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**CLIMATE CHANGE INTERACTIONS AT THE EDGE: WILDFIRE AND
SUBSISTENCE IN THE BOREAL FOREST, AND SEA-LEVEL RISE AND
NITROGEN LOADS AT THE CALIFORNIA LAND-SEA MARGIN**

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Abstract

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by

JOANNA L. NELSON

My dissertation furthers work in ecosystem resilience and social-ecological resilience to global change, in the systems of a) the northern boreal forest of interior Alaska, where climate change drives a changing wildfire regime; and b) a central Californian estuary, where N pollution and sea-level rise (due to climate change) converge at the land-sea interface, impacting rare salt marsh habitats and their provision of ecosystem services.

The first study explores impacts of a changing wildfire regime on a suite of wild species important for subsistence livelihoods, including game animals, furbearers, fish, and plants. Fire is a primary determinant of landscape pattern in the boreal forest. My review of 17 species indicated highly varied post-fire habitat requirements, implying that mosaics of differing stand ages best support a diversity of subsistence species. Obstacles to realizing a mosaic of different stand ages include a) increases in frequency of large-fire years due to climate change, producing homogeneous landscapes of younger trees, and b) fire suppression, producing homogeneous

landscapes of older trees. Neither of these scenarios provides the heterogeneous habitats necessary to maintain subsistence livelihoods; I conclude that integrating local knowledge with agency management could improve resilience to a changing fire regime.

The following two studies investigate coastal salt marshes' function as a "coastal filter" in central California, intercepting watershed-derived nitrogen (N) pollution and thereby buffering the major coastal problem of eutrophication. Nitrogen pollution and sea-level rise both impact coastal ecosystems, yet their interacting effects are poorly understood. In an experiment crossing simulated sea-level change and N addition, N addition had a significant, positive effect on plant growth, tissue quality, and total N sequestered. Simulated sea-level rise did not significantly affect biomass before a threshold of extreme sea-level rise simulation and subsequent plant death. Results suggest that coastal salt marsh plants serve as a robust N-trap and coastal filter in an experiment at one site, and that this function is not saturated despite extremely high background annual N inputs from agriculture. Findings at the landscape scale, in contrast, suggested that plants were saturated in their capacity to take up additional N in the estuary.

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CHAPTER 1

BOREAL FIRE EFFECTS ON SUBSISTENCE RESOURCES IN ALASKA AND ADJACENT CANADA

Introduction

Disturbance-generated landscape heterogeneity shapes ecosystem dynamics and processes, including organism movements and the population dynamics of wild species (Pickett and White 1985; Turner 1989). Wildfire is one of the primary ecological disturbances influencing landscape pattern and patch size in the North American northern boreal forest (Viereck 1973; Bonan and Shugart 1989; Kasischke and others 2002). Fire is therefore an important determinant of many ecosystem goods and services, ranging from air quality to habitat renewal and availability of game species. Many indigenous communities in the boreal forest of North America depend on these flows because of continued, widespread reliance on hunting and gathering for both nutrition and the maintenance of cultural identity (Fall 1990; Krupnik and Jolly 2002). Communities in boreal Alaska depend on more than 50 wild species for subsistence, including large game animals, furbearers, fish, and edible and medicinal plants (Scott and others 2001) (Figure 1). Fire-related changes in the community composition and structure of landscapes that supply these species are therefore likely to strongly affect subsistence opportunities and associated cultural continuity represented by hunting, fishing, trapping, and gathering of wild foods.

North American and Australian definitions of landscape ecology focus on causes and consequences of spatial pattern at variable spatial scales defined by the organism or process of interest (Turner 2005). In this article, we focus on the configuration of forest stands of different ages, where stand ages are determined by time since last fire, relative to the habitat requirements of animals, plants, and fish important to subsistence communities. We define the landscape in the context of subsistence as an area of radius approximately 50-150 km, set by the furthest distance rural subsistence hunters routinely travel to hunt, fish, trap and gather (Chapin and others 2004; M. Bifelt and J. L. Nelson, unpublished interviews).

Fire regimes in boreal forests are responding to anthropogenic climate change as well as to human ignitions and suppression activity. Air temperature has increased by approximately 2°C since 1950, and surface moisture has declined throughout much of the circumboreal zone, particularly in Alaska and western Canada (Serreze and others 2000). This warming correlates with a doubling of annual area burned in the boreal forest of western North America since 1965 (Murphy and others 2000). In Alaska the shift in the fire regime began in the mid-1980s, with 70% greater annual area burned for the period of 1985 to 2006 than from 1950 to 1984 (Kasischke and others 2006). A parallel shift in seasonality toward more late-season burning increased the severity of the more recent fires (Kasischke and others 2006; Kasischke and Turetsky 2006). In western Canada, fires now burn more than 95% of the area within a burn perimeter

(Eberhart and Woodard 1987; Kafka and others 2001), converting landscapes of multiple stand ages to early successional vegetation of a single predominant stand age. Projections suggest that air temperature will increase more rapidly during the 21st century (0.4-0.7°C decade⁻¹, up from 0.4°C decade⁻¹) (ACIA 2005). Fire scenarios in a warming climate suggest a future with more frequent, larger fires, and landscapes with a more homogeneous distribution of stand ages, more early-successional deciduous forest, and less mature spruce forest (Stocks and others 2000; Flannigan and others 2005) (Table 1).

Fire alters habitat for most subsistence species harvested by rural communities. Post-fire vegetational succession can follow multiple trajectories, but some pathways recur more frequently than others (Vioreck 1970). Succession ranges from self-replacement, in which the dominant tree species quickly resumes dominance (more common in extremely cold or dry soil conditions), to relay floristics, in which plant species show sequential patterns of dominance (Chapin and others 2006). In boreal forest relay floristics, succession resets with grasses, sedges, forbs and resprouting shrubs (Vioreck 1973), becomes increasingly shrub-dominated, then dominated by deciduous tree species and eventually reverts to late-successional deciduous or coniferous forest (Foote 1983). Although every fire event produces unique fine-scale patterning and trajectory of change, the successional dynamics described in the literature and summarized above provide a useful starting point for considering fire-directed landscape pattern. Changes in fire frequency, severity, and/or extent will

likely impact landscape-level vegetation patterns (Rupp and others 2002). We explore how a mosaic of post-fire patches in different stages of vegetational succession may contribute to the provision of subsistence goods and services to rural human communities in the boreal forest. In this article, we review fire effects on plant and animal species important to subsistence and explore how directional changes in wildfire regimes in the Alaskan and northern Canadian boreal forests could affect subsistence resource availability. We build on previous reviews indicating that different post-fire stand ages favor different wildlife species, each with specialized and often highly seasonal habitat requirements (Viereck and Schandelmeier 1980; Fisher and Wilkinson 2005). The co-occurrence of a full suite of subsistence species within distances accessible to permanent communities of hunters and gatherers should therefore depend on a sufficiently diverse post-fire landscape mosaic.

Although most research on wildlife responses to fire has focused on stand-level effects, we extend these results to the landscape scale, where possible, to assess the potential impact of changes in fire regime and management on local subsistence opportunities, paying particular attention to temporal trajectories of change.

Methods

We selected study species based on detailed subsistence use surveys conducted by the Subsistence Division of the Alaska Department of Fish and Game (<http://www.subsistence.adfg.state.ak.us/>) and on conversations with anthropologists, residents, and managers of the boreal forest region of Alaska. We focused on terrestrial and freshwater species resident in the boreal forest that are most frequently used, excluding migratory birds. We searched Web of Science, Biosis, and for aquatic species, Aquatic Sciences and Fisheries Abstracts with the terms “species AND boreal AND fire” where species was “moose”, “caribou”, “salmon”, “whitefish”, “blackfish”, “bear”, “wolf”, “furbearer”, “marten”, “fisher”, “lynx”, “wolf”, “hare”, “beaver”, “muskrat”, “grouse”, “ptarmigan” or “berries”. To capture material from unpublished reports and agency documents (“gray” literature), we searched annotated bibliographies (Magoun 1991; Saperstein and Joly 2001), unpublished reports (Foote 1983; Johnson and others 1995), and the Fire Effects Information System of the US Forest Service (<http://www.fs.fed.us/database/feis/>) for both data and citations, then repeated this cycle for all relevant articles located (both published and “gray”) until we stopped discovering new references.

Findings

Most available literature focuses on the effects of time since fire. Where possible, we also report effects of fire size, severity, and seasonality. Scant literature exists about

many subsistence resources including large carnivores such as bears and wolves; grouse and ptarmigan; and salmon, whitefish, and blackfish. However, certain key subsistence species have been studied in sufficient detail to support qualitative assessments of ways in which changing fire regimes could affect their availability.

Moose

Moose (*Alces alces*) are the main terrestrial subsistence species harvested in interior Alaska (Figure 1), contributing as much as 165 kg person⁻¹ year⁻¹ to the diet (median 39 kg person⁻¹ year⁻¹) (Scott and others 2001). Moose population increases have been observed in early successional forests (Spencer and Hakala 1964; Peek 1974; Loranger and others 1991), whereas mature conifer forest supports few moose (Scotter 1971a; Cederlund and Okarma 1988). Relatively recently burned areas (one to a few decades old) are described as more favorable for moose: those with resprouting and reseeded deciduous hardwoods including aspen, birch, willow, and in some cases, cottonwood that serve as winter forage (Leopold and Darling 1953; Spencer and Hakala 1964; MacCracken and Viereck 1990; Collins and Helm 1997). Protein and mineral concentrations of browse species decreased with time post-fire in one interior Alaskan study (MacCracken and Viereck 1990), suggesting that recent fire can enhance forage quality as well as availability. A great deal of research on fire effects on moose densities has been conducted in south-central Alaska, with less work in the boreal forest region of interior Alaska where large fires are more frequent (a

visual assessment of the fire-scar map of Alaska 1950-2006 shows the vast majority of large fires (greater than 450 ha or 1000 acres) in interior Alaska between the Brooks Range and the Alaska Range (Alaska Geospatial Data Center)).

Time since fire for optimal moose habitat and forage are most frequently reported in the range of 10-26 years, with subsequent declines in population density as stands mature (Figure 3A) (Spencer and Hakala 1964; Kelsall and others 1977; Gasaway and others 1989; Loranger and others 1991; Maier and others 2005). However, one source suggests that 60-70 years or longer are sometimes needed to produce favorable conditions (Spencer and Hakala 1964). Fire severity can strongly affect the time course of moose response. High-severity fires that burn the majority of the organic soil layer likely kill belowground vegetation and prevent sapling and shrub resprouting (although the bare mineral soil exposed is favorable for seeding of deciduous shrubs and trees (Johnstone and Kasischke 2005; Johnstone and Chapin 2006), delaying in turn use by moose. However, light fires can produce forage within months. MacCracken and Viereck (1990) reported abundant browse resprouting within 2 months after a 1983 fire in forests of quaking aspen (*Populus tremuloides*), paper birch (*Betula neoalaskana*), and white and black spruce (*Picea glauca* and *P. mariana*) in interior Alaska. Moose foraged in the burned area the winter after the fire. Moose browse was available during and immediately after a wildfire on the Tanana Flats, Alaska, in unburned islands within the burn perimeter and from resprouting in lightly burned areas (Gasaway and Dubois 1985). Moose increasingly

used the lightly burned areas for 4 years post-fire (Gasaway and Dubois 1985). In contrast, moderately and severely burned stands (~75% of the 1980 burn area) had little moose browse 1-5 years later (Gasaway and others 1989).

Spatial and seasonal variability in moose density in Alaska reflects several factors, including post-fire forage quality, landscape heterogeneity, and historical dynamics such as ease of travel, access to forage, predator avoidance, game management, human land use, riparian-area dynamics of flooding, erosion, and ice scour, and winter conditions such as snow depth, ice, temperatures and wind (Spencer and Hakala 1964). Physical barriers, such as downed trees, may hinder moose from gaining access to certain areas post-fire (MacCracken and Viereck 1990). Moose also have traditional travel routes and are unlikely to use a burned area if they have no pre-fire contact with that area (Gasaway and others 1989). In the Kenai Peninsula, Alaska, moose did not distinguish between post-fire stands of different ages, but their diet selectivity declined with increasing distance from cover, indicating that predation risk played a role in foraging dynamics (Weixelman and others 1998). Uplands and lowlands may also provide different conditions for moose: in riparian areas ice scour and other riverine processes provide vegetation renewal and desirable forage, whereas uplands rely on fire to renew browse (Collins and Helm 1997). One recent study examined female moose density in interior Alaska in relation to vegetation type, topography, occurrence and timing of fire, distance to rivers and towns, and landscape metrics (Maier and others 2005). Their analysis revealed that moose

density was highest in areas that had burned 11-30 years ago, with positive associations at all spatial scales examined and significant relationships at 15- and 23-km² scales. However, the densest populations occurred close to towns, at moderate elevations, and close to river corridors. Another study found river riparian corridors more important than fire history in explaining the variation in aerially surveyed November moose densities (Jandt 1992). In relation to subsistence, the difference between disturbance in uplands and lowlands (fire and ice scour, respectively) can lead to different perceptions of whether moose densities do in fact increase after fire: hunters who travel river corridors, in the fall moose hunting season, would be unlikely to perceive changes in upland moose populations. Eleven to thirty years after fire might seem a short interval for a land manager concerned with maintaining moose in a forest with a 30-200-year fire return interval; on the other hand, it might not, because managers' long term plans are often on the order of 15-20 years (Zavaleta, unpublished interviews). For hunters who are fixed in location by modern village infrastructure, 15-20 years represents a generation before they or their children have high likelihood of moose-hunting success, so recent increases in fire extent are of great concern to rural communities (Huntington and others 2006).

Caribou

Caribou (*Rangifer tarandus*) is the only large herbivore besides moose harvested by most boreal forest subsistence communities, contributing a maximum of 22 kg person⁻¹ year⁻¹ (median 3.5 kg person⁻¹ year⁻¹) (Scott and others 2001) (Figure 2), an order of magnitude less harvested meat than moose. In contrast to moose, caribou rely on winter forage in spruce-lichen forests that are typically at least 80 years old (Klein 1982; Schaefer and Pruitt 1991; Thomas and others 1996; Arseneault and others 1997; Joly and others 2003) (Figure 3B). Early researchers considered fire responsible for caribou declines (Leopold and Darling 1953; Lutz 1956). Researchers since the late 1960s typically conclude that fire is not responsible for caribou declines in North America, but agree that caribou appear to avoid burned areas for many decades or longer (Skoog 1968; Scotter 1971a; Johnson and Rowe 1975; Kelsall and others 1977; Miller 1980; Joly and others 2003; Rupp and others 2006). On time scales of centuries, fire could enhance the maintenance of lichen communities and nutritional quality of forage in boreal forest (Klein 1982). However, fire return times in boreal interior Alaska are typically 30-200 years (Yarie 1981; Viereck and others 1986; Kasischke and others 2002), so benefits on multi-century time scales are not realized in most areas.

Forage availability appears to be the key mechanism controlling fire effects on caribou density (Klein 1982; Joly and others 2003). The fructicose lichens (*Cladina* or *Cladonia*

spp.) preferred by caribou (Schaefer and Pruitt 1991; Thomas and others 1996) are very susceptible to fire and recover extremely slowly from it (Scotter 1971b; Viereck and Schandelmeier 1980). However, rate of lichen recovery depends on the characteristics of a fire. Within burns in Sweden, there was no lichen recovery 140 years after a severe wildfire, but recovery took only 20 years after a light, controlled burn (Skuncke 1969). Rate of lichen recovery could also vary along regional climate gradients. Slow recovery rates reported on the Seward Peninsula, Alaska and rapid rates in Newfoundland (Viereck and Schandelmeier 1980) could reflect the warmer climate in the latter site. Similarly, caribou lichen biomass (*Cladina* spp. and *Cetraria nivalis*) recovered and stabilized 61-80 years post-fire in the westernmost study area but only 41-60 years post-fire in the easternmost study area in one northern Canada study (Thomas and others 1996). The precise duration of reduced caribou use of burned areas will therefore depend on fire characteristics as well as landscape, climate, and previous fire history at both regional and more local scales. Factors other than forage availability may also affect caribou densities in post-fire patches: unfavorable snow conditions and downed trees have been suggested as detrimental to winter travel in burns (Schaefer and Pruitt 1991; Thomas 1996). One northern Canada study found that caribou made little use of forests younger than 60 years even when sufficient forage was present (Thomas and others 1996).

Furbearers: Wolf, Lynx, Hare, and Marten

These four species are harvested primarily for their pelts, either for household use in winter clothing or for cash income. We report their use on the scale of the community, because pelts are not divided and shared in the same way as edible harvests. Available ecological data suggest that all of these species benefit from relatively young to intermediate-aged burns (6-30+ years post-fire) for at least some of their habitat needs and life history stages.

Few data exist on fire effects on wolves (*Canis lupus*), although existing studies suggest that moose and caribou densities can both affect wolf use of post-fire areas. Wolf packs in the Kenai Peninsula, Alaska, used an area encompassing burns 9+ years old and 30+ years old and occurred in similar densities in each burn (Peterson and others 1984; Schwartz and Franzmann 1989). Wolves used burned areas more than expected during and 1 year after a northwest Alaskan taiga forest fire, but use dropped during the subsequent two winters before returning to pre-fire levels (Ballard and others 2000); the observed changes in wolf distribution were attributed to shifts in caribou distribution. Subsistence wolf catch is reported as an average of 8 individuals community⁻¹ year⁻¹ (Scott and others 2001).

Lynx (*Lynx canadensis*) in Alaska and Canada prey primarily on snowshoe hares (*Lepus americanus*) (Nellis and others 1972; Brand and others 1976; Paragi and

others 1997; O'Donoghue and others 1998). Both species exhibit preferences for mid-successional regenerating forest (Mowat and Slough 2003; Fisher and Wilkinson 2005), with hares selecting for denser growth (O'Donoghue and others 1998) and avoiding open, recently burned areas (<1-3 years) until post-burn regeneration can provide sufficient cover (Grange 1932; Keith and Surrendi 1971; Pietz and Tester 1983; Litvaitis and others 1985), suggesting that burns create high-quality habitat after 15-30 years. Trapper accounts from interior Alaska suggest that lynx can re-occupy burns as early as 5 years post-fire and remain abundant in burns up to 50 years old (Stephenson 1984). Lynx denning habitat, however, may differ from foraging habitats and may occur under deadfall debris in burns, in willow shrub thickets, or in mature forest (Koehler 1990, Slough 1999). Subsistence lynx catch is a mean of 29 individuals community⁻¹ year⁻¹, and snowshoe hare is a mean catch of 1412 individuals community⁻¹ year⁻¹ for pelts, and 4 kg person⁻¹ year⁻¹ as edible meat (Scott and others 2001).

Early researchers identified mature conifer stands as optimal for marten (*Martes americana*) and fisher (*Martes pennanti*) and recommended fire suppression to maintain populations of these furbearers (Lutz 1956). Further evidence emphasizes martens' and fishers' dependence on late-successional, coniferous forest for foraging, resting, and reproduction (Harris 1984; Arthur and others 1989; Buskirk 1994; Buskirk and Powell 1994). Both species need closed canopy tree cover and complex physical structure, usually of downed logs and branches, at ground level (Buskirk

1994). However, some evidence indicates that in the northern boreal forest marten can utilize more open, younger forests after wildfire (Magoun and Vernam 1986b; Latour and others 1994; Paragi and others 1996). Paragi and others (1996) found that marten abundance and activity in interior Alaska were greater in an area 6-9 years post-fire than in areas either 25-28 years or 100-115 years post-fire, although use of the recent 6-9 year-old burn was primarily by non-breeding juveniles. In another interior Alaskan site, marten hunted and rested within a 7-9 year-old burn (Magoun and Vernam 1986b). Martens may also use different stand ages at particular life history stages or use burns as suboptimal habitat (Fisher and Wilkinson 2005). Interviews with Alaskan trappers indicated that fire is generally favorable for marten (Stephenson 1984). Light to moderate fire might maintain a mosaic of habitats that marten utilize for travel, cover (under deadfall), foraging, and denning (Koehler and Hornocker 1977; Magoun and Vernam 1986a). Habitat preferences also reflect prey densities of microtine rodents (Cowan and Mackay 1950; Lensink and others 1955; Martin 1994). Yellow-cheeked voles (*Microtus xanthognathus*) and red-backed voles (*Clethrionomys rutilus*) in interior Alaska colonize and experience population increases in recently burned areas (West 1982; Lehmkuhl 2000). Marten catch is reported as an average of 636 individuals community⁻¹ year⁻¹ (Scott and others 2001). No data were found on fisher use of burned habitats in the northern boreal forest.

Beaver and Muskrat

Although beaver (*Castor canadensis*) and muskrat (*Ondatra zibethicus*) are primarily trapped for their pelts, we describe fire effects on their habitats separately from other furbearers because these organisms are aquatic. Beaver and muskrat are also eaten, although not as frequently as in past decades (M. Bifelt and J. Nelson, unpublished data). Annual beaver consumption varies considerably among boreal forest communities (range 0-50 kg person⁻¹ year⁻¹, mean 6.8 kg person⁻¹ year⁻¹). Muskrat catch is not recorded in the subsistence database. Fire is thought to benefit maintenance of wetland and aquatic edge habitat for beaver and muskrat in boreal forest (Kelsall and others 1977; Viereck and Schandelmeier 1980), but few studies exist. Beaver depend primarily on deciduous trees for food and necessary building supplies (Kelsall and others 1977). Two Canadian studies concluded that fire benefits beaver habitat where aspens are an early successional, disturbance-reliant species (Slough and Sadleir 1977; Barnes and Mallik 2001). Kelsall and others (1977) suggest that beaver are virtually absent from areas where coniferous forest dominates. However, in a study from Elk Island National Park, Canada, beaver lodge occupancy declined over a 12-year period of prescribed fires and did not return to pre-fire levels (Hood and others 2007). Muskrat data comes primarily from the southeastern US, where marshes are burned to promote muskrat habitat (Errington 1963). In one Manitoba, Canada study, summer marsh burning increased autumn muskrat populations (Ward 1968), and Athabascans in eastern Alaska traditionally burned

lake edges to improve muskrat habitat (Natcher 2004). Flooding, erosion, and ice scour could also be important disturbances in the aquatic habitats of beaver and muskrat, as reported for lowland moose, but we found no studies available.

Bears

Bears make up a relatively small part of the subsistence harvest of most interior Alaska communities, with a mean black bear (*Ursus americanus*) harvest of 2.3 kg person⁻¹ year⁻¹ and smaller harvests of grizzly (brown) bears (*Ursus arctos*). However, for individual households a single bear harvested can make a substantial contribution to food supplies, can be shared widely among neighbors, and represents an important cultural resource (Scott and others 2001). Available studies show that fire indirectly benefits bears by increasing foraging opportunities, due to benefits to moose density, increased moose calf productivity, and greater berry yield (genera *Vaccinium* and *Shepherdia*) (Schwartz and Franzmann 1989, 1990; Hamer 1996; Fisher and Wilkinson 2005). In Yellowstone National Park, Wyoming, large wildfires in 1988 caused elk mortality, and grizzly bears scavenged the elk carcasses (Blanchard and Knight 1990). On the Kenai Peninsula, Alaska growth and reproduction rates of black bears were greater in a 13-18 year-old burn than in a 35-40 year-old burn (Schwartz and Franzmann 1990). Fire may also improve denning habitat; in Alberta, Canada, black bears selected den sites in mature aspen (*Populus*

spp.) and spruce (*Picea* spp.) stands and avoided later successional muskeg sites (Tietje and Ruff 1980).

Grouse and Ptarmigan

Upland game birds, including grouse and ptarmigan species, make up a small (typically less than 3 kg person⁻¹ year⁻¹) part of the food harvests in interior Alaska. Long-term fire effects on these birds are mediated by vegetation changes (Vioreck and Schandelmeier 1980). Research in Alaska and Canada suggests that ruffed grouse, sharp-tailed grouse and spruce grouse each prefer different successional stages (Kelsall and others 1977). Sharp-tailed grouse (*Tympanuchus phasianellus*) thrive in fire-prone areas (Vioreck and Schandelmeier 1980). Periodic fires are beneficial to ruffed grouse (*Bonasa umbellus*) populations (Weeden 1965; Sharp 1971), which prefer early-successional aspen forest (Vioreck and Schandelmeier 1980). Limited evidence suggests that spruce grouse (*Falcienniss canadensis*) could prefer later successional stages (Ellison 1975; Kelsall and others 1977). Although very little research has been done on other upland bird species, fires that replace mature forest with shrubby growth probably benefit willow ptarmigan (*Lagopus lagopus*) through their forage of willow buds (Weeden 1965; Vioreck and Dyrness 1979).

Salmon, Blackfish, and Whitefish

Fish are the staple of interior Alaska subsistence diets, comprising 30 to more than 90% of total subsistence harvests (mean 61%) across 22 villages surveyed in 1982-1990 (Scott and others 2001) (Figure 1). Salmon alone make up 41% by weight (SD 24%) of subsistence harvests, with a mean harvest of 149 kg person⁻¹ year⁻¹.

Important species include king, coho and chum salmon (*Oncorhynchus tshawytscha*, *O. kisutch*, and *O. keta*, respectively), Alaska blackfish (*Dallia pectoralis*), broad whitefish (*Coregonus nasus*) and humpbacked whitefish (*Coregonus oidschian*).

Fire may affect aquatic environments through terrestrial vegetation removal; increased erosion or ash flow into streams and lakes; altered patterns of sedimentation, turbidity, and nutrient dynamics; reductions in dissolved oxygen via nutrient enrichment; leaf litter input; buildup of woody debris and other physical habitat alteration; and increased solar radiation due to canopy removal (Kelsall and others 1977; Minshall and others 1989; Gresswell 1999; Howell 2001). Fish mortality as a result of wildfire has been reported, but the mechanisms and magnitude of effects are generally unclear (Hakala and others 1971; Minshall and others 1989; Gresswell 1999).

Salmon species and whitefish species typically spawn on gravel beds (Alt 1994; Delaney 1994) and may be impacted by increased erosion and sedimentation.

Salmonids are sensitive to changes in water temperature (McCullough and others 2001). Even after highly severe fires, however, local extirpation of fishes is patchy and recolonization is rapid (Hakala and others 1971; Rieman and Clayton 1997; Gresswell 1999). A study of lakes in Alberta, Canada compared burned and logged catchments to undisturbed reference areas. Researchers found that, although fires could potentially cause nutrient enrichment or altered hydrology, the level of disturbance in a catchment explained less than three percent of the variation in fish assemblage structure (Tonn and others 2003). In another Alberta lake study, the only observed difference after burning was a decrease in small northern pike (Tonn and others 2004). Several researchers have called for long-term studies of fire effects on boreal aquatic environments (Lotspeich and others 1970; Gresswell 1999; Adams and others 2004).

Berries

Edible berries are the principal plant food harvested for subsistence in the boreal forest. They make up a small proportion of overall subsistence harvests by weight (mean 2.6 kg person⁻¹ yr⁻¹), but their gathering in summer is an important cultural activity across generations. Edible berries in the boreal forest of Alaska and adjacent Canada include at least six species; blueberry (*Vaccinium uliginosum*) and lingonberry (also known as low-bush cranberry, *Vaccinium vitis-idaea*) are the best studied and most important species to subsistence diets in interior Alaska. Most data,

however, deal with fire effects on vegetative plant parts rather than on fruit availability; the two are poorly correlated (Johnson and others 1995). Both species are found together in black spruce (*Picea mariana*) forests (Foote 1983), from lowland bogs to upland well-drained sites (Vander Kloet 1988) and alpine tundra. Both are facultative resprouters, resprouting from fire-pruned aerial stems or rhizomes (Viereck and Schandelmeier 1980; Calmes and Zasada 1982).

Sparse data indicate that blueberry and lingonberry produce more abundant berry crops in black spruce forest approximately 3-30 years post-fire than in dense deciduous or coniferous forests. Berry production requires an open canopy, adequate soil moisture, and the presence of a pre-fire *Vaccinium* population from which to resprout. In a Russian wildfire chronosequence, blueberry and *Oxycoccus quadripetalus* (cranberry) began fruit-bearing 3 years post-fire. Blueberry yield was 2.6-fold higher than in the unburned control a year after fruiting began, likely due to increased light availability that persisted for 17 years post-fire (Mironov 1984). Both types of berries were larger than those in unburned plots and more resistant to damage. In interior Alaska, berry fruiting by several species (genera *Vaccinium*, *Viburnum*, *Geocaulon*, *Cornus*, and *Empetrum*) was sufficient for four years after a severe fire in black spruce for red-backed voles to recolonize and overwinter in the area (West 1982).

Fire severity strongly shapes the timing of positive berry response to fire (Rowe 1983). After a light-to-moderate ground fire, blueberry and lingonberry may return to

or exceed pre-fire vegetative biomass in a few years (Uggla 1959); after a more severe fire, recovery may take more than 5-10 years (Viereck and Dyrness 1979; Schimmel and Granstrom 1996). Severe fires are likely to delay recovery of berry production by burning the organic mat and increasing damage to the belowground parts of plants (Calmes and Zasada 1982), especially in the more shallowly rooted *V. vitisidaea* (Uggla 1959; Friedman 1981). Where the organic mat is burned away to mineral soil, belowground stems and seeds of both species are typically killed, and seeds must disperse from outside the burn for recruitment to occur (Viereck and Schandelmeier 1980; Calmes and Zasada 1982).

Discussion

Subsistence species inhabiting boreal forests in interior Alaska and adjacent Canada exhibit distinct changes in post-fire population density and varied preferences for post-fire habitat of different ages (Table 1 and Figure 4). Two highly contrasting species, in terms of foraging needs, are moose and caribou. For example, wildfire is reported to benefit moose – a major component of boreal forest subsistence diets – within 10-30 years. In contrast, fire leads to decreased wintertime use by caribou, another important game species, for several decades or longer. These differences largely reflect contrasting diets, with moose favoring early successional, resprouting shrubs and saplings and caribou requiring late successional vegetation such as lichens in mature spruce forests. Also, moose populations have a greater potential to respond

numerically to fire than do caribou because cow moose can produce twin calves when in good nutritional condition (caribou rarely produce twins). Twinning rate in moose populations is negatively correlated to population density (Boertje and others 2007), but a burn could improve the nutritional condition of a herd by enhancing availability and quality of winter forage. Changing fire frequency could therefore have contrasting effects on human communities that differ in their relative harvests of moose versus caribou.

Most studies that we reviewed focused on stand-scale fire effects, through comparisons of use between burned and unburned stands. However, most subsistence species use multiple stands. Moose and snowshoe hares often use burn edges to capture improved forage in the burns and predator protection in adjacent unburned forest. Marten, lynx, and bear appear to use different habitats for foraging, including more open or younger stands, than for hibernation and breeding, when structural features often associated with mature forest are important. Other species, including caribou and most predators, move extensively among stands. Conclusions about fire effects on wildlife based on stand-level studies should therefore be extrapolated to landscape scales with caution. To conclude that a majority of subsistence species use and benefit from 10- to 35-year-old forest – and communities would therefore benefit from vast tracts of young- to intermediate-aged forest – would reflect wildlife foraging studies, but would overlook life-cycle needs for denning, calving, and predator protection (structure of old, fallen trees, edge environments, and sufficient

cover). One method for connecting stand-level preferences to landscape responses is with spatially explicit simulation models, the primary tools for exploring alternative future scenarios at the landscape level (Turner 2005). Rupp and others (2006) built a simulation model of caribou winter habitat availability in the Alaskan boreal forest under a range of fire regimes. Analysis revealed marked decreases in spruce-lichen habitat area and in spatial heterogeneity across a range of increases in fire frequency and size.

A review of subsistence species' response to fire is one piece of a complex suite of interactions in a social-ecological study of human-fire interactions in the boreal forest. Our findings suggest that human communities relying on multiple subsistence species are likely to benefit from access to a mosaic of forest patches that vary in time since fire. Two processes are currently altering landscape configuration: (1) Fire suppression is reducing annual area burned close to communities (DeWilde and Chapin 2006; Calef and others in press). If this continues, it will lead to a larger proportion of late-successional black spruce near communities (model prediction from Chapin and others 2003). (2) However, in areas without fire suppression, fires are becoming larger. Thus, both near and far from communities, it is increasingly likely that large areas of a single vegetation stage will predominate. Both very young (<15 years) and very old (mature black spruce) stands provide relatively few ecosystem services. Current trends are increasingly likely to present communities with these two stand types. The establishment in the mid-20th century of permanent

villages in rural Alaska radically changed traditional human mobility patterns; rather than moving among productive forest patches, community members have a fixed location from which to hunt, fish, or gather. Our findings suggest that communities are unlikely to find or gather abundant food resources if surrounded by large tracts of homogeneous black spruce, homogeneous young forest, or a combination of solely the two. Therefore, a sufficient diversity of patches must be available within travel distance. A mosaic of stand ages affects not only availability of subsistence plants and animals to rural communities, but also the organisms' access to and travel among patches as optimal and suboptimal habitats change in space and time (Wolff 1980). However, overall fire effects on subsistence also depend on factors like ease of travel: some subsistence communities report that post-fire conditions hamper travel and access (Chapin and others 2004). Downed trees, upturned roots, or dense regrowth can inhibit access to traplines, cabins, seasonal routes, and hunting sites.

A complicating factor in forecasting fire effects is fire heterogeneity, including topographic variation, variation in fire severity, areal extent of unburned islands, and fire edge indices. Here, we have treated burned patches as uniform in terms of fire effects upon successional trajectory, because we are assessing stand age in time since last fire. Therefore, directional change toward increased individual fire sizes, frequency, and total area burned would indeed lead to larger, more homogeneous forest patches. For example, several studies (incorporating models, historical data, or a combination) report that predicted climatic warming and fire regimes will likely

lead to homogenization of the boreal forest landscape with a higher proportion of early successional stands (Clark 1988; Overpeck and others 1990; Thompson and others 1998; Amiro and others 2001; Turner and others 2003). However, current research also indicates sources of variability. One interior Alaskan study showed that variance in burn severity increases with individual fire size (Duffy and others in press). A Canadian study showed that unburned islands are proportional to burn size (Eberhart and Woodard 1987). Johnstone and Kasischke (2005) showed that in a 1994 Alaskan fire in black spruce, variations in depth of burning in the organic layer led to variation in tree recruitment and shrub and herbaceous layer composition, leading to greater landscape heterogeneity. Post-fire range extension of lodgepole pine (*Pinus contorta*) has been documented in the southern Yukon (Johnstone and Chapin 2003), increasing the post-fire species diversity and landscape heterogeneity. Given the clear dependence of subsistence communities on landscape heterogeneity and the uncertainty in future fire-driven changes in habitat heterogeneity, this is clearly a fertile arena for research.

Fire Management Around Subsistence Communities

Dynamics of fire around human communities in the boreal forest reflect local human management and global-to-regional environmental change. The pattern of human influence on the fire regime is an increase in ignitions and a decrease in the area burned, with a footprint around settlements, highways, and major rivers. Human-

caused fire ignitions outnumber lightning-caused ignitions most strongly in a 5-km radius around a settlement (Calef and others in press). Beyond 20 km from a settlement, lightning-caused wildfires predominate, and these fires tend to burn an area, on average, eight times larger than human-caused fires. Therefore, area burned by fire is very low close to settlements and increases with distance until it peaks 35-45 km from villages (Calef and others in press). The case of fire suppression around communities was analyzed with the landscape model ALFRESCO, which simulates climate-fire-vegetation interactions in interior Alaska (Rupp and others 2002). When fire probability was reduced by 50% in the model to simulate effects of fire suppression, there was an increase in the area of unburned black spruce (Chapin and others 2003). Alaska's observed rapid climatic change has also caused increased air temperatures and reduced surface moisture (Serreze and others 2000), thawing of permafrost (Osterkamp and Romanovsky 1999), and increased incidence of insect outbreaks (for example, spruce bark beetle, Berg and others 2006), all of which increase fire risk due to drying of fuels. An important function of permafrost is as an impervious surface holding groundwater close to the soil surface (Viereck 1973); as permafrost thaws, the overlying soil is better drained and vegetation may dry. In insect outbreaks, feeding by bark beetles can alter accumulation of fuels through tree mortality and opening of the forest canopy to solar insolation (McCullough and others 1998). Finally, land use change – such as conversion to agriculture – and logging have altered the southern boreal forest of Alaska.

What are potential management options to support the flows of ecosystem goods and services in a changing environment? Policies that reduce the rate of climate disruption would address an important cause of recent changes. National and state fire policy tools that could address wildlife habitat needs include (a) wildland fire use, which shapes wildfires already burning through cutting of fire lines, fuel removal, and promotion of fire in desired locations; (b) prescribed fires, which are becoming politically and ecologically more difficult to conduct in Alaska; and (c) fuels thinning and management. Fires are allowed to burn and are simply monitored from the air in about two-thirds of Alaska, so the natural experiment of wildfire without suppression is already being conducted (DeWilde and Chapin 2006). Fires have been suppressed for decades in the vicinity of settlements, roads, and some rivers. The modeled result of fire suppression is an increase in the areal extent of late successional black spruce and white spruce (*Picea mariana* and *P. glauca*), which increases the potential for large future fires (Chapin and others 2003). Public education and stakeholder discussion will continue to be part of management options and decisions. After the Alaskan wildfire season of 2004, the largest on record, public meetings showed a call for more fire suppression around cities and towns (Todd and Jewkes 2006). One example of collaborative fire management comes from the Koyukuk and Nowitna National Wildlife Refuges in interior Alaska. There, one fire management officer has conducted fuels thinning treatments around communities in collaboration with the indigenous Tribal Council in each community. He also orchestrated a prescribed burn program in a slough area where fires in the 1940s and 1970s were suppressed. The

planned sequence of burns is intended to prevent unwanted fire effects on vegetation and to benefit marten, weasel, muskrat, moose, and migratory waterfowl and songbirds. Another example involves fire suppression to protect lichen habitat which serves as caribou winter forage: in a collaborative management agreement in 2006 between the Kanuti National Wildlife Refuge, Alaska Fire Service, and the regional Native corporation, Doyon, Inc., the lead Refuge biologist initiated an increase in fire suppression levels from “Limited” to “Modified” suppression (L. Saperstein and M. Spindler, USFWS, pers. comm.).

Further Research Needs

Although some information exists about the effects of fire frequency or time since fire on many key subsistence species in the boreal forest, many research gaps persist. There is a growing body of literature on the effects of fire severity on boreal species and ecosystem processes (for example, Johnstone and Kasischke 2005; Johnstone and Chapin 2006) and effects of fire size or shape on boreal species (Johnstone and Kasischke 2005; Maier and others 2005; Duffy and others in press). Little information exists to support inferences about how fires occurring in different vegetation types or stand ages might vary in their effects on subsistence resources. Almost none of the studies we reviewed address the effects of longer-term fire history or of repeated burns at changing intervals. In particular, very little data exist on large carnivores and aquatic habitats. Species interactions are extremely important for

population dynamics and therefore subsistence harvests, but we did not find comprehensive research on species interactions in post-fire environments for the 17 subsistence species reviewed here. Because there are few papers that address fire and subsistence species interactions (see Fisher and Wilkinson 2005; Hood and others 2007; Pastor and others 1988; Schwartz and Franzmann 1989, 1990; and outside the boreal forest, Bailey and Whitham 2002), our review generally covers one species at a time. Finally, existing studies are short in duration and occur at relatively small spatial scales. More long-term, spatially extensive observations will be needed to deduce patterns of response across all of these variables. In this respect, local knowledge and observations could complement and significantly add to the information available from ecological research to assess biodiversity trends linked to climate and fire regime changes and their impact on human well-being, (for example, Huntington and others 2004). Such an integrated approach could build the capacity to anticipate and plan for change.

Figures and Tables

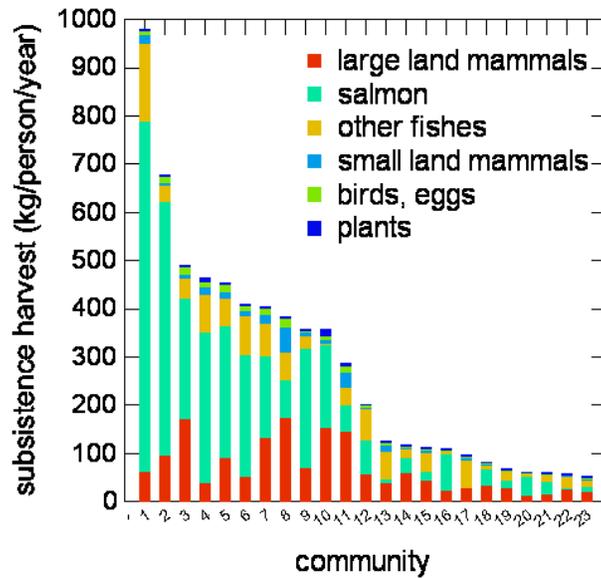


Figure 1. Composition of annual subsistence harvest for 23 rural communities in interior Alaska. Source: Alaska Department of Fish and Game Subsistence Division surveys conducted 1982-1990 (values may have changed considerably in the intervening period). Communities: 1-Tanana, 2-Hughes, 3-Huslia, 4-Minto, 5-Ft. Yukon, 6-Allakaket/ Alatna, 7-Grayling, 8-Anvik, 9-Galena, 10-Nikolai, 11-Holy Cross, 12-Shageluk, 13-Northway, 14-Bettles/ Evansville, 15-Tanacross, 16-McKinley Park, 17-Tetlin, 18-McGrath, 19-Tok, 20-Anderson, 21-Healy, 22-Chisana, 23-Dot Lake. There is over a 10-fold difference in the amount of subsistence resources used by different villages.

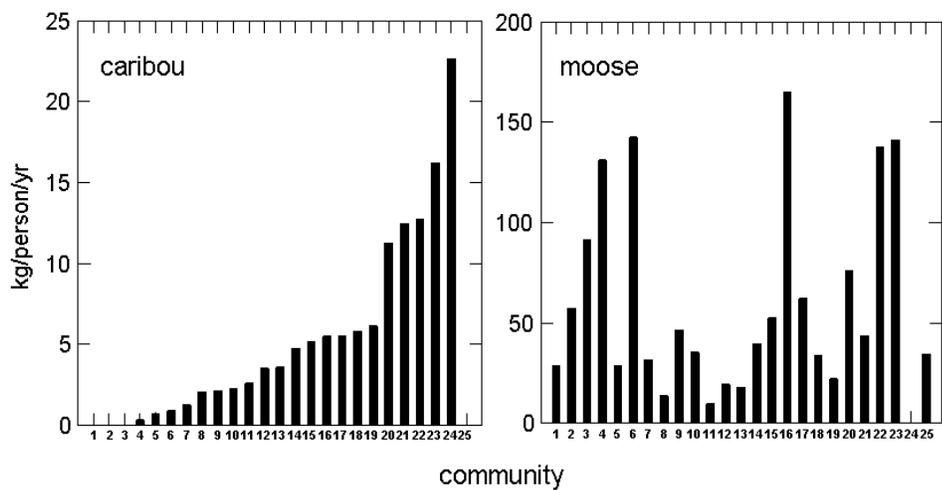


Figure 2. Annual harvest of moose and caribou by 24 rural communities in interior Alaska. Caribou data are shown in the left panel and moose data on the right; please note difference in scale on the y axis. Source: Alaska Department of Fish and Game Subsistence Division surveys conducted 1982-1990 (values may have changed considerably in the intervening period). Communities: 1-Ruby City, 2-Shageluk, 3-Hughes, 4-Grayling, 5-Tetlin, 6-Holy Cross, 7-McGrath, 8-Healy, 9-Allakaket/Alatna, 10-Nulato, 11-Anderson, 12-McKinley Park, 13-Dot Lake, 14-Tanacross, 15-Tanana, 16-Anvik, 17-Galena, 18-Northway, 19-Tok, 20-Ft. Yukon, 21-Bettles/Evansville, 22-Nikolai, 23-Huslia, 24-Chisana, 25-Minto (no caribou data available).

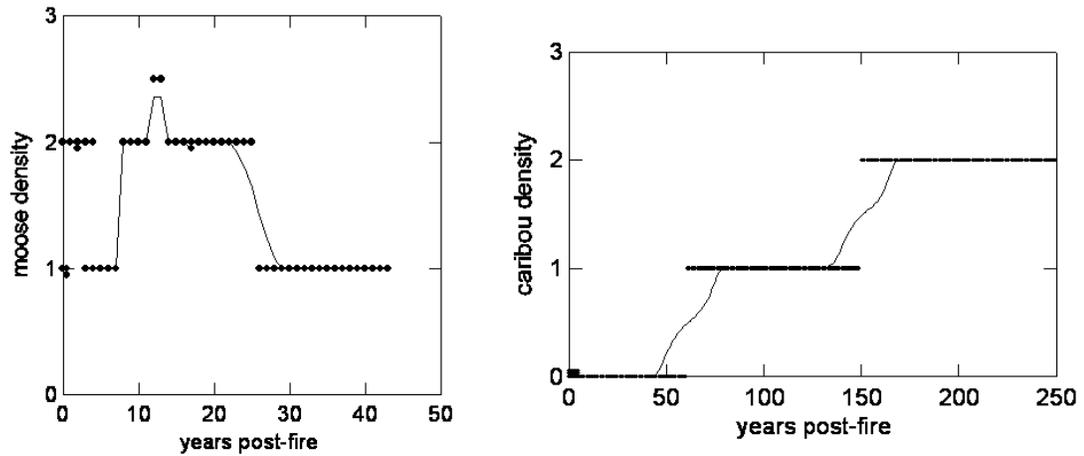


Figure 3. Effects of time since fire on (a) moose density (n=6 studies) and (b) caribou density (n=4 studies). Categorical density values: 0-absence of the species from study sites; 1-no change from pre-fire density/ presence with no indication of change from pre-fire density; 2-increased density relative to pre-fire density; 2.5-peak above other years with density greater than pre-fire values. Identical data points provided by more than one study are indicated with two vertically aligned dots in the figures. Points are fitted with LOWESS curves (tension = 0.3), which interpolate y-values from weighted averages of nearby reported y-values (Systat 10.2, Systat Software Inc.).

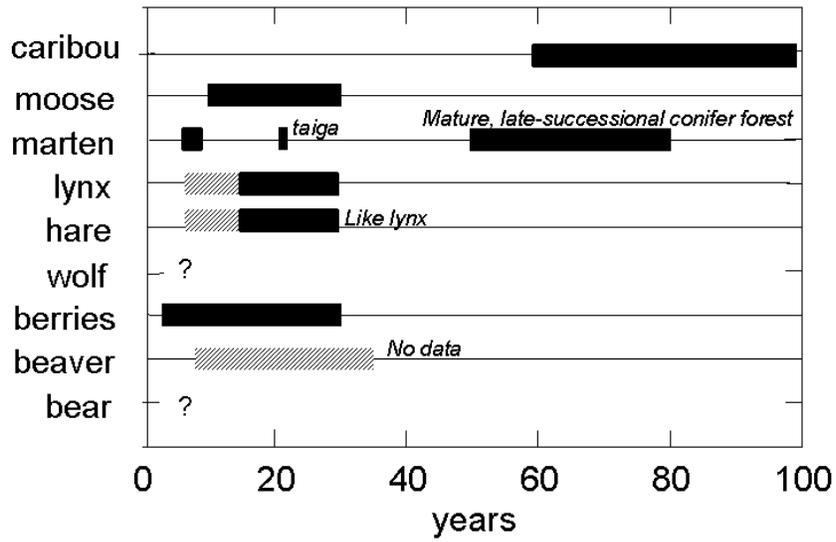


Figure 4. Approximate optimal periods post-fire for density or productivity of key boreal forest subsistence species, according to the ecological literature. Hatched bars indicate uncertain or hypothetical information.

Table 1. Summary effects of fire on terrestrial subsistence resources in the North American boreal forest

Organism	Summary
Moose	Increased densities 5-26 (especially 12-26) years post-fire; no evidence of moose declines immediately post-fire. Main mechanism appears to be browse availability.
Caribou	Winter use declines for ~60 (range 20-150) years post-fire due largely to forage (lichen) declines. Possible that stands >150 years old lose habitat value because lichens decline.
Lynx	Stands 15-30 post-fire generally produce good habitat for lynx and their prey of snowshoe hares in interior Alaska. Denning habitat may differ from foraging habitat.
Marten	Higher densities in 15-year post-burn sites than in 25-year or mature forest sites, but only non-breeding individuals found in the 15-year site. Suggests need for both mature and burned sites.
Grizzly bear and black bear	Consume berries and moose calves, both found in higher densities in early- to mid-successional stages. Bears are documented foraging in areas 5-40 years post-fire, and in Canada, selecting dens in mature aspen or spruce forest, suggesting mixed habitat needs.
Grouse	Little-studied; generally, sharp-tailed grouse use recent burns, ruffed grouse prefer intermediate-aged stands, and spruce grouse prefer mature forest.
Ptarmigan	Little-studied; willow ptarmigan may benefit from recent fire due to increase in shrubby habitat; willow buds (winter food).
Salmon, whitefish, and blackfish	Few data exist
Blueberry and Lingonberry (genus <i>Vaccinium</i>)	Berry yield may peak at 3-30 years after light-moderate fires, depending on light availability (openness of forest canopy), depth of organic mat burned, and pre-fire population from which to resprout.

Appendix

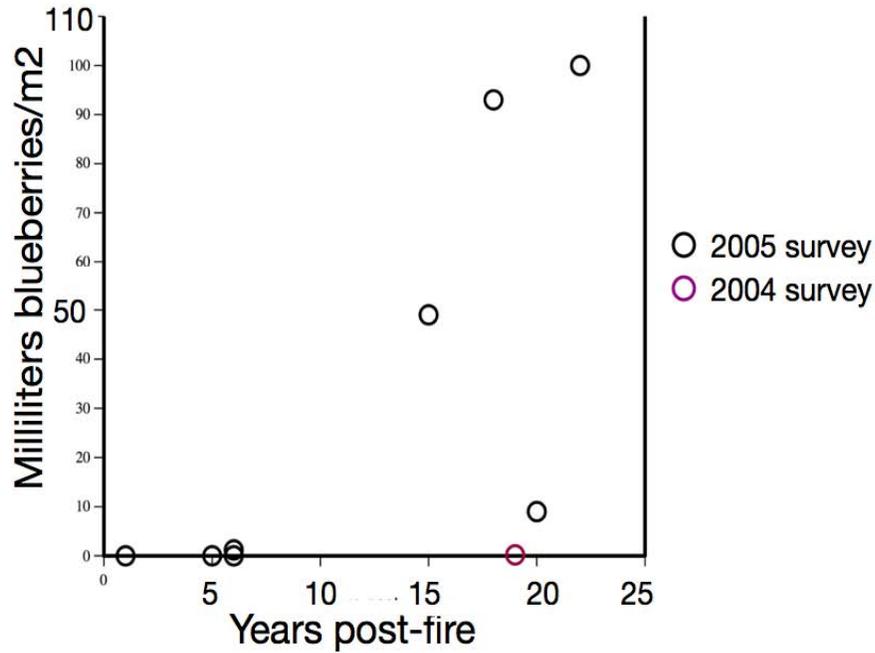


Figure 1. *Vaccinium uliginosum* (blueberry) berry density in post-fire succession in interior Alaska. Data series from 2005 survey shown in black circles; one data point from 2004 survey shown in gray. Surveys done primarily in the Koyukuk/Nowitna National Wildlife Refuges administered by the USFWS.

Table 1. Site locations of surveys, primarily in the roadless areas of the Koyukuk/Nowitna National Wildlife Refuges (KNNWR), Alaska.

Sites	Years since fire	Average volume [ml] of <i>Vaccinium uliginosum</i> m ⁻²
S. of the village of Galena	1	0
Shelter Cabin Lake (KNNWR)	5	0.01
Roundabout Mountain 1999 burn	6	1.2
Donnelly Flats 1999 burn	6	0
S. of 3-Day Slough, near Galena	15	49
Granite Creek near Fairbanks, AK	18	93
Round Lake (KNNWR) 2004	19	0.2
Round Lake (KNNWR) 2005	20	9
Rosie Creek LTER, Univ. of AK	22	100

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CHAPTER TWO

SALT MARSH AS A COASTAL FILTER FOR THE OCEANS: CHANGES IN FUNCTION WITH INCREASED NITROGEN LOADING AND SEA-LEVEL RISE

Introduction

Human activity has altered biotic and abiotic environmental controls at rates, scales, and in combinations that are unprecedented: the hydrologic cycle, biodiversity, land cover, the use of biological productivity, water quality, and the cycling of nitrogen (N) have all changed dramatically and at global scales (Chapin *et al.* 2000, Vitousek *et al.* 1997, IPCC 2007). Multiple global environmental changes converge in particular at the land-sea interface, with anthropogenic disturbances originating from both the marine and terrestrial realms. The land-sea interface, therefore, is an important place to study intensified global change interactions.

Nitrogen pollution and climate change are two dominant drivers of global change affecting ecosystems, yet their interacting effects at the land-sea interface are poorly understood. This is especially true of coastal salt marshes (Gedan *et al.* 2009). Coastal salt marshes are among Earth's most productive ecosystems (Teal 1962, Little 2000) and provide a number of ecosystem services including interception of watershed-derived nitrogen (N) and other pollutants before they reach the ocean (Kennedy 1984; Howes *et al.* 1996; Valiela *et al.* 2000; Brin *et al.* 2010). Coastal salt marsh ecosystems are among the most threatened in California, having lost 75 to

90 percent of their historic extent (Emmett et al. 2000, Zedler 1996). Globally, 21% of the human population lives within 30 kilometers of the coast, and increases in population are disproportionately high in coastal areas, so nearly all estuaries are impacted by human activities (Zedler and Kercher 2005).

Nitrogen pollution, often due to run-off from agricultural and urban lands, has increased dramatically in recent decades and poses one of the greatest threats to estuarine ecological function (NRC 2000; Cloern 2001; Howarth and Marino 2006). Human alteration of the global nitrogen cycle has led to exponential increases in plant-available nitrogen in the last three decades (Vitousek *et al.* 1997, Galloway *et al.* 2008). The leading sources of added nitrogen are the application of synthetic fertilizer in agriculture and disproportionately high human population growth rates in coastal areas, with associated runoff (Boesch 2002, Zedler and Kercher 2005).

Nutrient enrichment of coastal and estuarine systems can lead to dramatically altered biogeochemical cycles, disruptive blooms of phytoplankton and macroalgae, harmful algal blooms, and changes in food webs and biodiversity (NRC 2000). When nutrient additions fuel blooms of either phytoplankton or macroalgae, subsequent die-off and decomposition creates the rising problem of hypoxic or anoxic ocean regions, also called “dead zones” (Diaz *et al.* 2008; Rabalais *et al.* 2009; Howarth *et al.* 2011). In the USA, three quarters of all major estuaries have hypoxic “Dead Zones” (Bricker *et al.* 2007). Nitrogen supply in salt marshes affects plant productivity and biomass, and plant physiology, such as resource allocation and tissue N content (Hopkinson and Giblin 2008; Morris 1991; Haines & Dunn 1985). Eutrophication effects on salt

marsh sustainability are a current subject of study (e.g., Turner *et al.* 2009), but across all ecosystems, persistent exposure to high nutrient loading causes changes in biogeochemical cycling and trophic dynamics and can catalyze changes to alternative ecosystem states (Verhoeven *et al.* 2006).

Pathways of nitrogen interception in the coastal environment include plant uptake into tissue, denitrification by microbial communities, and burial in sediments (Bianchi 2007, Seitzinger *et al.* 1998). In the present study, we focus on plant uptake by emergent marsh plants. The role of subtidal estuarine vegetation functioning as a “coastal filter” is more thoroughly explored in the scientific literature (e.g., Short and Short 1984; McGlathery *et al.* 2007), with fewer studies to support or quantify this function of nutrient interception in intertidal marshes (but see Hopkinson and Giblin 2008, *c.f.* Lillibø *et al.* 2006; Drake *et al.* 2008; Brin *et al.* 2010). Building on this concept, studies suggest that the filtering processes of emergent salt marsh vegetation, higher in the intertidal, can support the survival and filtering processes of subtidal sea- and eelgrass beds (Valiela *et al.* 2000).

Climate change predictions for coastal salt marshes include both eustatic sea-level rise and increased variability in storms’ precipitation and sediment delivery (Meehl *et al.* 2007, Field *et al.* 1999). Sea-level rise is changing the character and location of the land-sea interface and therefore the existence, distribution, and potential migration of salt marshes (Day *et al.* 2008; Stevenson & Kearney 2009). Salt marsh existence depends on the interaction between sea level and sufficient sediment accumulation on the marsh plain. Not only is sea level important, but relative sea-level –

a lowering of the marsh plain due to subsidence, erosion, or decreased organic-matter delivery – will act in concert with sea-level rise to affect coastal ecosystems and their functions. A recent study projects a global sea-level rise by 2100 of 0.5 to 1.4 meters above the 1990 level (Rahmstorf 2007), which exceeds the 2007 IPCC maximum estimate of 0.6 meters. Incorporating the effects of glacier melt suggests an additional 0.1-0.25m of sea-level rise by 2100 (Meier *et al.* 2007), and melting predictions for ice sheets of Greenland and West Antarctica launch the range up to 3-7 m by 2100 (Oppenheimer 1998; Overpeck *et al.* 2006; Bamber *et al.* 2009), with a total of ~70 meters of sea-level rise should all ice sheets melt (Cazenave 2006). Sea level affects marsh distribution and density through the mechanisms of waterlogging and salinity stress (Mahall and Park 1976b; Mitsch & Gosselink 2000). Resilience of salt marsh to sea-level rise depends on sediment accretion or the ability of plants to migrate upland. Paleocological studies indicate that marshes distributed globally have kept pace with past sea-level rise through sediment accretion (Cahoon *et al.* 2006), including the San Francisco Bay estuary ~150 km north of Elkhorn Slough (Watson 2004). However, it is also an open question whether marshes can keep pace with sea-level rise without added mineral sediment inputs or increased organic-material accretion (Stevenson & Kearney 2009). Although sea-level rise may be gradual now, on a global scale, predictions include accelerating change as well as local variation (IPCC 2007). At our study site, Elkhorn Slough, marshes are unlikely to keep pace with sea-level rise because the Slough has physical, hard shoreline barriers – levees, tide gates, and rip-rap – that will likely obstruct marsh migration towards the uplands. Up-river

migration is possible (Caffrey *et al.* 2002); however, Elkhorn Slough has only one small, ephemeral river input (Carneros Creek) at the head. The Slough is also starved of sediment delivery (Caffrey *et al.* 2002). Finally, Elkhorn Slough is an ebb-dominated estuary (Nidzieko 2010), which tends to emphasize sediment loss with higher-velocity ebb waters.

Although both N accretion and sea-level rise are recognized threats to coastal marshes, their interacting effects are unknown. In our study, we address the question: How do sea-level rise and anthropogenic nitrogen additions affect the salt marsh ecosystem process of nitrogen uptake? This is the first study we are aware of to investigate the presence and type of interactions between the two stressors in an empirical, controlled experiment in temperate salt marsh. Salt marsh plant zonation has been clearly described, including the observation that increased waterlogging through relative sea-level rise detrimentally affects marsh plant growth and survival (Adam 1990; Lowe 1999). Our novel contribution is to look at both plant growth and N dynamics during inundation at the same time that inorganic N levels increased. Our objective was to investigate the potential for salt marsh plants to buffer estuarine and ocean waters from the effects of ever-increasing nitrogen loading from land. We quantified nitrogen uptake into plant tissue while plants were responding to treatments that simulated a) encroaching sea level and waterlogging; or b) increased sedimentation leading to a higher-elevation marsh platform.

In any sea-level-rise scenario, salt marsh plants will experience increased inundation depths and times. We expected the dominant plant, *Sarcocornia pacifica*

(Standley) (pickleweed), to decrease in both abundance (biomass) and extent (experimental sea levels where the plants survived) due to ecological drowning. We expected diminished nutrient uptake as plants were physiologically stressed and dying. We anticipated that experimentally raising the marsh plain (i.e., reducing the frequency of inundation) would improve halophytes' ability to take up nitrogen. Finally, we had a general expectation that nitrogen addition above background levels would increase marsh plant growth, providing antagonistic effects to marsh drowning in the field (e.g., Boyer *et al.* 2001, Covin and Zedler 1988) – but a threshold might exist, where chronic nutrient addition contributed to toxic effects or no longer contributed to growth.

Finally, nitrogen incorporated into plant tissue will continue to cycle when the plant dies or senesces, and decomposes, raising the question of whether plant-bound nutrients have truly been “intercepted” from the ocean. The slower turnover time of nitrogen bound in organic form is generally considered beneficial in buffering the rates and amounts of available-N delivery (Hopkinson and Giblin 2008). The timing of nutrient delivery and plant uptake does matter. *Sarcocornia* is most productive (with green, succulent, new tissue) in the summer months and dormant (with woody stems) in the winter (Boyer *et al.* 2001). Since there is a potential “mismatch” in timing in Pacific Coast marshes, where maximum plant production occurs in summer and peak nutrient runoff arrives with winter rains, we explored marsh response to N addition and sea-level rise simulations in the months of April, July, and Nov/Dec (spring, summer, and winter).

Materials and Methods

Study site: Elkhorn Slough (36°48' N, 121°47' W), located on the central coast of Monterey Bay, California, has one of the largest tracts of coastal salt marsh habitat in California, with 1,147 ha of marsh (Caffrey *et al.* 2002) (Fig. 1). The main channel of the Slough is part of the Monterey Bay National Marine Sanctuary and is surrounded by agricultural lands, with 24% of the slough watershed under production (Caffrey *et al.* 2002), primarily in heavily fertilized strawberries and vegetable row crops.

We established our experiment at Coyote Marsh, a high marsh in the Elkhorn Slough National Estuarine Research Reserve (ESNERR) (Fig. 5). Plant species at the site included *Sarcocornia pacifica* (pickleweed), which was the predominant cover, as well as *Jaumea carnosa* (fleshy jaumea), *Frankenia salina* (alkali heath), and *Distichlis spicata* (salt grass).

Experimental design: We crossed relative sea-level and nitrogen treatments in a fully factorial design to examine their potentially interacting effects on plant biomass and tissue nutrient concentrations. We used marsh elevation as a proxy for sea-level rise, and chose three elevations – with a fourth extreme sea-level rise simulation. Simulated sea levels were chosen to fall within the spectrum of IPCC (2001) scenarios (where +30cm was the maximum predicted), or an ecologically significant amount of sedimentation (Fogel *et al.* 2004) with predictions of more variability in precipitation and storm events (cite). The simulated sea levels were +10cm, 0cm (the ambient marsh plain) and -10cm,

simulating 10cm of sediment addition as might occur if more extreme storms increase sediment inputs to the marsh. The fourth simulated sea level, which we refer to as “extreme sea level treatment” was +30cm. Nitrogen additions simulated increased N in terrestrial surface runoff. The two levels of N treatment were $300 \text{ g N m}^{-2} \text{ yr}^{-1}$, in the form of ammonium nitrate (NH_4NO_3), or no added nitrogen under ambient conditions. The added N is equal to an average five- to ten-fold addition of the conventional fertilizer used in the region on strawberry or vegetable fields (Breschini and Hartz, 2002; T. Hartz, pers. comm.). We accounted for spatial variability across our site by establishing three blocks, each containing all treatment combinations (4 elevations and 2 N levels), for a total of 24 one- m^2 plots. Control plots evaluated a possible digging effect by digging up and then replacing otherwise-unmanipulated marsh vegetation. There was one control plot in each block: having determined that there was no significant digging effect for each analysis, we did not incorporate data from those plots.

Field methods:

Elevation: We created the artificial sea-level rise treatment (adapted from Fogel *et al.* 2004) by selecting a 1x1-m plot of marsh, removing vegetation with intact roots in a block of sediment, removing or adding sediment beneath the vegetation layer (depending on the treatment), and replacing the vegetation layer. A difference in marsh-plain elevation of 10cm has been shown to have ecological effects (Fogel *et al.* 2004). The side-walls of plots were held in place with hardware cloth and landscape staples.

Lowered plots did not have any drainage channels or other simulations of an ebb tide. Each plot was at least 3m away from any other plot.

Extreme sea-level rise simulation: Marsh plots lowered 30 cm simulated a sea-level rise that we estimate to be greater in magnitude than 30cm, because the plots did not drain and had no system to simulate an ebb tide. Plants were inundated in water with a salinity of ~35 (practical salinity units), typical of the main channel Slough and the Pacific Ocean. Plots did drain occasionally, with no intervention, in a pattern that was not correlated with any variables we measured. We refer to this scenario as “extreme sea-level rise simulation” since it is a rapid and almost-continual inundation of marsh.

Nutrient addition: We added ammonium nitrate (NH_4NO_3) to designated plots in the amount of 15 gN m^{-2} every two weeks. We did not fertilize during July and August of each year, because summer nutrient levels in the Slough are lowest and fertilizer applications are low, becoming high again in October (cite). Therefore, we added a total of $300 \text{ gN m}^{-2} \text{ yr}^{-1}$ to fertilized plots. We dissolved NH_4NO_3 pellets in 1L of main-channel Slough water and added them to treatment plots; we added 1L of Slough water to each ambient plot.

Biomass harvest: We measured the impacts of sea-level change and nitrogen addition on plant biomass, above- and belowground, and plant physiological measures of tissue nitrogen concentration and resource allocation. We harvested a 10x50cm swath

of aboveground vegetation from each meter-square plot on the following dates: July and November 2008, and April, July and November 2009. The swath was taken from a randomly-chosen quarter of a plot with the following constraints: the 50-cm edge was always internal to the plot to avoid edge effects, we harvested a given 10x50cm area only once in the two years, and we stopped harvesting when all plants in a plot were visibly dead. Once harvested, we sorted plants by species. We separated succulent (new) and woody (perennial) tissue for *Sarcocornia pacifica* only. All plant material was dried in a laboratory oven at 60°C for at least 48 hours; weighed; and a portion ground with a ball mill (Wiley). We put the ground plant material through a C:N analyzer (Elementar) in order to obtain tissue nitrogen concentration.

In the second year only (2009), we harvested root biomass with a 5-cm-diameter sediment corer, taking 20-cm-deep cores. We isolated plant material through root-washing by hand and categorized roots as fine or coarse. The approximate diameter cutoff between fine and coarse roots was 0.5 mm. We dried the roots in a laboratory oven at 60°C for at least 48 hours, weighed them, and ground all material in a ball mill (Spex 8000). We analyzed %N in November root data only (Costech ECS 4010).

Analytical methods: To assess treatment effects on plant aboveground biomass, we grouped all plant species (which includes succulent and woody tissue biomass of *Sarcocornia pacifica*) in each plot and used a General Linear Model with repeated measures in SYSTAT v12 (Systat Software. Inc., Chicago, IL, USA). We tested for a block effect, and where it was insignificant – in all analyses but one – removed it as a

factor. Therefore, independent factors were N-level, relative sea-level (RSL), and their interaction. We log-transformed biomass data to conform to a normal distribution. The repeated measures analysis incorporated all 24 plots over 5 harvests (July, November, April, July November). Similarly, to assess treatment effects on plant tissue nitrogen concentration (mg N per gram of plant tissue), we used a General Linear Model with repeated measures analysis, where data were log-transformed. We ran a post-hoc comparison for repeated measures, with a Bonferroni correction for pairwise comparisons, to assess which seasons might be different than each other. To assess experimental effects on root biomass and shoot:root ratios, we used a factorial ANOVA on each of two harvests. In any analysis where there were significant interactions, we explored the data visually to interpret patterns. We set the significance level for all analyses at $\alpha = 0.05$, *a priori*.

Results

Above- and belowground biomass production

Nitrogen addition increased aboveground marsh biomass (Fig. 2), (N-level $F=11.08$, $p=0.006$). Nitrogen-addition effects were strongest in Year Two of treatments, particularly in July during the summer growing season (Fig. 2). For example, in July 2009 at -10cm relative sea level, fertilized plots and unfertilized plots had mean biomass of $4.1 (\pm 0.67) \text{ kg m}^{-2}$ and $1.3 (\pm 0.41) \text{ kg m}^{-2}$, respectively – a three-fold difference.

In contrast, relative sea-level rise had no significant effect on biomass (RSL $F=1.04$, $p=0.39$) and did not influence the N response (N-level \times RSL $F=0.90$, $p=0.43$). The only harvest in which both treatments had any type of interactive or synergistic effect was the summer (July) of Year Two, where effects were additive: in the presence of N-addition, biomass decreased linearly with relative sea-level rise (Fig. 2). This pattern differed from the first year of the experiment, where in the absence of N-addition (ambient conditions), biomass decreased linearly with relative sea-level rise in both July and November (Fig.2). The simulated sea-level rise treatment was achieved by removing sediment from beneath the vegetation-and-roots mat, and the converse treatment (increased sedimentation) was achieved by adding sediment beneath the vegetation, as described in the methods section.

Although biomass varied among harvests, there was a clear seasonal pattern of N response, highest in the summer growing season, which was greatest in July of

Year Two. Pairwise comparisons of the significant N effect on biomass indicated that July of the first year was significantly different than all three of the second-year harvests (factor = season, $p=0.04$, $p<0.001$ and $p<0.001$). In the second year, April biomass was lower than July of that same year ($p = 0.04$).

Root biomass tended to increase with nitrogen addition in November (N level $F = 3.48$, $p = 0.09$), but relative sea-level rise did not have a discernible effect (RSL July $F= 0.47$, $p = 0.635$; RSL Nov, $F= 0.09$, $p = 0.915$) (Fig. 3). Root biomass in November 2009 was almost double that of July 2009: November's fertilized root biomass at -10cm relative sea level averaged $6096 (\pm 1527)$ g, compared to $3330 (\pm 419)$ g in July, a 183% increase.

Because of the strong effect of N increasing aboveground biomass in July and modest effect of increasing belowground biomass in November, N strongly increased shoot:root ratios in July (N level $F= 12.31$, $p= 0.004$) (Fig. 4). Changing relative sea level did not exert a significant effect on shoot:root ratios (RSL $F=2.14$, $p = 0.16$) or influence the N treatment (N-level x RSL $F = 0.51$, $p = 0.61$).

There was very little evidence for spatial variation in marsh growth, in that a test for a block effect was non-significant in all analyses save one (shoot:root biomass ratios in November 2009). Although there was a strong and interpretable overall response to treatments, salt marsh responses varied temporally, by season.

Extreme sea-level rise treatment

In the highest simulated sea-level rise of 30 cm, all salt marsh plants died in Year Two of the experiment, between spring and summer. N-addition led to greater

biomass in only one of three harvests with living plants, in winter of the first year (Fig. 5).

Plant tissue nitrogen

Nitrogen concentration

Nitrogen concentration (mg N g^{-1}) in aboveground plant tissue increased strongly in plots with N-addition (N-level $F = 35.81$; $p < 0.001$) (Fig. 6). Similar to results for biomass, simulated sea-level rise did not have an effect (RSL $F = 0.08$, $p = 0.92$), and there was no interaction between the treatments ($F = 0.47$, $p = 0.64$). There were significant within-subject (within-plot) effects of season ($F = 5.04$, $p = 0.002$), leading to an exploration of temporal variation: N concentration in July of the first year was significantly different than N concentrations in July and November of the second year (factor = season, $p < 0.001$ for each comparison), and N concentration in April of the second year was significantly different than July or November of the same year (factor=season $p < 0.001$ and $p = 0.002$).

Treatment effects on plant N concentration were most apparent in Year Two, as with biomass, but in the dormant season of November rather than the growing season of July. At a maximum – November 2009 in the +10cm sea-level rise plots – new pickleweed (*S. pacifica*) tissue had a concentration of $37.17 (\pm 23.9)$ mgN/g plant tissue when fertilized compared to $9.06 (\pm 0.27)$ mgN/g plant tissue in controls, a 410% difference.

N addition significantly increased root-N concentration in coarse roots only, in November (N-level $F=25.32$, $p<0.001$; RSL $F=1.50$, $p = 0.26$). There were no discernible treatment effects on fine roots (N-level $F=0.002$, $p=0.96$; RSL $F=0.50$, $p = 0.62$).

Extreme sea-level rise

In the highest simulated sea-level rise of 30 cm, N concentration in aboveground tissues increased significantly with added inorganic N only in April of the second year (N-level $F=20.41$, $p=0.01$) (Appendix 1).

Plant nitrogen sequestration

Total nitrogen sequestered in new growth of *S.pacifica* (gN m^{-2}) – a product of nitrogen concentration and new-growth biomass – increased strongly in response to N addition (N level $F= 13.88$, $p = 0.003$). Relative sea level had a marginally significant effect (RSL $F = 2.99$, $p = 0.09$), with no interaction between treatments (N-level x RSL $F= 0.581$, $p = 0.57$). There were significant effects of season and season-by-N level ($F= 17.53$, $p <0.001$ and $F= 4.10$, $p = 0.006$, respectively). At a maximum, fertilized plants stored more than four times as much nitrogen as controls: in July 2009 at -10cm relative sea-level rise, plants sequestered $22.8 (\pm 5.6) \text{ gN m}^{-2}$ compared to no-N plots with $4.8 (\pm 1.6) \text{ gN m}^{-2}$, a difference of 475 percent (Fig. 6). At that same time and plot elevation, biomass increased at a lower rate of 316 percent (4107 g m^{-2} average fertilized biomass vs. 1300 g m^{-2} average unfertilized biomass) (Fig. 2).

Extreme sea-level rise treatment

There was no significant effect of N addition on N stored in plots with 30cm of simulated sea-level rise ($F = 0.69$, $p = 0.45$). However, there was a within-plot effect of season ($F = 4.48$, $p = 0.05$) (Appendix 1).

Discussion

Important ecosystem functions and services provided by temperate salt marsh are at risk of being diminished by directional, ecological change. This is the first study to examine the interaction of N-accretion and sea-level rise on the capacity of temperate salt marshes to intercept land-derived N to protect ocean functioning. We present quantitative evidence of salt marsh plants' capacity to intercept excess N under conditions of chronic and increasing N loading. Our results suggest the plants serve as a robust N trap, or coastal filter. Additionally, in the case of Coyote Marsh, Elkhorn Slough, this function is not saturated.

However, if the marsh is drowned by rising seas – as it was in the most extreme sea-level rise simulation – the plants will no longer provide the ecosystem service of buffering the ocean from detrimental effects of eutrophication.

Nitrogen effects on salt marsh

In the present study, marsh buffers estuarine waters from N loading through the mechanism of plant uptake. In response to N addition, the dominant marsh plant, pickleweed (*S. pacifica*), increased N concentrations in succulent, annual tissue; all four marsh species increased growth and shoot:root ratios, with a larger proportion of N-rich shoots relative to low-N roots. Together, these three factors drove the

magnitude of N sequestered on a per area basis, which was four times higher in fertilized plots.

It is notable that in an estuarine environment with *high* concentrations of nitrate in the main channel water (up to 250-300 μM $\text{NO}_3\text{-N}$ in winter (Jannasch *et al.* 2008, and www.mbari.org/lobo)), salt marsh plants continued to be N-limited. High nitrate concentrations in the main channel fuel productivity that can be categorized as beyond “eutrophic” to “hypertrophic” (Nixon 1995). Even when “reference” plots are bathed in high concentrations of nitrogen, marsh plants treated with additional inorganic N show increased growth without any apparent toxicity effects.

The pathways by which N is delivered to salt marsh include surface runoff, groundwater, and inundation with estuarine-ocean water on flood tides. Therefore, although Coyote Marsh is subjected to flood tides no more than 4-6 times a month on average in winter, the marsh plants do get the 250-300 μM $\text{NO}_3\text{-N}$ as an ambient dose. In Elkhorn Slough, 66% of nitrate in the main channel comes from terrestrial sources (Plant *et al.* 2009), as distinct from ocean upwelling, so even the flood tides are a majority of “land-derived” N.

Notably high interception of externally added N has also been shown in the Great Sippewissett Salt Marsh, New England (Brin *et al.* 2010), even after 30 years of experimental fertilization treatments. However, in another New England study, salt marsh vegetation exposed to ~ 70 μM NO_3^- reached a saturation point for uptake, and became less effective at pollution control than the reference systems (Drake *et al.*

2008). In a study in Portugal, the capacity of salt marshes to retain N depended on the age of the marsh, where the oldest marshes retained the most (Sousa *et al.* 2008). All of the above studies focused on low-marsh *Spartina spp.*, cordgrass, whereas there is no *Spartina* in Elkhorn Slough; species differences need to be taken into account.

Other studies of nutrient enrichment in U.S. Pacific Coast, pickleweed-dominated salt marsh have shown that nutrient addition increases salt marsh productivity and alters community structure (Boyer *et al.* 2001, Boyer & Zedler 1999) and increased susceptibility to species invasions (Martone and Wasson 2008). In a greenhouse study, a toxicity threshold was reached upon adding $>6.67 \text{ g l}^{-1}$ of urea-N to pickleweed plants (K. Griffith dissertation). (All of these studies used an organic form of N, urea, which depends on microbial mineralization for plant availability.)

In contrast to aboveground measures, root biomass did not respond as strongly to N-addition treatment. There is disagreement in the literature about the vulnerability of salt marshes to eutrophication, which centers around belowground responses: some results indicate that nutrient-enriched sediments, such as treated sewage sediments, have no detrimental effects on marsh plants (Day *et al.* 2004), while other results show relatively lower root growth in marshes with nutrient addition (Turner *et al.* 2009, Turner 2010). A mechanism for detrimental effects, demonstrated in a long-term study in Louisiana, is that fertilized marshes allocate more to aboveground- than belowground-growth, decreasing organic matter in the sediments, leading to decreased elevation of the marsh plain – subsidence – and subsequent salt marsh loss through drowning (Turner *et al.* 2009). In contrast, our study showed either no effect

of N addition on root biomass (summer of year 2) or tended ($p=0.08$) to increase root biomass (winter of year 2).

There were seasonal differences in treatment effects, where in the summer growing season, we saw a more distinct response to experimental treatments of simulated sea-level rise and N addition. Since the first harvest was different than all those of the second year, we expect that the N-addition effects took time to build.

Salt marsh vulnerability to sea-level rise

Plants exposed to the less extreme simulation of sea-level rise (+10cm) survived throughout the two-year experiment, and their biomass did not differ significantly from that of the ambient marsh platform. These results suggest plant growth was not adversely affected by the sea-level rise treatment, and that – unsurprisingly – the rate and magnitude of biophysical change matter in terms of species' responses and survival. However, plant biomass reached a one-time maximum in plots with added sedimentation (summer of the second year), so the converse of relative sea-level rise promoted plant growth.

Although the simulated sea-level rises we imposed were sudden, rather than the gradual rate predicted (5-7mm/year eustatic rise in 50 years; IPCC 2007), the total amount of rise is on par with IPCC 2007 predictions (25-35cm in the next 50 years). Sea-level rise may outpace the ability of the marsh to keep pace, in terms of vertical accretion, through sedimentation. For example, researchers predict 1.5m of sea-level rise in the next century (Rahmstorf 2007), and those that incorporate ice-sheet

melting, through paleoclimatic data and models, pose > 7m of sea-level rise (Hansen 2005; Overpeck *et al.* 2006). If accelerating, directional changes outpace sedimentation or other physical, chemical, or biological foundations of marsh, our experimental results may provide greater insights and predictive power.

Extreme sea-level rise simulation

Salt marsh plants in Coyote Marsh, Elkhorn Slough, were vulnerable to the extreme sea-level rise simulation of +30cm, in that all plants died by the middle of the second year of the experiment. This result is consistent with the estuarine literature (Adam 1990; Lowe 1999; Mendelssohn & Morris 2000); however, our novel contribution was to look at N dynamics as plants were inundated.

Conclusions and implications for management

Our results have implications for management of both the elevation of marshes and nitrogen losses from land-use. For example, in Atlantic-Coast salt marshes, the ecosystem engineer, seasalt arrow grass, raised the marsh sediment level and improved growth of other marsh plant species (Fogel *et al.* 2004). Researchers and marsh conservation groups have proposed adding dredge sediments to marshes to increase their elevation relative to mean tidal height (Day *et al.* 2004; Tidal Wetlands Project 2008 (www.elkhornslough.org/tidalwetlandproject/index.html)). Dredge sediment addition has raised questions about nutrient, metal, and pollution concentrations in those sediments. Given sources of sediment that have acceptably

low levels of pollutants, sediment addition is an intervention that seems to support marsh survival and sustainability under conditions of relative sea-level rise.

In terms of seasonal effects, the peak marsh growing season is summer in Elkhorn Slough marshes, but the highest concentrations of nutrients are delivered with winter rains. Marsh plant uptake helps buffer nitrogen loading, as do terrestrial vegetative buffer strips in Elkhorn Slough (e.g., Los Huertos 1999), but they are not a comprehensive substitute for policies that reduce fertilizer N inputs and losses from land (Faeth ; Boesch 2002; Foley *et al.* 2005). Our two-year experiment shows that marsh plants are taking up excess N in each season studied.

In this study, the global changes of sea-level rise and nitrogen pollution have strong effects on salt marsh productivity and nutrient cycling. First, salt marshes buffer N loading through plant uptake; however, sea-level rise quickly diminishes salt marsh extent. Second, halophytes sequester more nitrogen – through growth and increased tissue N concentrations – with inorganic nitrogen addition. Third, there are seasonal variations in response to treatments – where plants grow more, sequester more nitrogen in standing stock, and respond more strongly to the combination of treatments in the summer growing season rather than the winter dormant season.

Salt marsh distribution will change with sea-level rise – coastal wetlands could establish in areas where they may not have been documented currently and disappear from protected areas (Craft *et al.* 2009) – making tools for flexible land-use and conservation of greater importance. Exploring policy synergies to mitigate greenhouse gas emissions and abate nutrient enrichment, at the same time, will be

valuable to both conservation of coastal marshes and improvement of ocean water quality (Faeth & Greenhalgh 2002; Foley *et al.* 2005; Ahrens *et al.* 2008; Gruber & Galloway 2008; Nicholls *et al.* 2011).

Figures

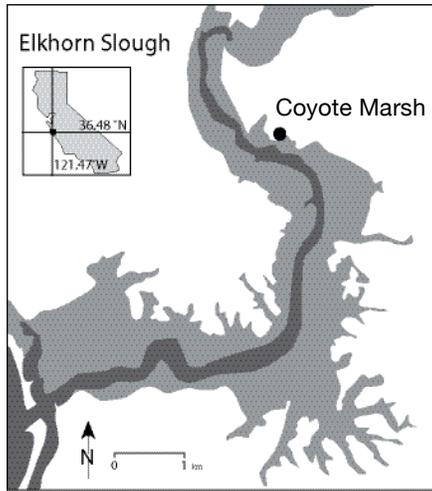


Figure 1. Elkhorn Slough, in Moss Landing, California, on the coast of Monterey Bay. The experiment site, Coyote Marsh, is located in the Elkhorn Slough National Estuarine Research Reserve.

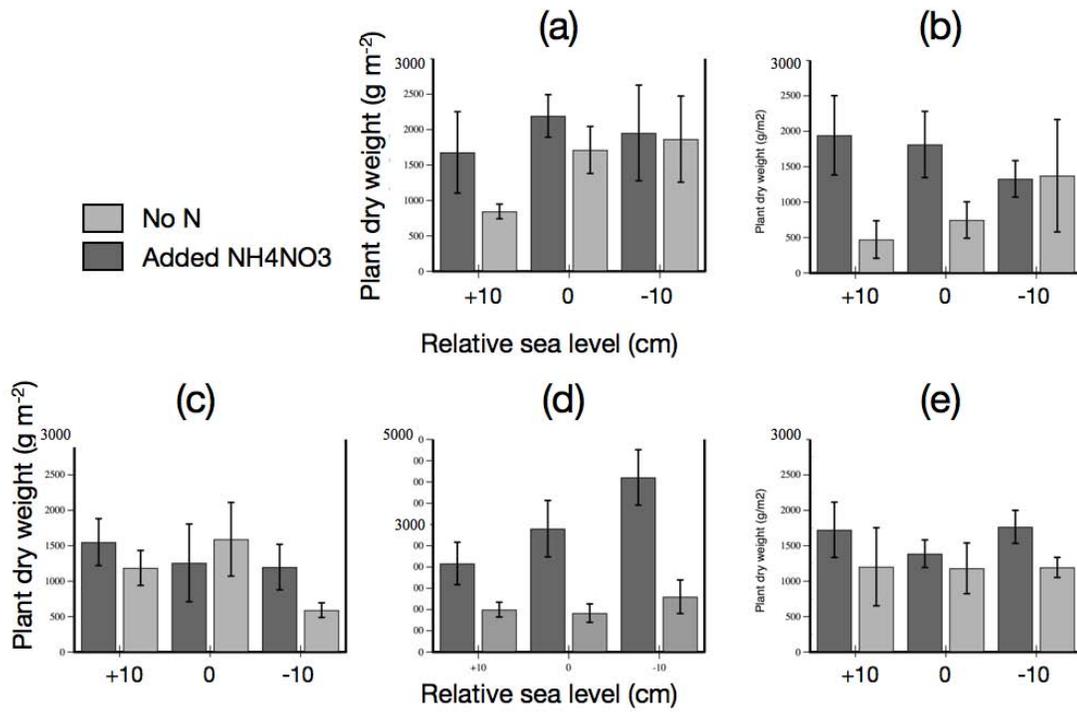


Figure 2. Aboveground salt marsh plant biomass (g m⁻²) in a) July 2008; b) Nov 2008; c) April 2009 d) July 2009; and e) Nov 2009 harvests. Error bars depict standard error of the mean.

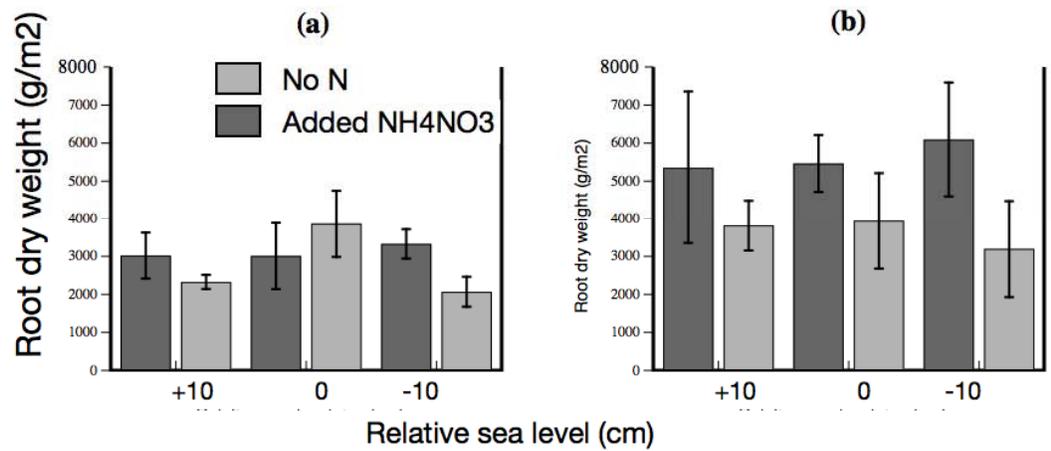


Figure 3. Salt marsh root biomass is almost twice as high in the dormant season of winter as in summer. Root biomass (g m⁻²) in a) Summer 2009; and b) Winter 2009. Error bars depict standard error of the mean.

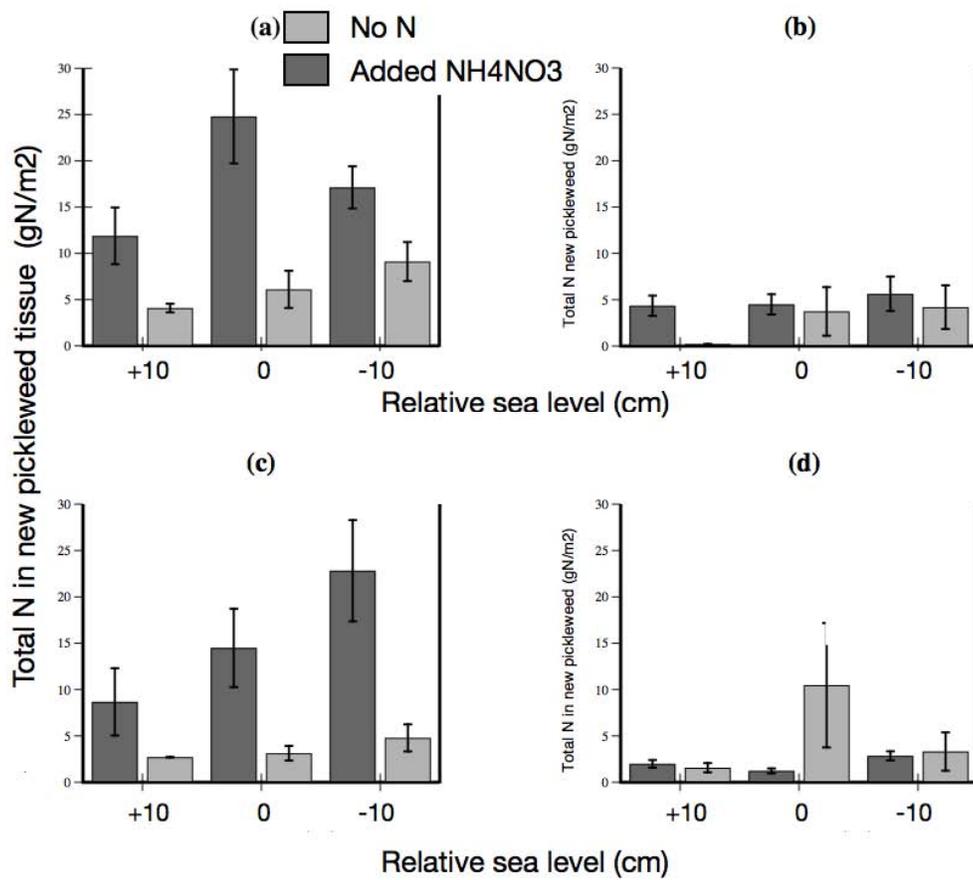


Figure 4. At a maximum, plants with added inorganic nitrogen sequestered more than four times as much as N as controls. Total N sequestered in *S. pacifica* new-growth tissue (gN m⁻²) in a) July 2008; b) November 2008; c) July 2009; d) November 2009.

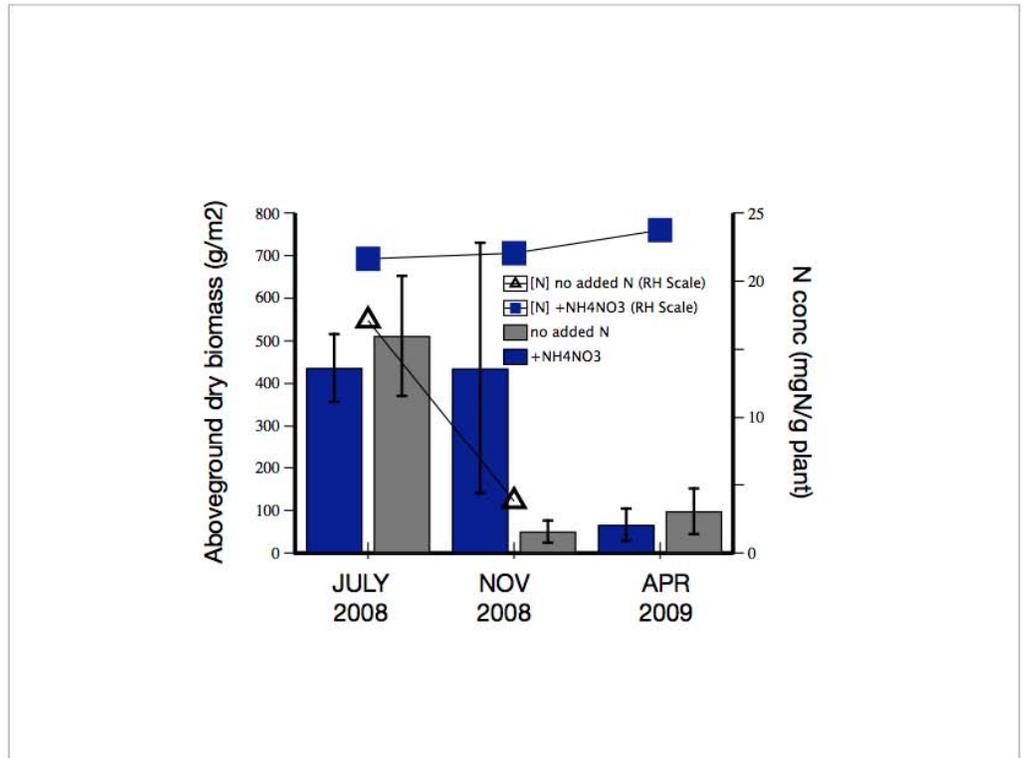


Figure 5. Simulation of +30cm sea-level rise resulted in the death of all salt marsh plants before the summer of Year Two of the experiment (bar graph), where plant tissue N concentrations increased with N treatment (XY graph). Salt marsh plant species are the dominant *Sarcocornia pacifica*, as well as *Jaumea carnosa*, *Frankenia salina*, and *Distichlis spicata*. Error bars depict standard error.

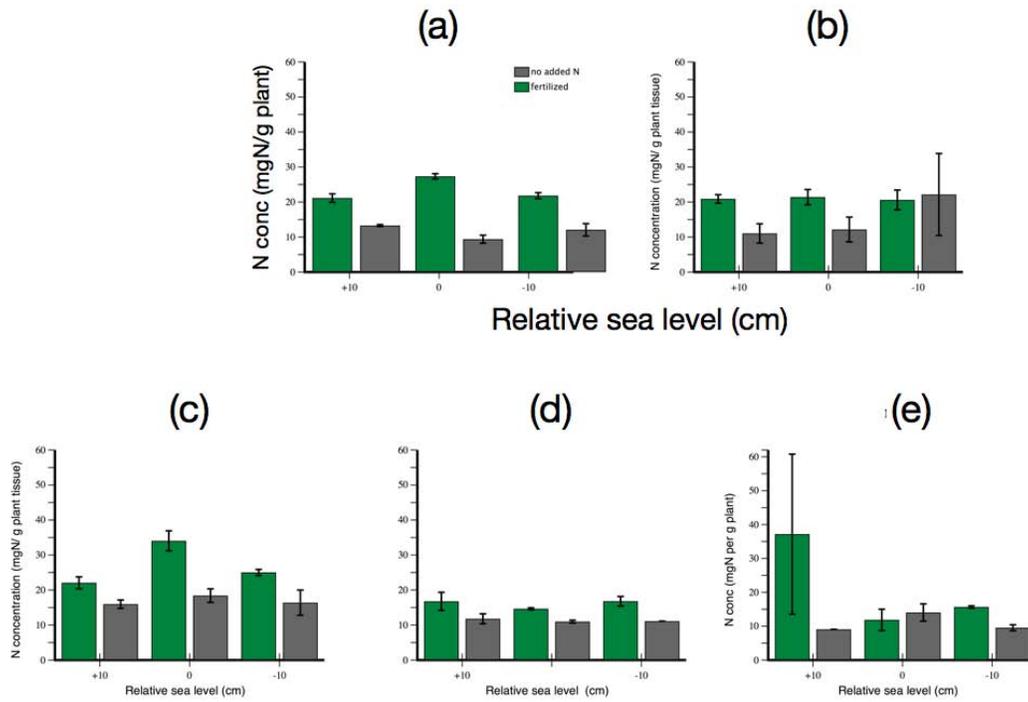


Figure 6. Nitrogen concentration in plant tissue (mgN g⁻¹ plant tissue) in a) July 2008; b) Nov 2008; c) April 2009 d) July 2009; and e) Nov 2009 harvests. Error bars depict standard error of the mean.

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CHAPTER 3

SALT MARSH AS A COASTAL FILTER: MARSH PLANT UPTAKE OF NITROGEN AT THE SCALE OF THE ESTUARY INDICATES SATURATED CAPACITY

Introduction

Ecological change and environmental degradation are accelerating as human activity profoundly alters physical, chemical, and biogeochemical cycles (Vitousek *et al.* 1997; Chapin *et al.* 2000; IPCC 2007). Multiple global environmental changes converge in particular at the land-sea interface, with anthropogenic disturbances originating from both the marine and terrestrial realms (NRC 2000). The coast, therefore, is an important place to study global change interactions, with a goal of understanding potential thresholds and nonlinearities in ecosystem responses in order to prevent unacceptable environmental change. Indeed, a study delineating nine major Earth System processes suggested that three processes have already crossed a threshold out of the “safe operating space for humanity”: the rate of terrestrial and marine biodiversity loss, climate change, and human interference with the nitrogen cycle (Rockstrom *et al.* 2009).

Nitrogen pollution and sea-level rise due to climate change are co-occurring and potentially interacting perturbations (Kennish 2002; Scavia *et al.* 2002; Howarth

et al. 2011), yet their combined effects in coastal salt marshes are poorly understood (Gedan *et al.* 2009). Eutrophication is the most extensive pollution problem in U.S. estuaries (NRC 2000; Cloern 2001), defined as an increase in the rate of supply of organic matter to an ecosystem (Nixon 1995). Nutrients fuel growth of phytoplankton and macroalgae in nearshore oceans. Subsequent microbial decomposition depletes dissolved oxygen, leading to coastal “dead zones” – hypoxic or anoxic zones of the ocean (Rabalais *et al.* 2009, 2010; Diaz and Rosenberg 2008). Dead zones now affect more than 245,000 km² worldwide (Diaz and Rosenberg 2008). In addition, nutrient pollution can contribute to harmful algal blooms, changes in trophic structure, long-term declines in coastal marine fisheries, and changes in biogeochemical cycling (Vitousek *et al.* 1997; NRC 2000; Howarth *et al.* 2011). Two-thirds of US estuaries are eutrophic (Bricker *et al.* 2007), and that proportion is growing. Among many important ecosystem services provided by salt marsh is the interception of land-derived nitrogen and other nutrients that enter watersheds and runoff from development and agricultural production (Zedler and Kercher 2005; McGlathery *et al.* 2007; Brin *et al.* 2010). The ability of salt marsh to buffer the perturbation of nutrient pollution needs to be quantified to assess its power to reduce severe environmental problems resulting from eutrophication in the coastal zone. Additionally, there is a need for further work on the extent to which salt marshes are also vulnerable to N pollution in runoff.

Salt marshes have been severely diminished in extent and degraded by coastal development, agricultural activity and other human uses, and increasingly by sea-level rise (Zedler and Kercher 2005). In California, salt marsh habitats are among the most threatened ecosystems, as endangered as coastal redwood forests, having lost 80-95% of their historic extent (Emmett et al. 2000, Zedler 1996). Coastal salt marshes are now threatened by sea-level rise resulting from climate disruption: static models suggest the loss of 50% of global marsh extent by 2100 (Nicholls et al. 2007; Craft et al. 2009).

Sea level affects marsh distribution and density through the mechanisms of waterlogging and salinity stress (Mahall and Park 1976b; Mitsch & Gosselink 2000). Resilience of salt marsh to sea-level rise depends on either of two pathways: a) sediment accretion in equilibrium with the rate of sea-level rise so the marsh maintains its relative elevation; or b) the ability of plants to migrate upland. In a), salt marsh survival depends on the interplay between sediment deposition and accretion, marsh elevation, relative sea-level rise, and the vegetation itself (Reed 1995; Morris et al. 2002; Cahoon et al. 2006; Kirwan et al. 2010). Marsh plants affect physical processes, for example by slowing water velocity, leading to sediment deposition (Leonard and Luther 1995; Allen 2000; Davidson-Arnott 2002; Morris et al. 2002). A positive feedback loop can develop where dense marsh vegetation promotes sediment accretion, building the marsh elevation in pace with a rising sea level, and promoting further growth of vegetation (e.g., Morris et al. 2002). Dynamic models of marsh

resilience thus suggest smaller losses of global marsh extent than static models (e.g., Kirwan et al. 2010). However, the opposite positive feedback can occur for degraded or drowning marsh vegetation, leading to accelerated marsh loss. Paleoecological studies indicate that marshes distributed globally have kept pace with past sea-level rise through sediment accretion (Cahoon *et al.* 2006), including the San Francisco Bay estuary ~150 km north of Elkhorn Slough (Watson 2004). However, it also remains an open question whether marshes can keep pace with sea-level rise without added mineral sediment inputs or increased organic-material accretion (Stevenson & Kearney 2009). Upland migration of salt marsh can be inhibited by engineered barriers, such as levees, and other coastal development (Zedler and Kercher 2005). Marsh survival or submergence in the face of sea-level rise (Reed 1995) seems to be site-specific in its context of geomorphology, sediment delivery, halophyte species composition, current elevation of a marsh platform, rate of relative sea-level rise (which incorporates land subsidence and eustatic sea-level rise) and ecogeomorphic feedbacks (Morris et al. 2002, Kerwin et al. 2010).

Salt marsh habitats therefore constitute important study communities for both documented and potential effects of global-scale, anthropogenic changes to the Earth System. Studying coastal salt marshes can provide insights into their dynamic nature, self-regulating capacities, and limits to their adaptability, which will influence the ways in which these ecosystems provide protective functions in the face of both terrestrial pollution and sea-level rise. A deeper understanding of the functioning of

these ecosystems may help us predict the limits of anthropogenic impacts they can absorb, and which types and levels of impacts could overwhelm the marshes' buffering capacity – such as drowning under relative sea-level rise, or crossing a threshold from nutrient interception to nutrient toxicity.

Given a body of evidence that marshes provide a nitrogen-filtering function between land and sea (Kennedy 1984; Mitsch *et al.* 2001; McGlathery *et al.* 2007; Sousa *et al.* 2008; Drake *et al.* 2009; Brin *et al.* 2010) and evidence that marsh sustainability is at risk, both globally and in particular regions (Zedler and Kercher 2005; Nicholls *et al.* 2007; Nicholls and Cazenave 2010), what might happen to the ecosystem service of salt marsh as a coastal filter? I investigated potential impacts of increasing nitrogen loading and sea-level rise, both independently of each other and in concert, in salt marshes surrounding Elkhorn Slough. The Slough extends beyond and encompasses the Elkhorn Slough National Estuarine Research Reserve (ESNERR), in Moss Landing, California. Specifically, I focused on how landscape-scale variation in 1) rates and magnitude of nitrogen delivery and 2) marsh intertidal height (a measure of tidal inundation) affect the growth of marsh plants and their nitrogen uptake.

Estuarine habitats can intercept nitrogen in three essential ways: via uptake into plant tissue, denitrification by microbial communities in sediments, and burial in sediments (Bianchi 2007, Seitzinger *et al.* 1998). My research focuses on plant uptake by emergent marsh plants. Nitrogen supply in salt marshes affects plant

productivity and biomass, and aspects of physiology, such as resource allocation and tissue N content (Hopkinson and Giblin 2008; Morris 1991; Haines & Dunn 1985). A gradient of N-concentration in the estuary of Elkhorn Slough, Moss Landing, CA, offers a window into the future of changing N-levels (both in concentrations of N and accelerating rates of delivery) and marsh response.

Elkhorn Slough, California

Elkhorn Slough serves as a model study system in several respects. ESNERR is one of a network of 28 estuaries in the United States that are a focus of research and conservation, in a partnership between federal and state agencies and scientific researchers (the NERRs, <http://www.nerrs.noaa.gov/>). In turn, the Elkhorn reserve belongs to a regional network of seven marine-focused academic institutions around Monterey Bay. My investigation was able to draw, therefore, on a rich foundation of data, records, and interpretations of environmental change. Surrounded by intensive conventional agriculture, the slough has some of the highest nutrient concentrations of any estuary in the United States (Caffrey *et al.* 1997; Caffrey *et al.* 2002; Fry 2003). Elkhorn Slough is listed by the US Environmental Protection Agency as an impaired waterway—impaired by nutrients, pathogens, pesticides, and sediment (US EPA 2011). Moreover, as the site of an estuarine reserve and part of the Monterey Bay National Marine Sanctuary, the Slough is the focus of organized governmental efforts to address environmental degradation primarily from agricultural practices: waterways draining into the National Marine Sanctuary repeatedly fail to meet water

quality standards (Caffrey 2001; Hunt *et al.* 1999). Five principal sources of N in the Elkhorn watershed and the Slough could affect salt marsh dynamics (Los Huertos 1999; Phillips *et al.* 2002; Plant *et al.* 2009):

- 1) Current discharge from agricultural tile drains (directly into the main channel of Elkhorn Slough closest to the mouth) – this is by far the greatest concentration of nutrient delivery to the Slough.
- 2) Historical legacy, from a history of agriculture in the region, beginning with commercial sugar beet production, and shifting to strawberry and vegetable row crop production.
- 3) A marine source from Monterey Bay, particularly with upwelling in the summer.
- 4) Current surface flows within the watershed, including the freshwater input of Carneros Creek at the head of the Slough.
- 5) Atmospheric deposition.

Two-thirds of nutrients in the slough are land-derived (Plant *et al.* 2009), so I focused on N inputs from agricultural tile drains.

Marsh elevation and relative sea-level rise

Major hydrological changes have also been wrought on the Slough. Because of the creation of the Moss Landing Harbor in 1947, with a straight channel mouth replacing the sinuous, natural mouth that originally wound from the estuary to the ocean, a muted tide range has increased to one resembling that of the outer coast, approximately -0.65m to +2m. The increase in tidal range and tidal prism serves as a simulation of sea-level rise. This suite of conditions provides a model of the problems and potential solutions I sought to investigate.

A gradient of vertical elevation through the marsh intertidal zone offers a window into the future of rising seas and marsh response to widely different immersion regimes. The elevation of a marsh relative to mean sea level is one of the most important contributors to plant productivity (Mendelssohn and Morris 2000; Morris et al. 2002). Stable intertidal salt marshes typically occupy an elevation on par with mean tide level (Adam 1990); in Elkhorn Slough, pickleweed (*Sarcocornia pacifica*) consistently occupies the elevations between mean high water (MHW) and mean higher high water (MHHW) (ESNERR monitoring program; US National Geodetic Survey). Studies exploring mechanisms for loss of *S. pacifica* marsh have focused on marsh elevation. Loss of *S. pacifica* marsh in Elkhorn Slough can be divided into two broad categories: a) bank edge erosion; and b) interior marsh thinning, where mud pannes develop between islands of plants. The first has been attributed to tidal scour with an increased tidal prism after the opening of Moss Landing Harbor in 1947, and the failure of several dikes in the 1980s (Philip Williams & Associates 1992; Crampton 1994). Hypotheses about interior marsh deterioration focus on the possibility of declining marsh elevation due to subsidence, earthquake events, or the interaction between vegetation loss and diminished sediment accretion (Crampton 1994; Lowe 1998; ABA Consultants 1989).

Interacting effects on salt marsh

Because nitrogen inputs and relative sea-level rise have demonstrated impacts on marsh growth and nitrogen uptake, I investigate the effects, singly and together, of N and relative sea-level rise on salt marsh provision of ecosystem services.

In this observational study, I address the following questions: a) Are salt marshes in Elkhorn Slough functioning as a coastal filter, improving coastal water quality, through the mechanism of increased nitrogen uptake into marsh plant tissues at higher levels of ambient N? b) Do plant biomass and sequestered N vary with elevation in the marsh intertidal zone, N concentrations in the main channel of the Slough, and/or an interaction between the two? c) On the scale of the estuary, are marsh plants responding in a pattern similar to that of the manipulative experiment of Chapter 2, with an unsaturated capacity for N uptake?

I hypothesized that salt marsh extent and function were positively correlated with water quality. Based on my experimental results (Chapter 2), I expected that nitrogen capture in plant tissue, as an indirect measure of water filtration, would increase with increasing N loads. I expected that plants located higher in the marsh intertidal would capture more N, as they have higher biomass relative to plants in the low marsh. I expected the effects of N and elevation on plant biomass to be additive. In order to assess the functioning of salt marsh as a coastal filter along N and elevation gradients, I investigated the responses of plant productivity, tissue quality, and N uptake.

Methods

Study site

Elkhorn Slough (36°48' N, 121°47' W), located on the central coast of Monterey Bay, California, has one of the largest tracts of coastal salt marsh habitat in California, with 1,147 ha of marsh (Caffrey *et al.* 2002) (Fig. 1). The main channel of the Slough is part of the Monterey Bay National Marine Sanctuary, the largest Sanctuary in the United States, and part of a recently established network of California Marine Life Protection Areas. Elkhorn Slough is surrounded by agricultural lands, with approximately 24% of the slough watershed (~4,170 ha) under production (Phillips *et al.* 2002), primarily in heavily fertilized strawberries and vegetable row crops. Elkhorn Slough has some of the highest levels of dissolved nutrients among United States estuaries (Caffrey *et al.* 1997, 2002; Fry 2003). The highest nutrient loads are delivered from agricultural tile drains located near the mouth of the Slough (Plant *et al.* 2009).

Study Species

Sarcocornia pacifica (Standley) – pickleweed – is a perennial, C3 plant in the family Chenopodiaceae. It is the dominant marsh cover around Elkhorn Slough, growing in a zone from mean high water to the highest high tides (generally, Mean Higher High Water (MHHW) is the upper limit) (Mahall and Park 1976b). *Sarcocornia pacifica* is distributed along the US West Coast from California to Baja California, Mexico

(MacDonald and Barbour 1974). Other marsh species included in this study are *Jaumea carnosa* (fleshy jaumea), *Frankenia salina* (alkali heath), and *Distichlis spicata* (salt grass). Cordgrass species, such as the native *Spartina foliosa* (native to the US west coast) or the invasive *Spartina alterniflora* (from the US east coast), are conspicuously absent (MacDonald and Barbour 1974).

Experimental design

I crossed the two factors of intertidal height within salt marsh (vertical height in reference to the North American Vertical Datum of 1988 (NAVD88 (m)) and main-channel N concentrations ([N]) to examine their potentially interacting effects on plant biomass and tissue nitrogen concentrations.

I chose nine sites around Elkhorn Slough, based on power analysis (see next subsection), along a gradient from higher to lower N-concentration in the main channel Slough (Fig. 1 and Table 1). The criteria for sites were that they had different N concentrations based on a two-year average of monthly samples; that they were adjacent to the main channel of the Slough and therefore exposed to the full tidal range (or the least tidally restricted possible, for the two sites of N. Azevedo Pond and Jetty Road), and that the marsh sites were directly adjacent to a water quality sampling station.

Nitrogen gradient

Elkhorn Slough NERR researchers collect monthly water samples at 18 monitoring sites, in an ongoing monitoring program with a 20-year history. Samples were run at

two different laboratories, Moss Landing Marine Labs (MLML) and Monterey County Consolidated Chemistry Lab (MCCCL) using methods described in Standard Methods 4500-NH₃ (Strickland and Parsons 1972) and US EPA protocols 350.3 and 300.0 (US EPA 1993). Regular cross-lab comparisons ensured high correlations between results. Eight out of the nine sites had dedicated water quality sampling sites adjacent to them. The ninth was created by interpolating between two established water quality stations. The site without an adjacent water-quality sampling site was Coyote Marsh, the site of a previous experiment (Ch. 2), to which I wanted to compare my observational findings. I used power analysis to determine the number of sites in the estuary necessary for 0.65 power to detect a difference in N level (JMP v.9, SAS Institute, Cary, NC, USA)

Averaging 19 months of water quality data out of the 24 months preceding my study (missing July-November 2010 from ESNERR database), two sites stood out as consistently having extremely high N concentrations – Hudsons Landing West and N. Potrero Road – and all other sites clumped more closely together with lower N concentrations (Table 1). Coastal nitrogen loads in the Monterey Bay and San Francisco Bay areas are estimated at 40-60 million metric tons yr⁻¹, high relative to other estuaries on the West Coast, and comparable to Gulf Coast and mid-Atlantic estuaries with high coastal population densities and agricultural runoff (Bricker *et al.* 2007). (For comparison, N loads from the Mississippi River delta – which contribute to the severe Gulf of Mexico “dead zone” – are 400-800 million metric tons yr⁻¹).

Nested elevation gradient within each of the nine sites

I used optical remote sensing data (1996 Light Detection and Ranging (LiDAR) data) in a Geographic Information System (GIS) to choose plot locations on a continuous gradient through low-, mid- and high-elevation marsh. Within the digital elevation model, I divided the continuous values from 1.0-2.4m (NAVD88) in the elevation gradient into thirds to ensure even distribution from the marsh-mudflat edge (low marsh) to mid-level marsh, to the marsh-terrestrial ecotone (high marsh). I transferred the plot selections to a handheld Geographic Positioning System (GPS, Trimble) in order to locate them in the field. In this way, I avoided selecting marsh heights by eye or by species composition, which could have contributed to circular logic. Therefore, I did not select plots with 100% cover of pickleweed, *S. pacifica*, having chosen them *a priori* based on elevation in a GIS. I used power analysis to determine the number of plots at each site necessary for 0.65 power to detect a difference between low- mid- and high-elevations along a continuous gradient (JMP v. 9, SAS Institute). At each site, I harvested at least 9 plots (Table 2 reports exact number) where 3 plots were replicates of low marsh, 3 of mid- and 3 of high. I assigned the range of <148cm (NAVD88) to low marsh, 148-185cm (NAVD88) to mid-elevation marsh, and >185cm (NAVD88) to high marsh, based on Elkhorn Slough survey data (Van Dyke and Wasson 2005, ESNERR monitoring program). With nine sites, I had an estuary-wide total of 96 plots.

Field and laboratory methods

Each of the 96 plots consisted of a 20x50cm area, where I harvested all aboveground vegetation to the sediment surface. I then harvested a subsample of root biomass with a 5-cm-diameter corer (mounted on a slide hammer), taking cores 15cm (+3cm/-5cm due to saturated sediments) in length. Once harvested, I sorted plants by species. I separated succulent (new) and woody (perennial) tissue for *Sarcocornia pacifica* only. I isolated roots by washing sediment cores through a stack of sieves (6-8 USA Standard Testing Sieves, from No. 10 (2mm) to No. 35(500 microns) with a closed tray on the bottom of the stack) by hand. All plant material was dried in a laboratory oven at 60°C for at least 48 hours; weighed; and a portion ground with a ball mill (Spex 8000). Samples were run on an Elementar C:N analyzer (vario MAX) when possible, due to sample size (minimum 250-300 mg material required) and on a Costech ECS 4010 if insufficient material available (2 mg required). Five samples were run on both instruments to verify instrument agreement. All plant harvests were completed in the month of March 2011, which precedes the summer's peak growing season.

Analytical methods

I used an analysis of covariance (ANCOVA) model, a type of general linear model (SYSTAT v. 12, Chicago, USA), in which the factors were intertidal height (continuous), main-channel N levels (categorical with 2 levels, "higher" and "lower"), an interaction term, and the covariate of site nested within N-level. Site (N=9) is a nested term, because only one average N-level is attributed to each site, and sites, therefore, are

replicates for one of the two categories of N-level. I investigated five response variables (N=92 plots, unless otherwise noted): 1) aboveground biomass a) with all sites and all plots included, and b) in only sites that were fully tidal, and only plots that were 100% pickleweed, for more comparable data (N=56 plots at 6 sites); 2) root biomass (N=84 due to hand-washing no more than 9-10 root cores per site); 3) root:shoot ratio of biomass (N=78); 4) tissue nitrogen concentration in new growth (succulent tissue) of aboveground *S. pacifica* (N=78); 5) nitrogen sequestered in standing stock aboveground (N=80). When neither the interaction between treatments or the nested effect of site (site nested within N-level) was significant, I tested only for the main effects of marsh elevation and main-channel nitrogen. I set the significance level for all analyses at $\alpha = 0.05$, *a priori*. When results were significant, I conducted post-hoc pairwise comparisons using Bonferroni corrections, which are appropriate for means with equal variances.

I conducted an additional analysis of mid-elevation plots only, at eight sites (N=24-30, depending on the analysis, when only mid-elevation is selected). I excluded N. Azevedo Pond from the analyses once it became clear that it was anomalous (see Discussion). I isolated mid-elevation plots because low-marsh plants may have been too stressed from inundation to take up N through growth or increased tissue-N concentration, and high-marsh plants are exposed to much less main-channel N. For example, low marsh at 1.0m (NAVD88) is inundated 53% of the time, and the high marsh at 2.0m (NAVD88) is inundated 1% of the time (ESNERR 2010) – creating a vast difference in the physical and chemical environment of marsh sediments. I expected mid-elevation marsh plants to be most responsive to nitrogen inputs. Having

selected one intertidal height, the ANCOVA factors were N-level and site nested within N-level.

To test relationships between aboveground biomass and elevation in a subset of 6 sites and pickleweed-only plots (1b, above), I used a meta-analytic method to evaluate regression slopes as an effect size metric (Bini *et al.* 2001; Becker and Wu 2007) across the 6 sites. For each site, I conducted linear regression analysis, with ordinary least squares (OLS) estimation, of the relationship between aboveground biomass (natural-log transformed biomass data) and vertical elevation in the marsh (SYSTAT v.12). I used the six slope coefficients and weighted each by the reciprocal of its variance (a product of $w_i * b_i$ where w is the weight ($1/\sigma^2$), b is the slope, and $i=1$ to 6). Finally, I conducted a one-sample t-test of the weighted slopes to test whether the overall effect size was greater than zero.

All response variables – with the exception of N concentration in succulent pickleweed tissue – required a natural-logarithm transformation to conform to the parametric assumption of a normal distribution. I normalized root biomass for the sediment core length (the product of root biomass and the reciprocal of the ratio of a given core length to the maximum length of 18 cm); normalizing assumes a uniform distribution of roots with depth, which is unlikely to be realistic, but addresses the important fact of core samples' different lengths.

Results

Aboveground biomass

Aboveground biomass in the six fully-tidal sites (N=56) increased significantly along a vertical gradient through the marsh intertidal, from the marsh-mudflat edge to the marsh-terrestrial ecotone ($t=2.01$, $p=0.05$). Aboveground biomass in all sites (N=92) did not respond significantly to either elevation ($F=0.004$, $p=0.95$) or concentrations of main-channel N ($F=0.02$, $p=0.89$) (Fig. 2). Site exerted a significant effect on aboveground biomass ($F=2.53$, $p=0.02$). (Fig. 2), where N. Azevedo Pond (abbreviated APN) had significantly lower biomass than Hudsons Landing West (HLW) (all pairwise *posthoc* comparisons given in Table 3).

Isolating mid-marsh elevation and *S. pacifica* succulent tissue alone, I would expect the most sensitive response to N level; increased Slough [N] tended to increase succulent biomass (N level $F=3.617$, $p=0.08$) and there was a significant effect of site ($F=3.16$, $p=0.04$), where N. Azevedo Main and South Marsh had lower biomass (Table 3).

Root biomass

Root biomass (N=84) decreased significantly at the highest N level (N-level $F=4.24$, $p=0.04$), but did not change significantly along a vertical gradient in the marsh intertidal (relative elevation $F=0.05$, $p=0.827$). There was no significant

interaction between the factors of elevation and N-concentration, and no significant effect of site (interaction $F = 1.83$, $p = 0.18$; site $F = 1.23$, $p = 0.30$).

At mid-elevations alone, the Slough N level no longer had a significant effect on root biomass (N-level $F = 1.16$, $p = 0.30$), but there was a significant effect of site ($F = 3.85$, $p = 0.01$) (Table 3).

Root:shoot ratios

The ratio of root to shoot biomass (root:shoot hereafter) (N=78) tended to decrease with the highest N level in the Slough ($F = 2.91$, $p = 0.09$), and did not respond significantly to marsh elevation ($F = 2.169$, $p = 0.11$). There was no significant interaction between the factors of elevation and N-concentration ($F = 1.69$, $p = 0.20$). Site had a significant effect on root:shoot ratios ($F = 2.90$, $p = 0.01$), although no sites were significantly different in a posthoc comparison.

In mid-elevation marsh, only site exerted a significant effect on root:shoot ratios (site $F = 2.65$, $p = 0.05$; N level $F = 0.02$, $p = 0.90$), and again, no sites were significantly different in a posthoc comparison.

Plant tissue N concentrations in S. pacifica succulent tissue

N concentrations (N=74) in *S. pacifica* annual, succulent tissue did not respond significantly to main-channel N ($F = 1.79$, $p = 0.19$) or to elevation in the marsh ($F = 0.04$, $p = 0.84$). There was no significant interaction between factors ($F = 0.03$, $p = 0.87$). There was a marginally significant effect of site ($F = 2.031$, $p = 0.07$).

At mid-elevations, the higher N level in the Slough led to significantly increased *S. pacifica* tissue-N concentrations (N-level $F=22.35$, $p<0.001$). Site also exerted a significant effect on tissue-N concentrations ($F=2.832$, $p=0.05$), where Jetty Road had lower tissue-N than other sites (Table 3).

Sequestered nitrogen in plant tissue

Total nitrogen sequestered in aboveground standing biomass (N=80) did not respond significantly to main-channel N concentrations ($F=0.20$, $p=0.66$) or elevation ($F=0.18$, $p=0.67$). There was no significant interaction between the factors ($F=0.68$, $p=0.41$). There was a marginal effect of site, ($F=1.99$, $p=0.07$) where N. Azevedo Pond tended to sequester less nitrogen in aboveground biomass than Hudsons Landing West (posthoc $p=0.06$). Removing N. Azevedo Pond from the analysis created a non-significant effect of site ($p=0.38$). Similarly, mid-elevation marsh plants did not respond significantly to treatments in terms of total N sequestered (N level $F=0.001$, $p=0.98$; site $F=1.158$, $p=0.37$).

Discussion

My findings indicate that N uptake into salt marsh vegetation was at a saturation point in Elkhorn Slough, toward the end of the winter rainy season, where there was no additional capture of N by plants at higher N exposure levels. Furthermore, my finding that root growth declined with higher N suggests a detrimental effect of the highest N levels on plant productivity. Root growth provides the basis for organic marsh sediments, builds marsh elevation, and therefore bolsters marsh resilience to relative sea-level rise (Cahoon *et al.* 2006). Therefore, negative impacts of nitrogen pollution on root growth could undercut marsh resilience to the simultaneous perturbation of sea-level rise. Since halophyte growth increased linearly with marsh elevation, low elevation indicates the likelihood of decreased plant productivity with sea-level rise. The results of decreased productivity with increased inundation agree with those from a previous field experiment at a single site, and contrast with previous findings where marsh vegetation demonstrated an unsaturated uptake of added N.

Nitrogen capture

Salt marsh could not capture more N at higher levels of exposure, suggesting that the pickleweed-dominated vegetation is no longer N limited at these concentrations and loads. Rather, the plants have reached their capacity to intercept

excess land-derived nitrogen. Root biomass, however, decreased significantly at the higher N level, which (in the absence of an aboveground-biomass change) suggests a negative response to additional N in this range of concentrations. Excess nutrients have been implicated in decreased marsh sustainability, where sustainability refers to the capacity of the marsh plants to recruit, grow and influence physical parameters that determine the elevation of the marsh plain (e.g., keeping pace with sea-level rise by accreting sediments (Leonard and Luther 1995; Reed 1995; Morris *et al.* 2002; Cahoon *et al.* 2006). There is disagreement in the literature about the vulnerability of salt marshes to eutrophication. This disagreement centers around belowground responses: some studies indicate that nutrient-enriched sediments, such as treated sewage sediments, have no detrimental effects on marsh plants (Day *et al.* 2004), while other studies, like mine, show relatively lower root growth – and root:shoot ratios – in marshes with nutrient addition (Turner *et al.* 2009, Turner 2010). A mechanism for detrimental effects, demonstrated in a long-term study in Louisiana, entails fertilized marshes allocating more to above- than belowground-growth, decreasing organic matter in the sediments, leading to decreased elevation of the marsh plain – subsidence – and subsequent salt marsh loss through drowning (Turner *et al.* 2009). Root:shoot ratios also decreased in response to the highest N level, although they showed a weaker response than roots alone. This finding lends further support to the hypothesis that eutrophication reduces marsh sustainability (Turner *et al.* 2009; Turner 2010). Similar results are observed in both agriculture and other

ecosystem types, where N addition frequently reduces root growth and root:shoot ratios (Chapin 1980; Lambers *et al.* 2008).

S. pacifica succulent-tissue N concentrations did increase significantly at the highest level of N in the Slough main channel, but only in mid-elevation plots, suggesting an influence of elevation in plants' ability to respond to ambient N concentrations. One possibility is that low-elevation plants are physiologically stressed and high-elevation plants have minimal exposure to tidal inundation, so that only mid-elevation plots have both enough exposure and enough ability to respond to additional N inputs. My finding that *S. pacifica* succulent-tissue N concentration across all elevations in the marsh intertidal zone did not respond significantly to N concentration in the Slough is consistent with the conclusion that pickleweed was N-saturated. Furthermore, because N capture, represented by N sequestered in a standing pool of aboveground biomass, did not respond significantly to N concentrations in the Slough, I conclude that the filtering capacity of the marsh is functioning at full capacity or is overwhelmed.

Marsh biomass generally exhibits less sensitive responses to perturbations or treatments in the winter dormant season relative to the summer growing season (Boyer *et al.* 2001; Chapter 2). However, since the highest concentrations of N are delivered in winter rains (Fig. 9), the month of March was a key time to document marsh plant responses to pulses of nutrient inputs. This year, 2011, had particularly high rainfall; March rainfall was 15 cm relative to a long-term average of 6cm, and the total 2010-2011 "rain year" was 53 cm relative to an average of 41cm (J. Haskins,

ESNERR monitoring program, 14-yr average of rainfall). To explore and quantify any potential “mismatch” in timing in Pacific Coast marshes, where maximum plant production occurs in summer and peak nutrient runoff arrives with winter rains, it was important to assess plant uptake at a peak runoff time. Quantifying marsh plant response to Slough [N] and elevation in the summer growing season could confirm the patterns found in this spring study and clarify potential growth patterns.

Effects of intertidal elevation

Marsh plants’ response to elevation in the intertidal zone was only detectable in a set of marshes that were exposed to full tidal range and in plots that were monospecific *S. pacifica*. My finding is consistent with the majority of the estuarine literature that identifies marsh platform elevation as one of the most important factors determining marsh distribution, plant species composition, vulnerability to invasion, marsh vegetation’s ability to self-regulate in terms of continued recruitment and survival, and optimal growth (Chapman 1974; Mitsch and Gosselink 2000; Weinstein and Kriger 2000; Pennings and Bertness 2001). My finding of a positive relationship between biomass and intertidal height also agrees with other observational studies in Elkhorn Slough that indicate a positive trend (Crampton 1994) or significant relationship (ABA Consultants 1989; Lowe 1998) between marsh elevation and percent cover of halophytes. In a transplant experiment (Lowe 1998), plants at the lowest elevation, 12 cm below a comparison marsh, died within two years, while those in elevated boxes grew vigorously. Some researchers have argued that there are

more complex controls on marsh spatial pattern (Zedler *et al.* 1999), an important consideration for landscape-scale studies.

Models forecasting marsh response to sea-level rise incorporate a unimodal relationship between marsh biomass and elevation in the northeastern and southeastern United States, where mid-level marsh has the highest biomass (SLAMM, Morris *et al.* 2002, Craft 2009). My finding of a positive, linear relationship between biomass and intertidal height in fully-tidal sites with monospecific (*S.pacifica*) plots suggests a different empirically-based parameterization for Elkhorn Slough.

Site effects

Site exerts a strong influence on salt marsh response in Elkhorn Slough. Among the nine sites, N. Azevedo Pond appears to be anomalous. N. Azevedo Pond is tidally restricted, separated from the main channel of Elkhorn Slough by a railroad track built on a levee. A neighboring pond, <0.25 km away and with similar hydrology, exhibits a dramatic cycling of diel oxygen levels, from supersaturated during the day to undetectably low at night, a state termed “hyperventilating” (Beck and Bruland 2000). Tidal restriction has been shown to have impacts on ecological community composition in Elkhorn Slough (Ritter *et al.* 2008) and eutrophication expression (Hughes *et al.* 2011), and appears to have an impact on marsh plant growth. In this way, local management of tidal restriction at the site scale exerts a stronger influence on ecosystem function than variation in N concentration or marsh

elevation. Because factors other than N availability and tidal height appear to account for biomass variation, an exploration of site effects might yield other important covariates influencing biomass.

Comparing manipulations of N and marsh elevation in the field with this observational study

In this study, I found that N uptake into salt marsh is at a saturation point, and furthermore, that the highest N level led to root growth declines. In contrast, in the manipulative experiment (Chapter 2), N additions stimulated increased plant growth relative to controls in every case except where the plants were drowning in extreme simulated sea-level rise. In that experiment, *Sarcocornia* continued to exhibit N limitation throughout two years of the experiment and at experimental N additions 5-10 times the amount of N applied to conventional farmlands. Added N stimulated not only increased biomass, but also increased tissue-N concentration.

Different scales of investigation often yield qualitatively different patterns. The manipulative experiment was located in one marsh over a span of two years. I applied inorganic N treatments biweekly throughout the year, with the exception of summer when N levels are lowest. In a previous study of the function of invasion resistance by Elkhorn Slough marshes subjected to trampling and nutrient additions (Martone and Wasson 2008), only two sites out of six showed increased *S. pacifica* biomass with nutrient (urea) additions; Coyote Marsh, where I completed the manipulative experiment, was one of those two sites. In contrast, the observational

study incorporated greater spatial extent, located in nine marshes, and sampling occurred in a single month (March 2011). Ambient nitrogen was delivered in pulses throughout the winter, primarily associated with rain events. The contrast in patterns suggest that short-term growth of marsh plants in the experimental site is strongly nitrogen limited but that other, as yet unidentified factors account for spatial patterning of salt marsh vegetation in Elkhorn Slough. These could include patterns of storm exposure, sediment redox, and exposure to multiple forms of pollutants such as toxic metals and pesticides. Ecological studies frequently show that short-term experimental responses different from geographic patterns. For example, fresh-water lakes generally respond to both short-term and long-term addition of nitrogen or phosphorus (Elser *et al.* 2009), but over the long-term respond only to nitrogen (Schindler *et al.* 2006, Parker *et al.* 2009), showing a difference between proximate (short-term) and ultimate (long-term) controls (Vitousek *et al.* 2010). Zedler and others (1999) proposed an improved model of spatial pattern for Californian salt marshes that incorporates not only vertical elevation, but also topography, especially the influence of tidal creeks, and conspicuous species.

Conclusions

My findings indicate that across a range of intertidal elevations, Elkhorn Slough salt marsh vegetation is not sequestering additional main-channel nitrogen into biomass in the pre-growing season and root biomass declines at the highest N level. Therefore, during this time, the marsh was at or beyond its capacity to intercept N pollution. The one exception to findings of saturation was an increase in tissue-N concentration in new-growth pickleweed at mid elevations in the marsh; new growth generally exhibits more sensitive responses than perennial tissue. The nine sites I sampled provide a fair representation of the Slough as a whole, distributed through the mouth of the estuary, mid-estuary, and the head of the estuary. Elkhorn Slough, however, is unlikely to be representative of US west coast estuaries due to major hydrological alterations in the last century, its lack of cordgrass species (*Spartina spp.*), and its particular history of land-use, especially with intensive agricultural cultivation. Since *Spartina spp.* are ecosystem engineers (Mendelssohn and Morris 2000), results from this study make an important contribution to learning about US west coast, pickleweed-dominated marshes, especially those where *Spartina spp.* are not present or are patchily distributed. In my observational findings, the impact of the highest level of N in the Slough – where N inputs globally and regionally are forecasted to continue to increase – is not buffered, since salt marsh N-capture is at the limits of its capacity. I have quantified the capacity of the salt marsh to sequester N and also shown detrimental effects of the highest level of N on root growth, which

has non-linear feedbacks to the relative elevation of the marsh plain (roots contribute to building organic marsh sediments (Cahoon *et al.* 2006)). Impacts of eutrophication included decreased root growth at higher N levels.

Climate change is expected to exacerbate existing pollution problems (Scavia *et al.* 2002). Although many climate change effects are underway and not reversible, we can reduce nutrient pollution into coastal waterways (Rabalais *et al.* 2010).

Elkhorn Slough offers a window into future changes with sea-level rise and anthropogenic N additions, with an engineered straight channel at the mouth that has increased tidal range and inundation, and some of the highest N concentrations in North American estuaries. Both perturbations diminished aboveground and root growth of halophytes, which detrimentally affected their provision of ecosystem services.

Figures and Tables

Hudsons Landing West	HLW
N. Azevedo Pond	APN
N. Azevedo Main Channel	NAM
Kirby Park	KP
Coyote Marsh	CM
South Marsh	SM
Reserve Bridge	RBR
Jetty Road	JR
N. Potrero Road	PRN

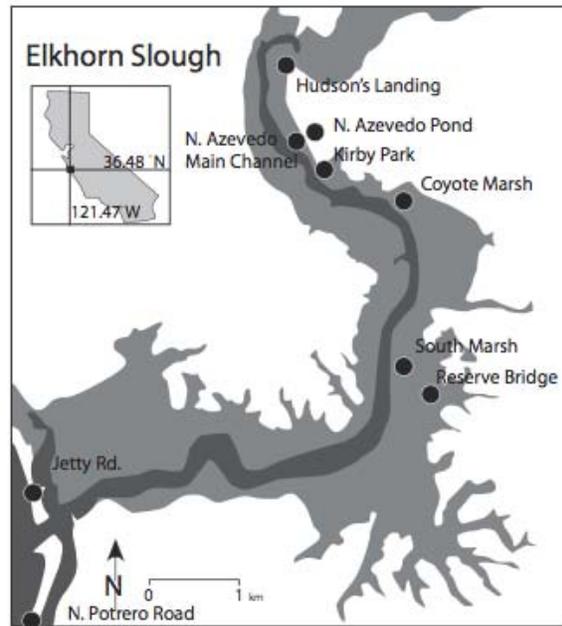


Figure 1. Location of Elkhorn Slough, Moss Landing, California, and study sites (dark grey circles). Table lists the nine study sites with abbreviations used throughout figures.

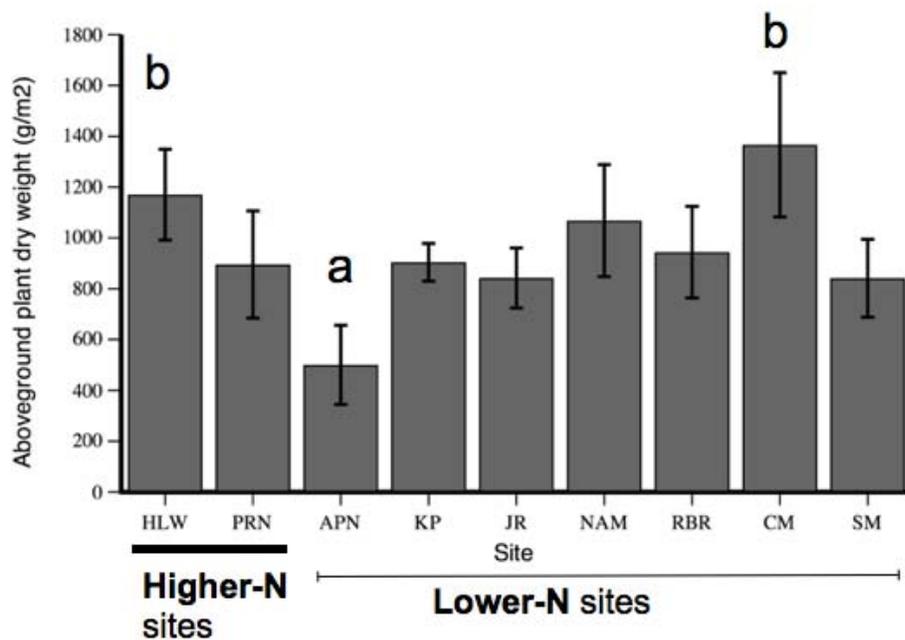


Figure 2. Aboveground biomass (g m^{-2}) averaged across all intertidal elevations for each site. Error bars indicate one standard error of the mean. Letters (a, b) which differ from each other have statistically different biomasses.

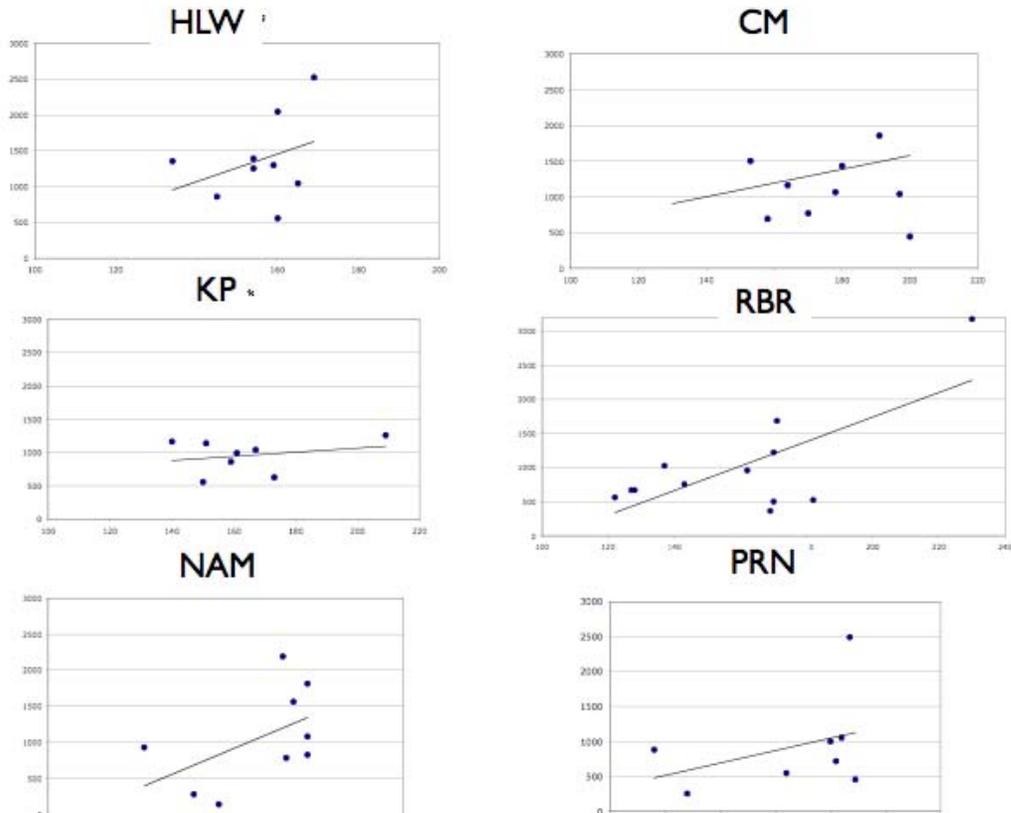


Figure 3. Aboveground biomass (g m^{-2}) as a function of vertical intertidal height (NAVD88) in six fully-tidal sites. Line in each panel represents the slope of a linear regression (ordinary least squares estimation).

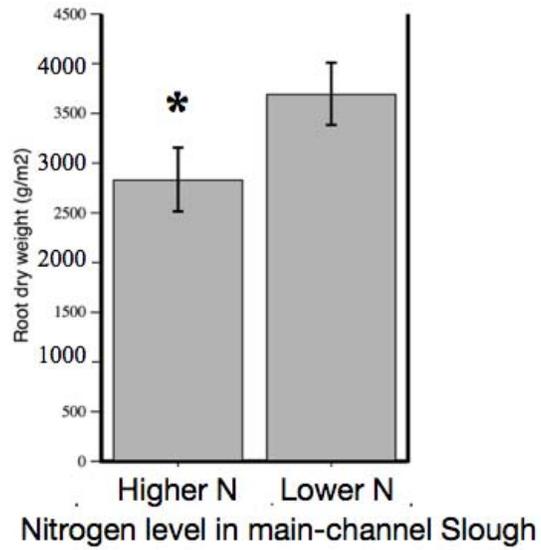


Figure 4. Root biomass (g m^{-2}) of salt marsh plants pooled by N level. Error bars indicate one standard error of the mean. Asterisk denotes a significant difference between biomass across N levels.

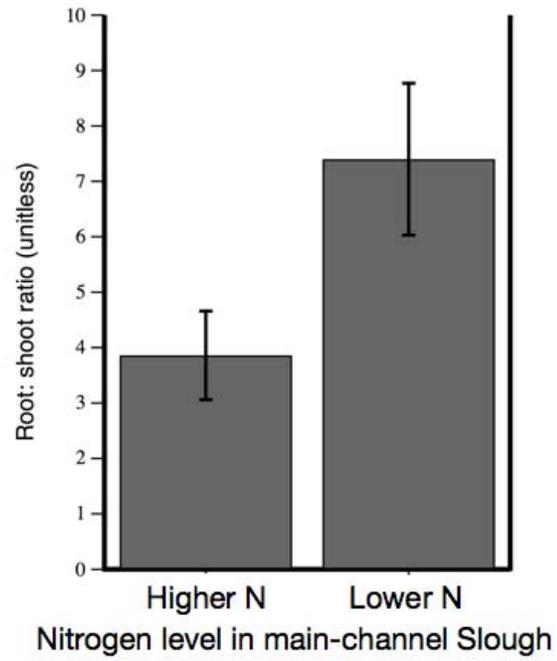


Figure 5. Root:shoot ratios (unitless) pooled by N-level. Error bars indicate one standard error of the mean.

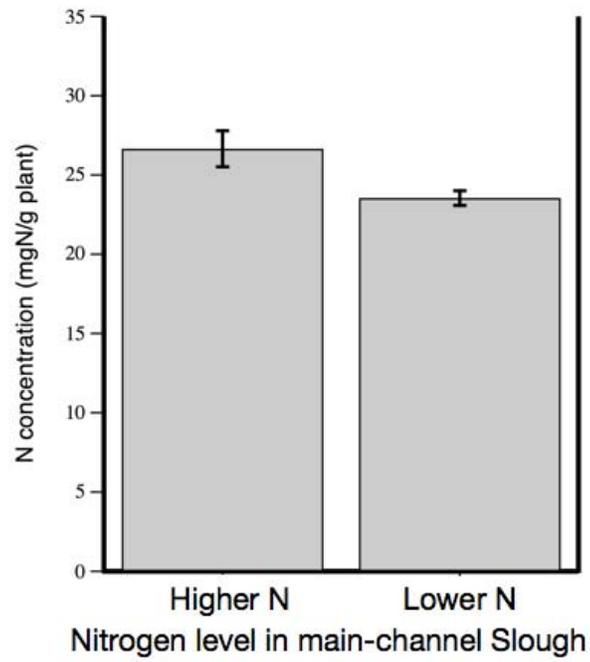


Figure 6. N concentration (gN g^{-1} plant) in *Sarcocornia pacifica* succulent tissue, pooled by N level. Error bars indicate one standard error of the mean.

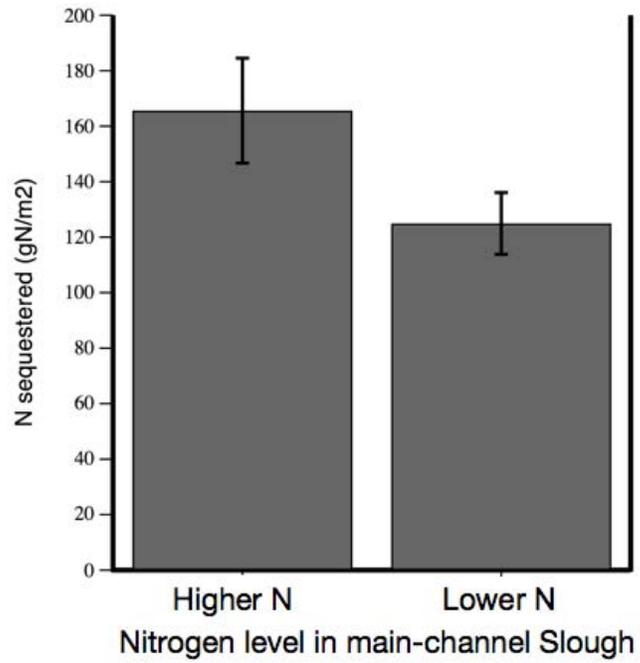


Figure 7. Total nitrogen sequestered in standing stock aboveground biomass (gN m^{-2}) pooled by N level. Error bars indicate one standard error of the mean.

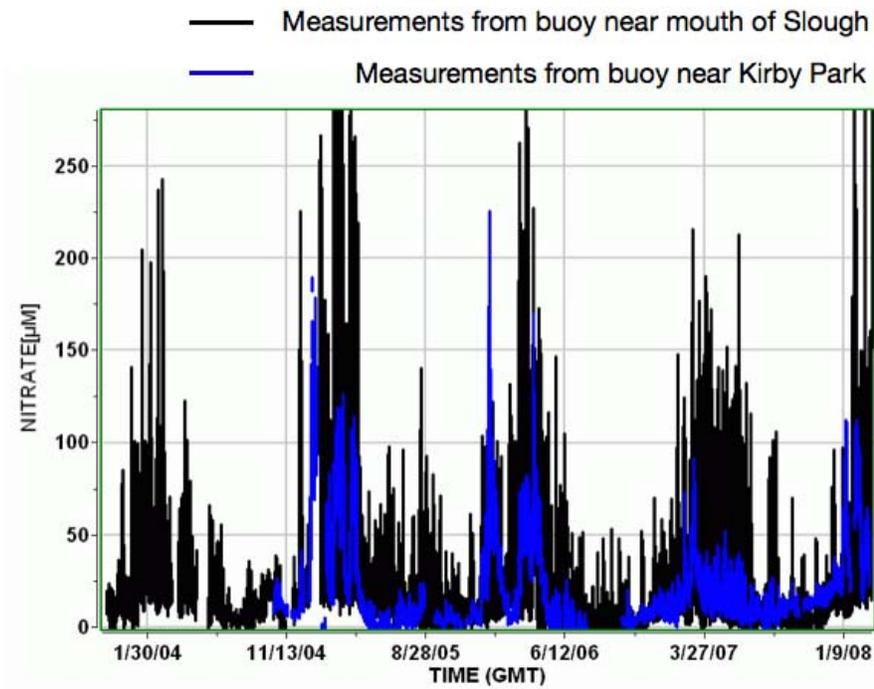


Figure 8. Nitrate concentrations (mM) in Elkhorn Slough from Land-Ocean Biogeochemical Observatory (LOBO) moorings, 2004-2008. Data and LOBOviz interface, K. Johnson, Monterey Bay Aquarium Research Institute (www.mbari.org/lobo).

Table 1. Slough total N (mg L⁻¹ as N)

Site abbreviation	Site	Slough total N
PRN	N. Potrero Road	21.69
HLW	Hudsons Landing West	1.15
APN	N. Azevedo Pond	0.25
KP	Kirby Park	0.36
JR	Jetty Road	0.41
NAM	N. Azevedo Main Channel	0.62
RBR	Reserve Bridge	0.59
CM	Coyote Marsh	0.48
SMWQ	South Marsh Water Quality	0.59

Table 2. Number of plots harvested at each of nine sites

Site abbreviation	Site	# of plots
PRN	N. Potrero Road	9
HLW	Hudsons Landing West	12
APN	N. Azevedo Pond	9
KP	Kirby Park	10
JR	Jetty Road	9
NAM	N. Azevedo Main Channel	10
RBR	Reserve Bridge	15
CM	Coyote Marsh	11
SMWQ	South Marsh Water Quality	9

Table 3. *Posthoc* pairwise comparisons ($p < 0.05$) following a significant effect of site (N level) in ANCOVA.

1) In (Aboveground biomass)		Bonferroni-corrected
Site(i) (N(i))	Site(j) (N(j))	p-value
N. Azevedo Pond (lower N)	Hudsons Landing (higher N)	0.04
2) [N] <i>S. pacifica</i> succulent tissue	8 sites (exclude APN)	Mid-elevation marsh only
Site(i) (N(i))	Site(j) (N(j))	
Site-nested (i)	Site-nested (j)	
Coyote Marsh	JR	<0.001
Coyote Marsh	HLW (higher N)	0.002
Coyote Marsh	PRN (higher N)	<0.001
Jetty Road	KP	<0.001
Jetty Road	NAM	<0.001
Jetty Road	RBR	<0.001
Jetty Road	SMWQ	<0.001
Jetty Road	HLW (higher N)	<0.001
Jetty Road	PRN (higher N)	<0.001
NAM	HLW (higher N)	0.036
SMWQ	HLW (higher N)	0.046
3) In (<i>S. pacifica</i> succulent biomass)		
Site(i) (N(i))	Site(j) (N(j))	
Coyote Marsh	JR	<0.001
Jetty Road	KP	<0.001
Jetty Road	NAM	<0.001
Jetty Road	RBR	<0.001
Jetty Road	SMWQ	<0.001
Jetty Road	HLW (higher N)	<0.001
Jetty Road	PRN (higher N)	<0.001

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