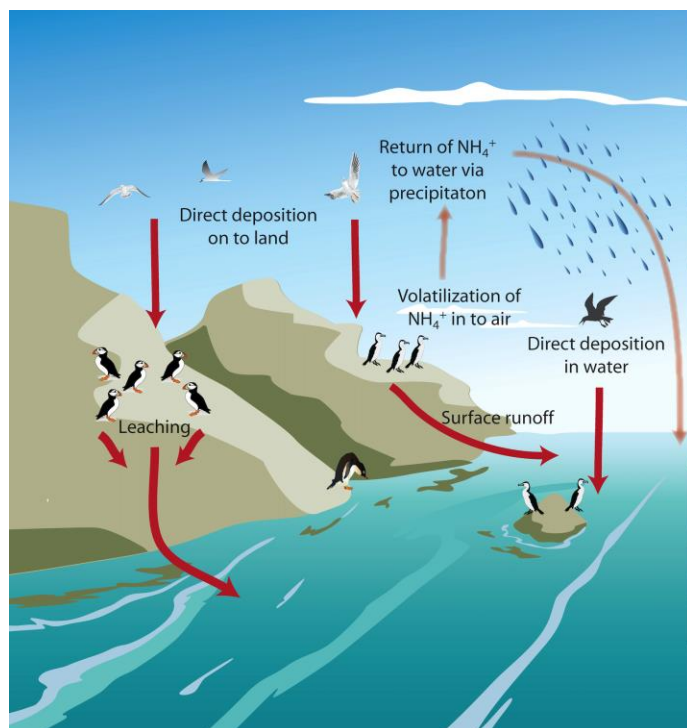


Figure 5. While we focus here on marine to terrestrial subsidies, it is important to recognize that this connectivity is circular. For instance, with seabirds, one of the most well established vectors of nutrients from land to sea, their nutrients also cycle back to aquatic ecosystems, often playing critical roles in supporting nearshore communities and fisheries, particularly in shallow water ecosystems (e.g. in this system, the terrestrial subsidies may indirectly support intertidal or kelp forest communities)

ecosystem connectivity. In the Gaviota system, Native American human populations almost certainly were historically important in providing ecosystem connectivity in this region, through fishing, foraging, hunting and migration. Given the long duration and relative recency of Native American occupancy of this region, understanding the role of this historic human connectivity would very likely be informative to understanding the modern ecological conditions. Unfortunately, we are unaware of good data quantifying the magnitude or nature of these historic anthropogenic nutrient transfers.

Finally, we recognize that the current land use – while relatively low intensity - is not without significant impacts on connectivity. We recognize that current human use – including grazing, fishing, boating, water extraction, roads, human waste, and human perturbation of wildlife - likely already has some, unquantified impact on connectivity as does more pervasive forms of global change (e.g. climate change is likely changing current baseline productivity in the system).

Through all these changes, humans likely also change the relative importance of existing animal subsidies. Additional work would certainly be needed to assess the relative importance of various forms of human disturbance, and their mitigation, might impact connectivity. However, for the purpose of this report we simply aim to assess current levels of marine to terrestrial connectivity and its importance for current ecological communities. We do not discuss how this may, or may not, relate to any prior historical baselines.

Section II: The role of spatial subsidies in Mediterranean ecosystems

Global Mediterranean Climate Zones

The Gaviota Coast has a quintessential Mediterranean climate, with distinctive cool, mild winters and warm, dry summers. The dominant chaparral ecosystem is a result of this mild climate, characterized by drought resistant plant life, mostly shrubs, with short, broad leaves. Other Mediterranean systems with similar abiotic and biotic characteristics are found on the west coasts of most continents between 30 and 40 degrees latitude (Figure 6) (Beck et al., 2018). Based on a review we conducted of the published literature on spatial subsidies (Appendix 1), we find that subsidization is common and important in Mediterranean ecosystems; even though Mediterranean climate zones make up a small percentage of the climate zones on earth, about 10% of the research on spatial subsidies focuses on habitats therein (Figure 7). Coastal habitats within Mediterranean climates are often characterized by dry perennial shrublands (e.g. chaparral); along the Pacific coast of North and South America these shrublands are adjacent to extremely productive marine regions influenced by upwelling (e.g. kelp forests). This contrast creates a gradient of resources ideal for facilitating spatial subsidies from the sea to the land. We find that in other Mediterranean coastal regions, the majority of subsidies reported in this climate zone (of 31 total studies) are from marine to terrestrial habitats (Figure 8). The majority of research in Mediterranean climates investigates marine to terrestrial subsidies, specifically

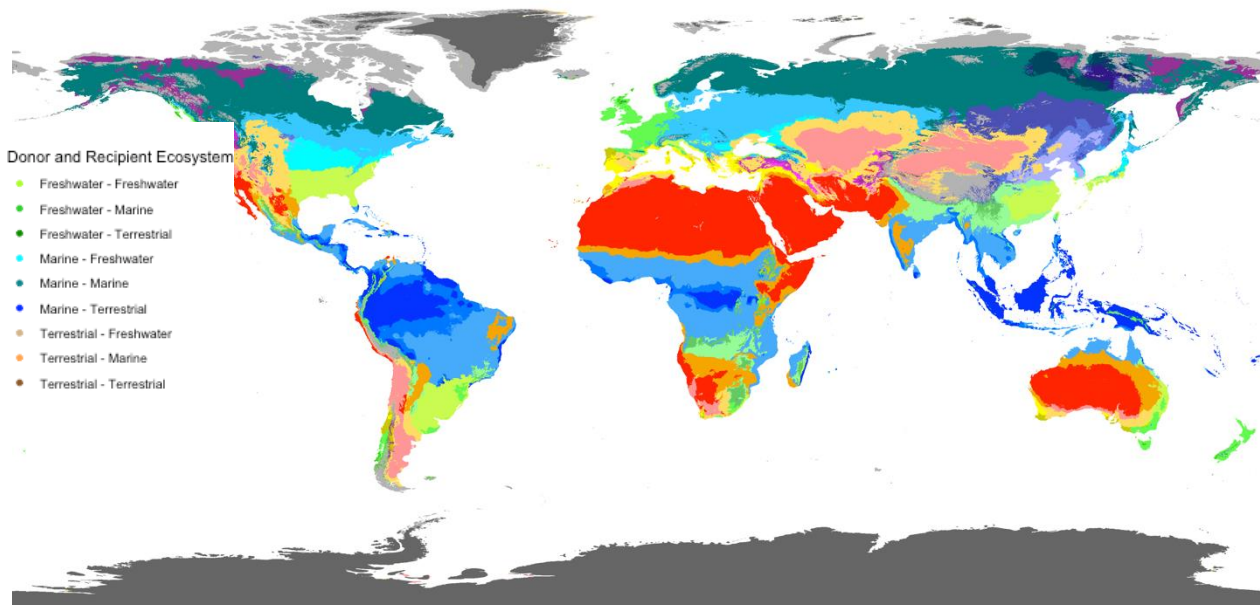


Figure 6. World map of Koppen-Geiger climate zones. Shades of yellow represent the three Mediterranean

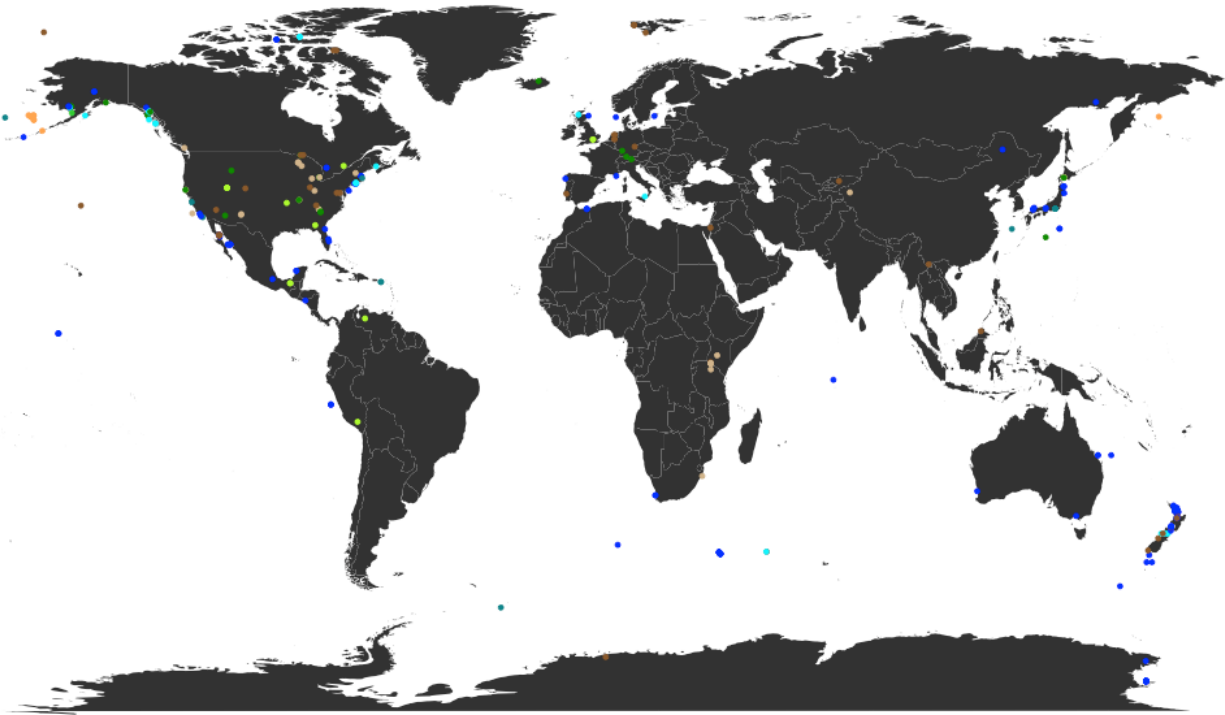


Figure 7. Global locations of scientific research on spatial subsidies, including the general type of subsidy based on a review of primary literature conducted for this report (See supp informatio). Shades of green represent subsidies from freshwater ecosystems, shades of blue represent subsidies from marine ecosystems, and shades of brown represent subsidies from terrestrial ecosystems.

the pathway that seabird guano follows as it moves inland (reviewed in Section III). Recipients of subsidies in Mediterranean ecosystems are diverse, ranging from intertidal invertebrates to inland riparian vegetation, suggesting that although documented subsidies in Mediterranean climate zones are mostly marine- and seabird-derived, they affect a variety of habitat types. Research on the ecological effects of subsidies in Mediterranean islands documented changes in diverse responses such as in vegetation abundance (García et al., 2002), lizard clutch size and gigantism (Pafilis et al., 2011), rodent communities (Stapp and Polis, 2003), and arthropod assemblages (Rgeas et al., 2003).

The California Coast

Central and Southern California coastlines are known for chaparral shrubland and productive, species-rich subtidal and intertidal zones. Both ecosystems have strong seasonal and intrannual patterns. In the terrestrial systems there are pronounced drought periods from May to October, causing reduced primary productivity, which in turn creates periods of stress or food shortage for terrestrial consumers. Central California is also in the midst of a prolonged multiyear drought period, likely surpassing that seen for centuries in this region. In other systems, spatial subsidies have been shown to be of critical importance for terrestrial consumers during such times of stress, although to our knowledge there is no work in California documenting this pattern. The Gulf of California has been the location of much of the canonical research on sea-to-land spatial subsidies for Mediterranean climate zones. Research on this

particular ecosystem has demonstrated how rich ocean waters can subsidize xeric coastal desert habitats, allowing multiple trophic levels to persist despite low local primary productivity. While the productivity gradient is more extreme in the arid deserts of Baja California, there are many similarities with the Gaviota Coast, and the products of this research can be applied to dry coastal shrublands like the California chaparral.

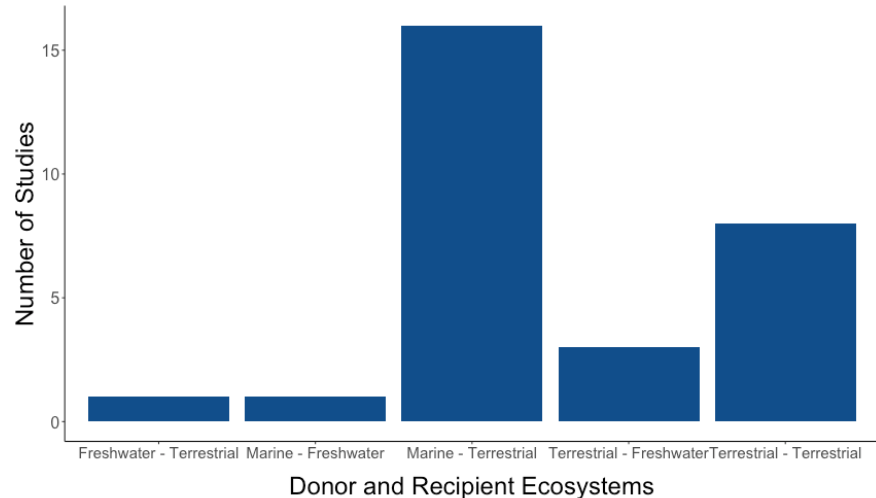


Figure 8. Frequency of donor and recipient ecosystem types in scientific papers that focus on spatial subsidies in Mediterranean climate zones (n = 31).

In general, marine to terrestrial subsidies in California are usually centered around the deposition of kelp wrack. Shore-washed kelp either directly or indirectly subsidizes terrestrial consumers at several trophic levels, from detritivorous arthropods to mammalian apex predators. In marine systems there are stronger storms and tides in winter, and particularly December to February periods; these storm events are critical for marine wrack inputs creating strong pulses of subsidies (described in more detail below) that, in other systems have been shown to transform subsidized ecosystems (Spiller et al., 2010). After this storm period, wind driven coastal upwelling follows, with strongest upwellings in April to June (although there is high variability due to frequent reversals in wind patterns). Upwellings in California are driven by equatorward alongshore wind stress that brings nutrient rich deep waters to the surface, and thus increase the productivity of nearshore marine environment and ultimately increase amounts of marine subsidies to coastal environment (García-Reyes and Largier, 2012). Notably, local topography strongly influences both upwelling patterns and wrack inputs creating high local variability. While general patterns are summarized below, with regional data mentioned when available, site specific data would be necessary to calibrate seasonality of spatial subsidies along the Gaviota Coast. The remaining months of the year are more variable among years in productivity and tend to have lower storm and tidal surges, creating lower but steady delivery of marine subsidies (press subsidies). In addition to intraannual variation, there is strong interannual variation in both productivity and subsidy delivery driven by ENSO cycles and long-term drought cycles. Additionally, recipient reliance on marine subsidies is highly seasonal and likely peaks in the dry, hot summer months, although this phenomenon is not directly studied in California. However, in Baja California, subsidy deposition and subsidy use is highly seasonal and dependent upon ENSO events.

Spatial subsidies require habitat connectivity, which is directly threatened by many anthropogenic impacts. Coastal development and urban sprawl especially disrupt ecosystem integrity and function as they often result in habitat fragmentation. Both donors and recipients are impacted by development; for example, shoreline armoring disrupts the natural pattern of wrack deposition, and road expansion

prohibits terrestrial consumers from accessing marine-derived subsidies and moving nutrients inland. The resultant decline in abundance of many of these consumers due to habitat fragmentation will only exacerbate reduction in subsidies, likely creating a negative feedback loop of ecosystem function loss. In addition, climate change is likely to greatly impact resource subsidies in California. Simultaneously, droughts are predicted to become longer and more severe, likely increasing reliance on potentially dwindling subsidies. Longer, more frequent storms will likely tear large amounts of macroalgae free at a rate faster than it can replenish itself, decreasing species diversity and subsidy deposition in the long term (Byrnes et al., 2011).

Section III: The primary spatial subsidy sources (donors) on the Gaviota Coast

In this section of the report, we summarize the major marine-derived resources (sources of nutrients that originated in the ocean) that are known to be used by terrestrial consumers, or that otherwise travel across the land-sea interface, along the Gaviota Coast or similar ecosystems. These resources are highly likely to be used by terrestrial consumers living along Santa Barbara coastlines.

Marine Algal Wrack

Nearshore kelp forests provide a near-constant supply of subsidy, via algal wrack, to intertidal ecosystems. In turn, endemic and visiting consumers transport those resources to nearby terrestrial ecosystems. In Southern California, algal wrack is comprised of 90% giant kelp (*Macrocystis pyrifera*), feather boa kelp (*Egregia menziesii*), and eelgrass (*Phyllospadix* sp.) (Lastra et al., 2008). Kelp wrack cover is consistently higher on beaches near subtidal kelp reefs (Dugan et al., 2003). According to monitoring done by Lastra *et al* (2008), between 2 and 9.2 kg of algal wrack is deposited on Santa Barbara beaches over a three day period, and at a single time point, there is an average of 21.4 kg of recently deposited wrack on a 100 meter segment of beach. Dugan *et al* (2011) took into account consumption by wrack invertebrates and estimated that total algal input to beaches is 840 kg/year. As mentioned previously, kelp wrack deposition is highly seasonal. Cover of sand by kelp is highest along the Gaviota Coast in the winter, likely due to strong winter storms. On some beaches, wrack cover declines to almost zero in late spring and early summer. The biomass estimates calculated by Dugan *et al* (2011) are likely low because their surveys were done during summer months. Wrack deposition is strongly affected by ENSO events. Wrack cover was only 30-40% of normal during the 1997-1998 El Niño, and recovery to previous levels was slow (Revell et al., 2011).

Algal wrack supports a significant community of consumers in the sandy beach ecosystem, which otherwise lacks primary producers almost entirely. The nutrients provided by washed-up kelp subsidize first order consumers (beach macro- and meiofaunal invertebrates) directly, but the effects of this subsidy extend significantly inland due to mobile predators of wrack-associated taxa (Figure ZZ) (Krumhansl and Scheibling, 2012). Talitrid amphipods (specifically *Megalorchestia benedicti*, *Megalorchestia californiana*, *Megalorchestia columbiana*, and *Megalorchestia corniculata*) are the most important consumers of intertidal algal wrack, along with two isopod species (*Tylos punctatus* and *Alloniscus perconvexus*), one wrack-associated polychaete worm, and several species of adult and larval insects (Dugan et al., 2003). These arthropods process algal wrack so quickly that 87% of experimentally

deployed *Macrocystis* sp. blades were consumed overnight (Lastra et al., 2008). Wrack deposition also delivers carrion and subtidal invertebrates and fish that become tangled in the macroalgae to the beach and provides an essential source of food for beach scavengers (see below). In addition to subsidizing intertidal consumers, algal wrack provides shelter and a humid microclimate for many beach invertebrates. The sandcrab, *Emertia analoga*, is often found in association with wrack patches even though it does not actually consume kelp. In fact, overall mobile invertebrate

species richness increases with algal wrack cover on Santa Barbara beaches (Dugan et al., 2003). Coastal strand vegetation also benefits from the patches of sand moisture created by wrack. Once shredded and remineralized by invertebrates and bacteria, algal wrack increases pore-water nutrients that benefit vegetation growing in otherwise xeric habitats (e.g. dune grass) (Lowman et al., 2019). Windblown wrack can even provide initial structural support for sand hummocks (embryo dunes) that eventually become dunes, with a base level of decaying algae or remineralized algal-derived nutrients to jumpstart dune vegetation growth (Dugan and Hubbard, 2010).

While it is difficult to quantify the net nutrient and caloric contributions of algal wrack to the beach, it is important to note that wrack is the single most important source of primary productivity for this habitat. Beaches have extremely low local primary productivity due to the mobile nature of sand grains and their inability to support plant root systems, so these ecosystems rely entirely on inputs from nearshore marine habitats (Griffiths et al., 1983). Dugan *et al* (2011) investigated the contributions of algal wrack to pore water nutrients on Gaviota Coast beaches, and found a significant correlation between algal wrack biomass and dissolved inorganic and organic nitrogen. While background nitrate concentrations in nearshore waters are usually 1-2 μM (peaking to 20 μM during upwelling events), Gaviota Coast beaches with dense wrack cover had pore water nitrate concentrations up to 6553 μM . Many of these nutrients are likely washed back into the ocean, but, as stated previously, some contribute to the growth of coastal strand plants and move inland via terrestrial grazers. The macrophyte species that make up the bulk of algal wrack range in their caloric content. *Macrocystis pyrifera* constitutes the majority of wrack biomass, and contributes 2.85 kilocalories per gram of dry weight (Paine and Vadas, 1969). The more calorically dense alga, including *Egregia mensizii*, *Ulva* sp., *Porphyra* sp., and *Phyllospadix* sp., are less common in wrack, but are consumed at a faster rate by invertebrates, so could represent a limiting resource (Michaud et al., 2019). Overall, algal wrack provides an essential service, concentrating nutrients in an otherwise nutrient poor system and creating hotspots of bottom-up productivity (Gómez et al., 2018).

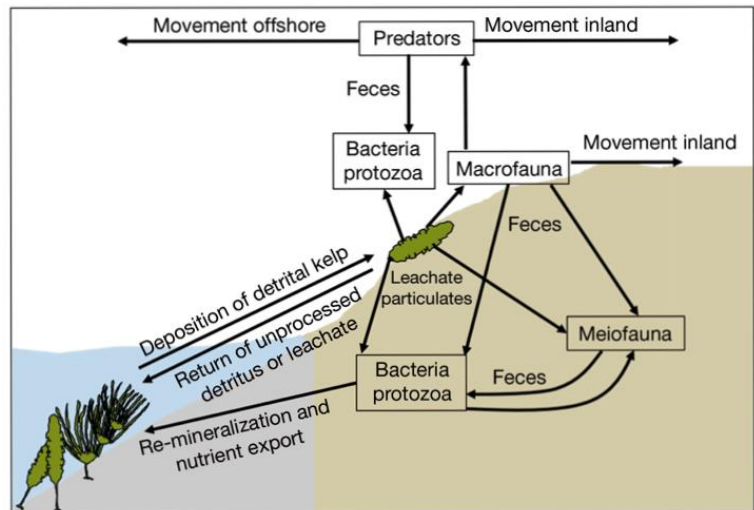


Figure 9. Energy flow associated with faunal and microbial processing of kelp detritus in sandy beach ecosystems. Adapted from Krumhansl and Scheibling (2012).

Live Rocky Intertidal Fish and Invertebrates

The rocky intertidal zone along the Gaviota Coast is a rich ecosystem, and one of the most productive in the world. While there are not many studies quantifying the extent to which terrestrial predators exploit concentrated rocky intertidal prey at low tide in this specific region, studies from other locations suggest that many consumers present on the Gaviota Coast rely on food from the tide pools. Notably, most of the apex and mesopredators active along the Gaviota Coast are generalist hunters, including bears, raccoons, possums, mountain lions, bobcats, badgers, coyotes, and birds of prey. For instance small predators and omnivores such as mice, rats, and foxes have been shown to play critical roles in structuring intertidal ecosystems in the North Pacific, suggesting that large amounts of nutrients may be moved inland directly by predation in the intertidal (Kurle, 2009; Kurle et al., 2008a). To our knowledge the quantity of nutrients moving directly from intertidal or subtidal via predation by primarily terrestrial consumers has not been quantified in this region, but it is likely important.

Marine-Derived Carrion

Carcasses of dead marine life provide pulsed deliveries of nutrients to the beach ecosystem, where scavengers process and distribute the resources. Carrion deposition attracts and concentrates consumers in space and time, temporarily, and possibly permanently, altering consumer density (Schlacher et al., 2013). In some ecosystems these inputs can be massive; for instance, Polis and Hurd

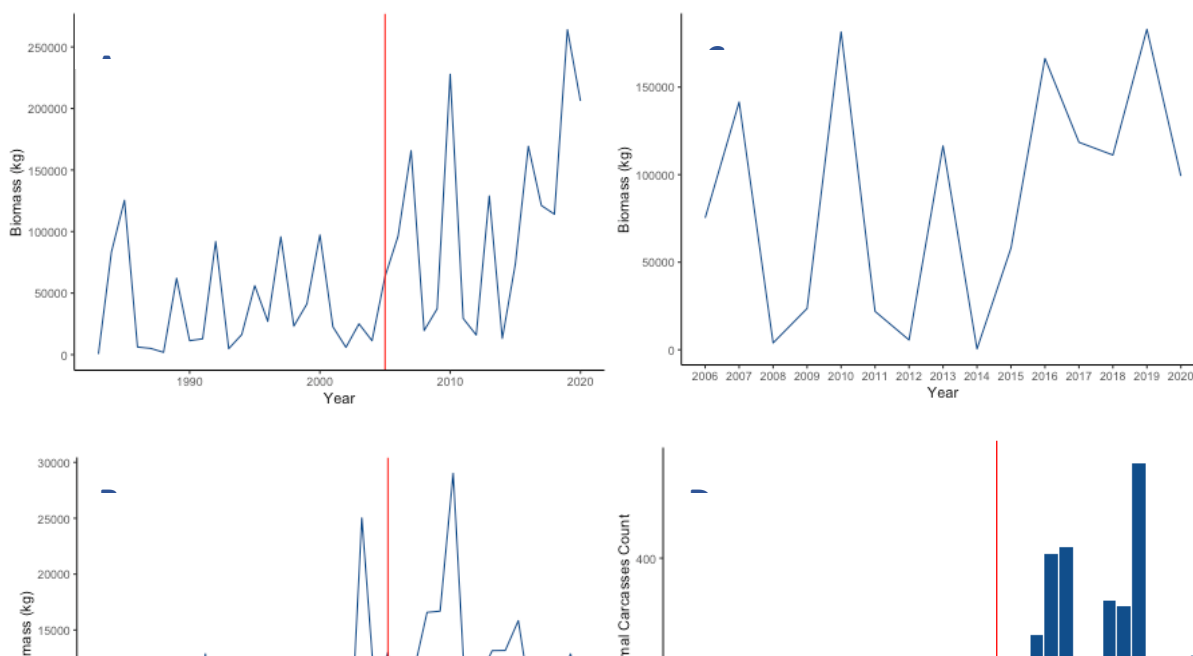


Figure 10. Annual marine mammal carcass deposition on Santa Barbara County beaches recorded by the NOAA Marine Mammal Stranding Network and the Channel Islands Marine and Wildlife Institution (CIMWI) from 1983-2020 including biomass of (A) all marine mammals (B) pinnipeds and porpoises (excluding rare, high biomass whale strandings), (C) carcasses left in place by responders from 2006-2020, and (D) the total number of marine mammal carcasses deposited annually. The red vertical line indicates when NOAA/CIMWI data collection methods changed in 2005.

(1996) estimated that beaches received between 110 and 530 grams of vertebrate carrion per meter per year based on surveys of beaches in the Gulf of California.

The largest and most obvious source of carrion on the Gaviota Coast is marine mammal strandings. On the West Coast, the majority of marine mammals that wash ashore are pinnipeds, specifically the California sea lion (*Zalophus californianus*). California sea lions, sea otters (*Enhydra lutis*), and harbor seals (*Phoca litulina*) represented 90% of carcasses found washed ashore between 1980 and 1986 (Bodkin and Jameson, 1991). According to the database maintained by the West Coast Marine Mammals Stranding Network and NOAA, an average of 112 (± 141) marine mammals wash up dead every year in Santa Barbara County (Figure 10D). Strandings of marine mammal carcasses are more commonly encountered in late winter and early spring, but depositions are highly pulsed. Bodkin and Jameson (1991) found that over half of the carcasses were recovered during less than a quarter of their monthly surveys. About half of all sea lion carrion washed ashore in a single year (1983, mostly subadult males). Sea otter carcasses were mostly comprised of pups and juveniles washing up in early spring and late summer, respectively. Harbor seal carcass strandings peaked in April and were mostly pups (Bodkin and Jameson, 1991). The West Coast Marine Mammal Stranding Network data suggests that there may be a multi-year pattern in deposition of mammal carcasses on beaches (Figure 10B and C). It is possible that this pattern is due to a spike in marine mammal deaths due to domoic acid poisoning, which demonstrates a similar interannual cycle (Smith et al., 2018). Unlike macroalgae wrack, mammal carcasses are processed relatively slowly. Dead marine mammals remain on the beach for an average of 28 days on California's coast, but can stay in place for up to 135 days (Bodkin and Jameson, 1991).

Due to the fact that most large mammalian carcasses are mechanically removed from beaches for disposal, there is a lack of research on the natural colonization of these carcasses by scavenger species. However, Quagiotto *et al* (2017) recently found clear evidence of successional scavenger assemblages at a seal pup carcass on the beach in the United Kingdom. The carcass was fed upon by crows and several gull species, crabs, larval and adult insects; all soft tissues were consumed or mummified in 47 days. Along the remote Gaviota Coast, large scavengers and predators alike are likely subsidized by marine mammal carrion, and there is anecdotal evidence that mountain lions (*Puma concolor*) rely on marine mammals in the Dangermond Preserve (pers. comm. Dangermond Preserve Staff). When left in place and allowed to decompose, marine mammal carcasses contribute an estimated average of 87,112 kilograms of biomass to the Santa Barbara County beach ecosystem per year.

Dead seabirds wash ashore regularly on the Gaviota Coast, and their decaying bodies subsidize a cohort of invertebrate and vertebrate scavengers. Common murrelets are the most abundant carcass found dead on California beaches, representing 27% of surveyed bird carcasses and are found most often in summer months. Grebes, unidentified gulls, and cormorants are also common. In the late fall and winter, Pacific loon, common loon, and Northern fulmar carcasses were commonly found washed ashore. Dead seabirds typically remain onshore for an average of 15 days before they are consumed or washed back out to sea (Bodkin and Jameson, 1991). Seabird carcasses are located and consumed by mostly avian scavengers such as corvids, raptors, and vultures, but Ford and Zafonte (2009) found some evidence of mammalian scavengers (raccoon, gray fox, river otter) as well. This study, however, concluded that

invertebrate scavengers (e.g. talitrid amphipods) played little role in disarticulating or decomposing seabird carcasses on the beach.

Like marine mammals and seabirds, fish die at sea and occasionally wash ashore. However there has been little research into this process for Gaviota Coast ecosystems. The majority of studies investigating the ecology of fish carrion have been conducted in Australia along coastal habitat similar to the Gaviota Coast. Research conducted on Eastern Australian beaches demonstrated that fish carrion attracted and aggregated invertebrate and vertebrate scavengers in space and time. Most experimentally placed fish were consumed in less than 24 hours, suggesting that large-scale patterns of fish-carrion-deposition are understudied because these smaller allochthonous resources are processed so efficiently by consumers (Schlacher et al., 2013). Even grunion, a charismatic surf-zone fish that spawns in beach sands *en masse* between February and August, are relatively poorly understood when it comes to their non-human predators. While these fish are not necessarily carrion (in that they are still alive when they come ashore) grunion are relied upon by several species of birds. Because grunion make easy prey during their emerged spawning events, grunion runs are closely tracked by the black-crowned night heron (*Nycticorax nycticorax*), the great blue heron (*Ardea herodias*), the snowy egret (*Egretta thula*), and the Western gull (*Larus occidentalis*) (Martin and Raim, 2014). At Solimar beach, huge numbers of a predator beetle, *Bledius fenyessi*, were associated with grunion eggs and larvae buried in the sand (Dugan et al., 2003). There is also anecdotal evidence that feral pigs consume their eggs, indicating a pulsed resource that is transported inland by an invasive species (pers. comm. Dangermond Reserve Staff).

Unfortunately, little research has been done on the carcasses of pelagic and rocky intertidal invertebrates that wash ashore, even though they have a notable seasonal presence in beach wrack. Nielsen et al. (2017) studied “animal wrack” deposition along the northern California coastline, and found that 0.018 – 0.45 square meters/meter of animal debris—consisting of hydroids, mollusk shells, jellies, and invertebrate molts—washed up on the beach and was most abundant in May. The bodies of these organisms are likely processed by arthropod scavengers along with macroalgal wrack. Planktonic invertebrates like the By-the-Wind-Sailor (*Vellella velella*), other jellies, and pyrosomes (floating colonial tunicates), wash ashore in seasonal pulses due to strong offshore winds (pers. obs.). Although their nutrient content is likely to be negligible, these massive strandings could provide a small pulse of subsidy to the shoreline ecotone.

Seabird Guano and Gametes

Seabirds forage at sea but either roost or nest in terrestrial habitats, typically in coastal or island ecosystems. These birds actively transport nutrients from the open-ocean and intertidal environment, concentrating them in patches on land, and subsidizing both terrestrial plants (via guano) and terrestrial consumers (via gametes and dead offspring) with marine-derived resources. The majority of research on seabird guano nutrient subsidies has been conducted for island ecosystems, as these ecosystems tend to have higher densities of seabirds as they provide provide natural escapes from predators during vulnerable nesting and roosting periods (Mulder et al., 2011). That being said, some species, including the charismatic Western snowy plover (*Charadrius nivosus nivosus*) and California least tern (*Sternula antillarum*) nest on mainland beaches and presumably have similar effects on mainland ecosystems. In

addition to their guano, these two shorebirds provide seasonal pulses of nutrients to the sandy beach and nearshore habitats in the form of eggs, vulnerable nesting adults, and chicks. Plovers nest on open sand with little vegetation from early March to late September (US Fish and Wildlife Service, 2007). Due to the extreme conspicuousness of their nests, plover nests are vulnerable to predation, and predators include gray foxes (*Urocyon cinereoargenteus*), coyotes, striped skunks (*Mephitis mephitis*), spotted skunks (*Spilogale sp.*), raccoons (*Procyon lotor*), California ground squirrels (*Citellus beecheyi*), long-tailed weasels (*Mustela frenata*), American crows (*Corvus brachyrhynchos*), common ravens (*Corvus corax*), ring-billed gulls (*Larus delawarensis*), California gulls (*Larus californicus*), western gulls (*Larus occidentalis*), glaucous-winged gulls (*Larus glaucescens*), gull-billed tern (*Gelochelidon nilotica*), American kestrels (*Falco sparverius*), peregrine falcons (*Falco peregrinus*), northern harriers (*Circus cyaneus*), loggerhead shrikes, merlins (*Falco columbarius*), great horned owls (*Bubo virginianus*), burrowing owls (*Speotyto cunicularia*), great blue herons (*Ardea herodias*), eastern red foxes (*Vulpes vulpes regalis*), Norway rats (*Rattus norvegicus*), and Virginia opossums (*Didelphis marsupialis*) (US Fish and Wildlife Service, 2007). Corvids are by far the most important predators of plover nests, and demonstrate increased activity with human presence. Breeding plover abundance varies, but in Santa Barbara County it can be as high as 245 breeding adults (at Vandenberg Airforce Base in 2006) (US Fish and Wildlife Service, 2007). Least terns historically nested in large colonies along large swaths of uninterrupted beach, but this nesting pattern was disrupted by coastal development in California, resulting in fragmented nesting sites and an interruption of the subsidies likely provided by these birds. As of 2005, there were about 7,100 nesting pairs of least terns in Southern California, 62 of which were located in Santa Barbara County (US Fish and Wildlife Service, 2006).

Although the Gaviota Coast doesn't support large seabird colonies such as those on the Channel Islands, pelicans, cormorants, gulls, and terns routinely roost onshore and deposit guano in concentrated patches on the California mainland. Therefore, we can extrapolate research from nearby island studies to the Gaviota Coast ecotone. Seabird guano delivers bioavailable nitrogen and phosphorous in extremely high amounts due to their colonial nature, in a process known as ornithotrophication. Seabird roosting and nesting sites concentrate these nutrients to an extent that they can increase productivity in terrestrial plant communities, which in turn subsidizes herbivores, with cascading effects at higher trophic levels (Croll, 2005). In fact, excretion of bioavailable nutrients within seabird colonies is so significant that it affects global biogeochemical processes (Otero et al., 2018). In addition to the nutritional subsidies provided by guano, seabird colonies are also often rich with decaying matter from dead adults and chicks, which provides concentrated resources for detritivores, scavengers, and in some cases vegetation (Polis and Hurd, 1996).

Section IV: Terrestrial species likely dependent on marine resources

In this section of the report, we have listed several consumer species that are connected in some way to marine-derived resources. We have also indicated how likely these species are to be impacted by increased human activity, including trampling, noise, and road improvements. We have divided these species up as follows:

Species that are likely to be particularly important as vectors of marine-derived subsidies

For the purposes of this report, we define animal vectors as those animals that actively move subsidies from the marine ecosystem towards terrestrial habitats. This can include either actively moving carcasses or vegetation, consuming resources and defecating/nesting significantly inland, or consuming resources and then becoming prey to inland predators.

Talitrid Amphipods

Talitrid amphipods represent a major transference of energy from subtidal kelp forest ecosystems to coastal terrestrial habitat. These crustaceans are the most important, in terms of both abundance and biomass, consumers and processors of macroalgal wrack that is deposited on the beaches of the Gaviota Coast. Talitrids, along with several other, but less important invertebrates, can consume washed-up kelp in less than 24 hours, processing kelp at a rate of 0.6 kilograms per day (Dugan et al., 2011). The process of consuming kelp involves shredding it into tiny pieces, which releases nutrients into the pore water of sandy beaches, making it bioavailable for microalgae and bacteria in the sand. Talitrids can reach abundances of over 10,000 individuals per meter, which, along with other wrack invertebrates, equates 660 to over 21,000 grams of invertebrate biomass per meter of beach (Dugan et al., 2003). Macroalgal wrack-associated invertebrates are consumed by several terrestrial consumers, including shorebirds, terrestrial birds, lizards, and predatory arthropods (Dugan and Hubbard, 2016). Some species, like Western snowy plovers, rely on wrack-associated arthropods as a main component of their diet (Dugan et al., 2003). Talitrids are highly specialized and concentrated in space, but due to their biomass and desirability as prey for a variety of terrestrial predators, they are extremely important vectors of marine-derived subsidies to inland habitats.

Lizards

Three species of lizards opportunistically forage in the intertidal zone along the Gaviota Coast: *Sceloporous occidentalis*, the Western fence lizard, *Elgaria multicarinata*, the Southern alligator lizard, and *Anniella pulchra*, the California legless lizard. The Western fence lizard and Southern alligator lizard are commonly observed among rocks, driftwood, supralittoral wrack, and coastal vegetation hunting for arthropods (pers. obs.), although there is little literature to support these observations. Both of these lizards have cosmopolitan distributions and varied carnivorous diets, and likely move nutrients inland. There are scattered populations of California legless lizards in Northern Santa Barbara dunes, and since these lizards are insectivorous, they are likely consuming arthropods concentrated around the dunes in decomposing algal wrack (Hunt, 2008; Lentz, 2013). Although legless lizards have very narrow home ranges and, being fossorial, likely do not move nutrients further inland, they do consume invertebrates and, via defecation, move those nutrients underground where they become available to dune plants.

Small Mammals (Ground Squirrels, Lagomorphs, Mice, and Rats)

In general, common rodents like squirrels, mice, and rats are opportunistic omnivorous foragers with wide home ranges and lots of predators, which makes them particularly suited to transport nutrients across ecosystem boundaries. Coastal populations of mice (*Peromyscus* sp.) in California are likely subsidized by marine resources. In the Gulf of California, intertidal invertebrates make up an average of 17.6% of *P. maniculatus* diet, and radio isotope analysis suggests that these mice are effective vectors of

marine-derived nutrients inland. Norway rats are known to consume intertidal invertebrates throughout the world. In Central Chile, these rats eat a variety of fish, crabs, mollusks, and echinoderms (Navarrete and Castilla, 1993). On certain islands in the Aleutian archipelago, Norway rats have become invasive and stable isotope analysis suggests that they consume intertidal invertebrates to a significant degree (Hopkins and Kurle, 2016). While invasive rodents likely facilitate movement of intertidal nutrients inland, Norway rats also predate upon nesting shorebirds, disrupting the subsidy provided by those birds, so they may have a net neutral effect on the inland movement of subsidies (Kurle et al., 2021, 2008b). Regardless, invasive Norway rats are almost entirely subsidized by marine-derived resources. Herbivorous rodents like ground squirrels and lagomorphs can often be seen consuming vegetation along upper beach boundaries (author pers. obs), and likely consume plants that are subsidized by nutrients derived from marine inputs.

Crows and Ravens

Corvids are opportunistic scavengers and can be found capitalizing on almost any food source. As a result, they are commonly seen consuming carcasses of marine animals that have washed up on the beach (Dugan and Hubbard, 2016). In fact, crows and ravens were one of the first scavengers observed at freshly placed bird carcasses in an experiment done by Ford and Zafonte (2009), and they often removed the entire carcass from the beach to consume elsewhere. Due to their proclivity for carrion and their ability to transport carcasses inland, they likely play a significant role in the movement of nutrients across the coastal ecotone. Crows and ravens also hunt in the intertidal zone, both in boulder fields and tide pools, for small invertebrates and fish (e.g. rockweed gunnells), and have been seen flipping over rocks to access these resources (author pers. obs).

Species likely to be particularly dependent on marine-derived spatial subsidies

Below we review species that are dependent on subsidies, focusing on those which rely on marine resources as a significant part of their diet, or who rely on consumers of marine resources as a significant part of their diet

Bears

Although there have been no reports in the literature of bears foraging in the California intertidal, bear commonly depredate intertidal fish and invertebrates along the west coast (Carlton and Hodder, 2003). Gaydos and Pearson (2011) list black bears (*Ursus americanus*) as one of the mammals that “relies on the Salish Sea” in Washington state, reporting observations of bears flipping over rocks in search of crabs, clams, and barnacles. In British Columbia, bears consume forage fish spawn and kelp wrack amphipods, both of which are correlated with increased bear activity in the intertidal (Fox et al., 2015). Bears consume intertidal prey with enough regularity that they impact the abundance of crabs and intertidal fish on British Columbia islands (Suraci et al., 2017). Black bears have huge home ranges, and are well known for their role in transporting salmon-derived subsidies. However, in the absence of salmon, it is likely that coastal California black bears rely heavily on protein from the surf zone and the rocky intertidal. There are some reports of bears foraging on the beach in very remote areas on the Gaviota Coast, primarily on marine mammal carrion (pers. comm. Dangermond Preserve Staff).

Raccoons

Typically, raccoons are successful mesocarnivores in anthropogenically impacted areas where apex predators are less active. Therefore, they are unlikely to be important in the Gaviota Coast ecosystem as it currently stands. Moreover, raccoons have declined to low abundance regionally due to recent distemper outbreaks. However, if increased human visitation were to result in reduced apex predator abundance and activity, raccoons could assume a more prominent role in the predator landscape. In other West Coast habitats where raccoons are common, including more populated areas of Santa Barbara county, raccoons commonly forage in intertidal habitats. Weinstein et al (2019) found internal parasites in Santa Barbara raccoons that strongly suggested they were consistently feeding on mollusks, crustaceans, and fish. In fact, raccoons have been observed eating intertidal crabs, clams, amphipods, barnacles, pricklebacks, clingfish, and kelp wrack-associated arthropods throughout California and the West Coast (Carlton and Hodder, 2003; Dugan and Hubbard, 2016; Gaydos and Pearson, 2011; Suraci et al., 2014). Raccoons forage in the intertidal regularly enough that they have a notable impact on community structure; their presence is correlated with a lower abundance of crabs and prickleback fish on islands in British Columbia (Suraci et al., 2014).

Vultures

In California, turkey vultures (*Cathartes aura*) are an unmistakable sentinel of animal carrion nearby. Turkey vultures are opportunistic and will consume animal carcasses even in extreme states of decay. Due to their volant nature, these birds likely move nutrients from derived from all types of marine carrion (mammals, birds, fish, invertebrates, etc) to inland habitats. There is only one published reports of turkey vultures scavenging along the coastal ecotone in California, wherein several vultures perched on and consumed a floating pinniped carcass in Big Sur (Gunderson, 2019). However, it is common to see vultures circling above Gaviota Coast beaches (authors pers. obs.). In the Gulf of California, subordinate and juvenile individuals, unable to successfully compete for access to carcasses of large terrestrial animals, relied almost entirely on carcasses from marine and intertidal environments (Blázquez et al., 2016).

Coyotes

Recently, coyote (*Canis latrans*) have become more reliant on marine-derived subsidies in California. In more arid coastal environments, like those in Baja California, coyote rely heavily on marine resources, including bird and mammal carrion, kelp wrack and associated lizards, birds, and insects, beach crabs, rocky intertidal invertebrates, and intertidal fish. Marine and beach taxa comprise up to 49% of coyote scat (Rose and Polis, 1998). Populations in coastal deserts tend to increase closer to the coast, suggesting that marine input does indeed subsidize coyote where other prey resources are scarce. In Northern California, coyote may be responding to an absence of other apex predators, such as bears, that would have historically exploited marine-derived prey. Where there are seal and sea lion rookeries, coyote populations consume both live and dead pinnipeds, where they had historically not relied significantly on marine resources (Reid et al., 2018). Additionally, coyote are generalist predators and prey upon several intermediate consumers of beach and intertidal subsidies, including seabirds, lagomorphs, and rodents (Bekoff, 1977). Coyote travel large distances, up to 4 kilometers per day (Bekoff, 1977), and coastal-dwelling individuals likely play a role in the movement of marine resources inland.

Mule Deer

Deer are anecdotally reported, usually by nature photographers, to visit the intertidal along the Gaviota Coast. Systematic studies on why exactly Californian deer species frequent the beach and the tide pools are lacking. However, mule deer (*Odocoileus hemionus*) in Washington regularly graze on green algae in the Salish Sea (Gaydos and Pearson, 2011). Red deer (*Cervus elaphus*) in Scotland regularly forage on marine macroalgae, but there seem to be differences in preference for algae among individual deer, who also appear to learn this preference from their parents (Conradt, 2000). Deer likely rely on macroalgae in a seasonal manner, depending on the availability and nutrient content of terrestrial vegetation (Ceacero et al., 2014). Macroalgae is probably most important to California cervids during the summer months when local vegetation is slightly more scarce.

Mountain Lion

Mountain lions (*Puma concolor*) have large individual home ranges and a wide range of prey species. Mountain lion mainly depredate mule deer, which make up 60-75% of their diet depending on the season, but will opportunistically hunt almost any animal, including fish (Currier, 1983). While camera trapping in British Columbia intertidal areas, Fox *et al* (2015) captured a mountain lion foraging in the intertidal. According to an unpublished report created for the WildCoast project in Pacific Rim National Park, British Columbia, mountain lions predate heavily on pinnipeds; their scat consisted of 24% harbor seal (*Phoca vitulina*) and 7% California sea lion (*Zalophus californianus*) (Wilton, 2007). Locally, mountain lions have been observed feeding on live and deceased pinnipeds (pers. comm. Dangermond Preserve Staff).

Species of regional conservation concern in the region that are likely vectors or recipients (direct or indirect) of marine-derived subsidies in this ecosystem.

Gray Fox

Gray fox (*Urocyon cinereoargenteus*) are charismatic, if skittish, terrestrial occupants of Gaviota Coast nearshore habitat. Gray fox have been reported in coastal deserts in Baja California eating live marine invertebrates, mostly sea cucumbers, at low tide (Rose and Polis, 1998). According to Dugan and Hubbard (2016), they eat a wide variety of intertidal invertebrates. Invertebrates, lagomorphs, and small rodents are important components of gray fox diet in California, and as these prey are subsidized by marine inputs in several ways, foxes are more likely to be a downstream recipient of subsidy impacts, rather than a direct recipient. Gray fox foraging is impacted by human activity, and they are less likely to use habitat that experiences human visitation (Fariás et al., 2012). While these animals are not endangered, they rely on connectivity between inland habitats, beaches, and coastal marshes. Foxes also consume many small rodents and birds that rely on coastal strand habitat (Fritzell and Haroldson, 1982).

American Badger

The American badger (*Taxidea taxus*) is primarily terrestrial, but is also a voracious generalist predator. They consume a variety of small vertebrates and invertebrates, including rodents, birds, fish, reptiles, and insects (Long, 1973). Due to the generalist nature of their diet, badgers likely consume beach-associated prey at multiple trophic levels, although there is currently no evidence of badgers foraging in the intertidal zone.

Western Spotted Skunk

The Western spotted skunk (*Spilogale gracilis*) is a species of special concern in the state of California. These charismatic skunks are omnivorous foragers that frequent ocean beaches along their coastal range, and have been reported to wade or swim (Dalquest, 1948; Howell, 1906). Spotted skunks feed on larval and adult insects, especially beetles, and small mammals, but will also scavenge from carrion.

California Condor

Any resource that might subsidize the endangered California condor (*Gymnogyps californianus*) should be carefully considered. A scavenger, the condor is drawn to carrion, and have been recently reported to regularly feed on the carcasses of marine mammals (Dugan and Hubbard, 2016). In Monterey County, California sea lion carcasses made up 84% of marine mammal carrion consumed by condors. They were also observed eating gray whale (*Eschrichtius robustus*) and sea otter (*Enhydra lutris*) carcasses (Burnett et al., 2013). In fact, feeding on dead marine mammals could potentially be what saved the California condor from extinction when their historical carrion resources, terrestrial megafauna, went extinct (Emslie, 1987). Coastal condor populations tend to have lower exposure to heavy metals than their terrestrial counterparts, and have higher survival rates (Bakker et al., 2017). However, the bodies of contemporary marine mammals may concentrate mercury, pesticides, and other toxins to levels that are fatal the condor, so it is unclear whether provisioning mammal carrion for this endangered species will contribute to population reduction instead of increase (Kurle et al., 2016).

Western Snowy Plover

The Western snowy plover is a federally protected threatened species that nests intermittently along the California coastline. The snowy plover consumes primarily beach wrack-associated invertebrates and, to a lesser extent, intertidal fish (US Fish and Wildlife Service, 2007). As previously mentioned, the snowy plover relies on coastal strand and dune habitat to nest and raise its young. Snowy plovers both rely on subsidies from the ocean via kelp wrack associated invertebrates, and are themselves a beach-derived subsidy to inland predators that consume nesting plovers and eggs. Even since the local plover population's recovery has become a priority for coastal managers, numbers have consistently decreased (*Five Year Review - Western Snowy Plover*, 2019). This decrease is likely due to their open-nesting strategy and increased beach grooming and human visitation, as well as an increase in predation.

Coastal Range Newt

The coastal range newt, (*Taricha torosa*) a subpopulation of the California newt, is a species of special concern in the state of California. This amphibian is exclusively coastal, and although it does not live on or visit intertidal areas, it could be affected by any disruption in connectivity between marine and terrestrial ecosystems. California newts consume a wide variety of aquatic invertebrates (crustaceans, snails, clams, insects, etc), some of whom could be indirectly subsidized by marine resources. Additionally, California coastal range newts move in groups during the breeding season, and can be seen crossing roads and highways (Pimentel, 1960). Habitat fragmentation, especially due to roadways, is highly likely to negatively impact this sensitive species.

Two-striped Garter Snake

The two-striped garter snake (*Thamnophis hammondi*) is highly aquatic, feeding almost exclusively on fish and amphibians. Other coastal garter snake species (e.g. *Thamnophis elegans*) are known to forage on fish and invertebrates in the rocky intertidal areas of the Pacific Northwest (Gregory, 1978). It is likely that the two-striped garter plays a similar role in Gaviota Coast intertidal systems when it has access to such habitats.

Species with evidence of marine subsidy use on the Gaviota Coast

Camera trap footage taken before the writing of this report demonstrates anecdotal beach and rocky intertidal habitat use by consumers that are normally categorized as terrestrial. This footage captured two organisms actively consuming intertidal and marine derived resources. Mule deer (*Odocoileus hemionus*) were filmed consuming vegetation in the mouth of an estuary. A single coyote (*Canis latrans*) was filmed carrying a dead seabird carcass inland, presumably to consume or feed others. Camera trap footage also showed several visitors to intertidal habitats, including bobcats (*Lynx rufus*), woodrats and packrats (*Neotoma* sp.), mountain lions (*Puma concolor*), raccoons (*Procyon lotor*), striped skunks (*Mephitis mephitis*), and badger (*Taxidea taxus*). Explanations for terrestrial consumer presence on beaches or in the rocky intertidal include predator escape, foraging, or temperature regulation. Hobby photographers have captured footage of small herds of mule deer drinking and grazing on algae at Asilomar Beach in San Luis Obispo County.

Additionally, Dangermond Reserve has conducted extensive camera trapping in the intertidal zone since the founding of the reserve, and has a significant database of footage. While reviewing this dataset is outside of the scope of this report, the images therein could provide robust empirical evidence of connectivity between land and sea in a relatively intact coastal environment. Additional camera trapping work would greatly assist in identifying regionally important species involved in nutrient transfer, as well as identifying the spatial and temporal variation in delivery of these nutrients.

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Appendix 1: Importance of Marine to Terrestrial subsidies on the Gaviota Coast

Supplement – Methods

Global Biogeography of Spatial Subsidies Literature Search

To assess the importance and distribution of studies on spatial subsidies globally, we performed a literature search starting using four major recent reviews on spatial subsidies, especially marine to terrestrial subsidies. Specifically, we gathered metadata for every source cited by the following four reviews: Subalusky and Post (2019), McInturf *et al.*, (2019), Mulder *et al.*, (2011), and Kolb, Young, and Anderson (2011). Next, we back-cited each source identified in these literatures, collecting all additional primary research references therein that concerned resource subsidies and that were not already in our database. We also forward-cited each of the original papers, collecting additional primary studies that had cited each of the four reviews to this date. We eliminated all studies that did not describe new empirical data. From each source thus identified, we collected the following information: subsidy type, subsidy donor, subsidy recipient, subsidy vector, ecosystem boundary that subsidy travels across (i.e. marine to terrestrial), coordinates of study location, and dates of study. For studies that described several separate subsidies or looked at the same subsidy in different locations, we created a separate entry. We then used the coordinates of each subsidy studied to make a global map representing where spatial subsidies are likely common or important. This map (Figure 7 in text) was created in R, version 4.1.0, with packages ggmap, maps, and rnatualearth.

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