A Conceptual Model of Natural and Anthropogenic Drivers and Their Influence on the Prince William Sound, Alaska, Ecosystem

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Abstract
Prince William Sound (PWS) is a semi-enclosed fjord estuary on the coast of Alaska adjoining the northern Gulf of Alaska (GOA). PWS is highly productive and diverse, with primary productivity strongly coupled to nutrient dynamics driven by variability in the climate and oceanography of the GOA and North Pacific Ocean. The pelagic and nearshore primary productivity supports a complex and diverse trophic structure, including large populations of forage and large fish that support many species of marine birds and mammals. High intra-annual, inter-annual, and interdecadal variability in climatic and oceanographic processes as drives high variability in the biological populations. A risk-based conceptual ecosystem model (CEM) is presented describing the natural processes, anthropogenic drivers, and resultant stressors that affect PWS, including stressors caused by the Great Alaska Earthquake of 1964 and the Exxon Valdez oil spill of 1989. A trophodynamic model incorporating PWS valued ecosystem components is integrated into the CEM. By representing the relative strengths of driver/stressors/effects, the CEM graphically demonstrates the fundamental dynamics of the PWS ecosystem, the natural forces that control the ecological condition of the Sound, and the relative contribution of

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natural processes and human activities to the health of the ecosystem. The CEM illustrates the dominance of natural processes in shaping the structure and functioning of the GOA and PWS ecosystems.

Key Words: conceptual ecosystem model, Prince William Sound, ecological risks, relative risks, environmental stressors, Exxon Valdez oil spill, Great Alaska Earthquake.

INTRODUCTION

Prince William Sound (PWS) is a semi-enclosed fjord estuary on the southern coast of Alaska along the Gulf of Alaska (GOA) (Figure 1). Designated by the National Oceanic and Atmospheric Administration (NOAA) as one of the Large Marine Ecosystems (LME) of the world (Sherman 1993; see also http://www.lme.noaa.gov/), the GOA constitutes a highly productive ecosystem (Stabeno et al. 2004) that sustains immense populations of seabirds, marine mammals, and fishes (NWF 2003; Mundy and Cooney 2005). The globally significant resources of the northern GOA region are preserved in six U.S. National Parks (Aniakchak, Katmai, Lake Clark, Kenai Fjords, Wrangell-St. Elias, and Glacier Bay) (http://www.nps.gov/state/AK/), plus a unit of the Alaska Maritime National Wildlife Refuge (http://alaska.fws.gov/nwr/akmar/units/gulf.htm) and the Kachemak Bay National Estuarine Research Reserve (http://www.nerrs.noaa.gov/KachemakBay/welcome.html). PWS itself contains 14 Alaska State Parks, characterized by the AK Department of Natural Resources (http://www.dnr.state.ak.us/parks/units/pwssmp/smppws.htm) as remote “fjords, bays, coves, lakes, glaciers, mountains and hundreds of islands (that) provide a rich and unspoiled beauty,” and PWS is almost completely encompassed within the Chugach National Forest (http://www.fs.fed.us/r10/chugach). Thus, while there is a long history of human activities and anthropogenic stressors, clearly the PWS ecosystem is highly valued by society because of its unique characteristics, magnificent wildlife, commercially important resources, and relatively pristine condition.

Two extraordinary episodic events occurred in PWS in recent decades, the Great Alaska Earthquake of 1964 and the Exxon Valdez oil spill (EVOS) of 1989. Each had major impacts on the ecological condition of PWS. The earthquake was magnitude 9.2 on the Richter scale and involved large (up to 10 m) vertical displacements over an area of ~520,000 km², including all of PWS (State of Alaska 1964; Stanley 1968; USGS 2009). These displacements significantly affected many habitats along the PWS coastline, such as salmon streams, intertidal and subtidal areas, and other coastal habitats. EVOS was the largest and one of the most ecologically consequential oil spills in U.S. history, with more than 250,000 barrels of crude oil released into northeastern PWS, resulting in major impacts on virtually all species of marine birds and mammals as well as shoreline habitats (NOAA 1992; Wells et al. 1995; Spies et al. 1996). Because PWS is a highly dynamic system, the spilled oil was largely eliminated from shorelines by natural processes and clean-up activities in the initial months to few years after the spill (NOAA 1992; Neff et al. 1995), but there remain ongoing discussions over the nature and importance of any continuing effects from EVOS, now two decades later.
Figure 1. Map of Prince William Sound, Alaska, and associated areas of the Gulf of Alaska out to the continental shelf. Figure created for this article by Allison Zusi-Cobb, ABR, Inc., Environmental Research & Services, Fairbanks, AK, USA.
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In the present article, we begin with an overview of the PWS ecosystem based on the literature and the co-authors’ expertise and experience, and we explore the full suite of drivers and stressors, both natural and anthropogenic, that impinge on the PWS ecosystem, including the episodic earthquake and EVOS events. We then conceptualize the forces that shape and control the PWS ecosystem through the development of a conceptual ecological model (CEM) that represents the natural drivers, human activities, environmental stressors, and ecological components of importance in the ecosystem. This type of CEM is built around direct stress-response relationships, following the U.S. Environmental Protection Agency (USEPA) ecological risk assessment framework (USEPA 1992, 1998; Gentile et al. 1993; Suter 1999a,b). Such CEMs have been successfully used to communicate the understanding of an ecosystem to both scientists and non-scientists, to identify major uncertainties, to prioritize research activities, and to develop testable hypotheses for further analysis. In some cases conceptual models have been used as the basis for developing predictive, quantitative models for use in scenario/consequence analyses in support of ecological risk assessments (e.g., Harwell et al. 2010). Our purpose here is to present a CEM targeted at both the scientific and decision-making communities that elucidates the relative importance of the various factors that affect, control, and even dominate the PWS ecosystem; that is, after considering virtually all of the natural and anthropogenic factors that affect PWS, we aimed to distinguish those that truly drive the ecosystem’s structure and functioning from those that have lesser influence. This conceptualization also provides a context into which the initial risks and potentially any residual risks from the 1964 earthquake and EVOS may be placed.

PHYSICAL CHARACTERISTICS OF PRINCE WILLIAM SOUND

PWS is a large, complex, semi-enclosed, glacial fjord-type of estuary covering more than 9,000 km², with steep, convoluted shorelines dropping from narrow beach shelves to depths of more than 800 m (Figure 1). The central Sound is ~60 km by 90 km, with depths typically >200 m and a maximum depth of ~750 m in northern PWS. The entrances to PWS are guarded by the continental shelf, sills, or both, each ~180 m deep. Numerous islands are scattered throughout PWS, and bays, fjords, and many glaciers are interspersed along its rugged coastline. The Sound communicates with the GOA shelf through Hinchinbrook Entrance to the east and Montague Strait and several smaller passes to the west.

The principal habitats and resources of PWS and the GOA include: coastal watersheds; shorelines, including intertidal zones (ITZ) and shallow subtidal zones (STZ); pelagic systems; the Alaskan Coastal Current (ACC); and offshore areas embracing the continental shelf break and beyond to the continental slope and deep ocean basin (Weingartner et al. 2002; Stabeno et al. 2004; Mundy 2005). The complex mosaic of habitats occurs along a wide spectrum of salinity, temperature, and substrate gradients, with extensive intertidal areas and a substantial pelagic zone (see CORI 2007 for detailed coastal habitat classification and mapping of PWS). PWS shoreline habitat types include sheltered rocky shores, sand/gravel beaches, gravel/cobble/boulder beaches, exposed rocky shores, exposed wave-cut platforms, sheltered tidal flats, and marshes. The ecosystem is characterized by a diversity of
plant and animal populations covering the full spectrum of trophic levels and by significant variability that occurs spatially, seasonally, and interannually.

Climate

The PWS climate is maritime, with high precipitation, strong winds, and relatively moderate temperatures, considering the latitude (∼60°N) (Steiner 2002; Mundy and Olsson 2005). Contemporary GOA climate is defined by atmospheric and oceanic circulation on a global scale. The GOA is at the end of the Pacific storm track, where storms tend to remain as they weaken, primarily because of the coastal mountains surrounding the area (Stabeno et al. 2004; Weingartner 2007) (Figure 1). There is a pronounced seasonal cycle, with cyclonic winds from fall through spring, resulting in wind-induced upwelling of deep, nutrient-rich water in the central GOA and downwelling of surface waters along the coast (Stabeno et al. 2004; Weingartner 2007). During the rest of the year, winds are variable, with weak-to-moderate cyclonic systems between periods of high pressures, during which intermittent upwelling occurs along the coast.

Two periodic changes in ocean and atmospheric conditions are important for understanding variability in GOA climate: the Pacific Decadal Oscillation (PDO), and the El Niño Southern Oscillation (ENSO) (Wilson and Overland 1986; Mantua et al. 1997; Hollowed et al. 1998; Stabeno et al. 2004). ENSO events originate in the eastern equatorial Pacific and have a 2–5 year periodicity. The PDO signal is largest in the northern North Pacific, including the GOA, and has a decadal-scale periodicity (Mantua et al. 1997). The PDO has two phases, warm or cold, each of which has major implications for wind, temperature, precipitation, and oceanographic patterns in the northeastern Pacific Ocean. Mantua et al. (1997) presented evidence for two full PDO cycles in the past century: cool or negative PDO regimes, prevailing from 1890–1924 and again from 1947–1976; and warm or positive PDO regimes, dominating from 1925–1946 and from 1977 through the mid-1990s. Peterson and Schwing (2003) documented a rapid and striking transition in late 1998 to a cool regime, in which coastal waters of the California Current and the GOA cooled by several degrees, although a return to warm conditions occurred from 2001–2007 (see http://jisao.washington.edu/pdo/PDO.latest for PDO data from the University of Washington-NOAA Joint Institute for the Study of the Atmosphere and the Ocean).

A positive PDO regime is characterized by above-normal upper-ocean temperatures in the GOA and PWS. An intense low-pressure system centered over the Alaska Peninsula leads to warming in the GOA and PWS, with strong onshore winds and increased precipitation (Stabeno et al. 2004; Mundy and Olsson 2005). During the warm, positive PDO, coastal downwelling and offshore nutrient upwelling are enhanced. The latter should stimulate offshore primary and secondary productivity and foraging, while enhanced coastal downwelling may lead to a reduction in productivity and foraging on the shelf (Stabeno et al. 2004; Mundy and Olsson 2005). In contrast, a negative PDO regime is characterized by below-normal upper-ocean temperatures, winter high pressures, moderate onshore winds, and moderate precipitation. Coastal downwelling and offshore nutrient upwelling are reduced, possibly resulting in a reduction in offshore production but an increase in shelf production.
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(Stabeno et al. 2004; Mundy and Olsson 2005). These two climate patterns, plus climate variability from annual to multi-decadal time scales, combine with the significant influence of the coastal terrain to give the GOA and PWS a highly variable and sometimes severe climate. Moreover, multiple forcing factors with different characteristic frequencies operating simultaneously may create coupled climate-ocean regime shifts, such as the warm shift that occurred during the 1970s (Minobe 1997; Bograd et al. 2005).

Oceanography

PWS is an important part of the GOA ecosystem, acting as a potential sink and source for dissolved and suspended materials carried by shelf waters (Mundy 2005). The mountains and glaciers surrounding PWS constitute its watershed, and considerable precipitation runoff and snow melt drain into the Sound through numerous small streams. A substantial supply of relatively fresh water, derived from river discharges along the coast of SE Alaska and the Copper River to the east of PWS, also enters the system via the along-shelf transport of the ACC (Weingartner 2007). For comparison, the annual discharge of fresh water into the GOA is somewhat larger than that of the Mississippi River into the Gulf of Mexico (Royer 1982; Stabeno et al. 2004).

Circulation in PWS is complex because of the rough bathymetry, convoluted coastline, numerous islands, tidal regime (with a maximum tidal range of 6.1 m), and spatially and temporally varying winds and freshwater runoff. These features lead to small-scale surface convergences, eddies, upwelling, and downwelling varying in time and space in response to annual wind and runoff patterns. Water circulates in a generally anticlockwise central gyre, with subtidal currents advecting shelf water through Hinchinbrook Entrance in the east, around the Sound, and over rough bottom topography before exiting through Montague Strait and other southwest ocean passages (Bograd et al. 1994; Niebauer et al. 1994; Jin and Wang 2004) (see Figure 1). The mean circulation is enhanced by runoff entering along the perimeter of PWS. Occasionally, summer circulation reverses to clockwise, with surface waters entering through Montague Strait and exiting via Hinchinbrook Entrance (Vaughn et al. 2001).

The primary source of GOA shelf-PWS exchange is the ACC, with much of the current flowing through the central Sound. PWS also communicates directly with deep continental slope waters through the entrance to Hinchinbrook Canyon, predominantly in the summer (Niebauer et al. 1994). Because deep waters are relatively rich in nutrients, they can be important to the PWS nutrient budget as well as provide an advective pathway for oceanic plankton. Niebauer et al. (1994) suggested that up to 40% of the Sound’s volume is exchanged in the summer and 200% in winter. Although these estimates are imprecise, they imply that the shelf-Sound exchange is efficient and that PWS is intimately coupled to shelf processes. The turnover rate for the entire volume of water in PWS is several times per year.

Salinity plays a special role in the PWS ecosystem. Based on their model sensitivity analyses, Jin and Wang (2004) showed that salinity is the most important factor determining central Sound circulation patterns. Because water density in PWS is primarily controlled by variations in salinity rather than temperature, salinity controls
vertical density stratification, which influences the extent to which vertical mixing occurs, thereby controlling both the nutrient supply and the amount of time that phytoplankton remain in the euphotic zone. Horizontal salinity gradients affect current patterns and can establish fronts that are often important foraging areas for a variety of marine organisms. Thus, changes in freshwater discharge or oceanic salt supply affect the water density distribution in the Sound, with potential effects on the ecosystem across trophic levels. Frequent and intense winter storms can mix the upper layers to depths of 200 m. As the water column stabilizes in spring, the mixed layer becomes shallower and contiguous with the sunlit photic layer, usually ≤50 m. The reduced depth of the nutrient-rich mixed layer, along with increasing solar energy input, gives rise to major spring (generally April) plankton blooms that form the fundamental primary and secondary productivity base of the pelagic marine food web (Eslinger et al. 2001).

Biophysical Coupling

The Sound Ecosystem Assessment (SEA) oceanographic study of PWS and northern GOA (Cooney 1999; Kline 1999; Eslinger et al. 2001; Vaughan et al. 2001) showed that physical processes, including surface stratification, upper-layer circulation, and GOA–PWS exchange, are capable of regulating the spatial distribution and abundance of the biological components in PWS, including Pacific herring. Eslinger et al. (2001) showed that phytoplankton and zooplankton variability in PWS is primarily determined by winds and associated convective currents and air temperatures during a relatively short period each spring. They noted the importance of GOA-derived nutrients and/or carbon to juvenile fish in PWS, and that interannual differences in fish populations reflect variability in transport processes delivering nutrients or plankton into nearshore waters. During some years, the import of macronutrients into PWS from the GOA supports phytoplankton blooms in the normally nitrogen-limited Sound, which in turn supports the zooplankton and forage fish communities. However, in other years, the carbon in the stocks of PWS zooplankton and fishes is derived primarily from sources outside PWS (Eslinger et al. 2001). Using stable isotope ratios (¹³C/¹²C), Kline (1999) showed that half of the carbon in PWS zooplankton and fish was autochthonous in 1994, whereas in 1995, most of the carbon came from the GOA during the spring bloom via the Alaskan Coastal Current or deep-water influxes. Modeling by Eslinger et al. (2001) indicated that bottom-up (nutrient-limited) processes controlled interannual zooplankton variability after 1992, but failed to do so during the 1980s, when allochthonous carbon likely dominated.

In either case, the critical timing, duration, and intensity of upwelling, nutrient and freshwater inputs, vertical mixing, and other physical processes result in high interannual variability in secondary production. For example, numbers of wild pink salmon returning to PWS to spawn ranged from ~2 million in 1988 to >23 million in 1984, i.e., an order-of-magnitude interannual variability (EVOSTC 2002). Cooney et al. (2001a) and Willette et al. (2001) hypothesized that the high interannual variability in pink salmon is largely driven by trophodynamic interactions involving plankton populations, which are controlled by upwelling and other hydrodynamic processes. This is consistent with the findings of Morita and Fukuwaka (2006).
that climate variability largely drives pink salmon population dynamics. Further, Ware and Thompson (2005) demonstrated a tightly coupled phytoplankton-fish productivity relationship for the coastal Northern Pacific, including the GOA and PWS. This trophic coupling is maintained by an onshore nutrient supply driven by current-induced upwelling, coastal eddies, winter winds, and upper-ocean stability associated with the large freshwater discharges along the coast.

In general, the fluctuations of primary productivity in PWS are strongly influenced by outside factors. Since the open GOA is iron-limited, resulting in high-nitrogen, low-chlorophyll conditions, the events that lead to upwelling along the shelf, and consequently supply more relatively iron-rich water to the surface layer and enhance primary productivity, are important for the PWS ecosystem (Cooney 2005). The Sound is probably not iron-limited, so contributions from the GOA might be expected to enhance or dilute PWS productivity. McRoy et al. (1999), in an assessment of phytoplankton productivity in PWS for the period 1972 to 1997, found a linear correlation between bloom primary productivity in March and the North Pacific Index ($r^2 = 0.82$). This suggests a strong relationship or forcing on spring productivity in GOA and PWS by the NE Pacific Ocean. Cooney et al. (2001b) also demonstrated a 5-fold interannual variability in an 18-yr time series of springtime settled zooplankton volumes for eastern PWS. From 1981 to 1993 (but not thereafter), settled zooplankton volumes in PWS were strongly and positively correlated with the strength of the Bakun upwelling index (Cooney 1995).

The biophysical coupling of large-scale atmospheric and oceanic circulation in both the GOA and PWS is also seen through climate variability. Finney et al. (2002) used sediment cores to link climatic variability to fish productivity, extending their historical catch record analyses to reconstruct salmon abundance for 2200 years. They concluded that climate has a strong role in the forcing of NE Pacific fish populations. In an overview of the physical variability and ecosystem responses in the NE Pacific, McGowan et al. (1998) indicated that large-scale oceanic biological responses to low-frequency climate variability include the geographical ranges and spatial patterns of species, anomalies in secondary productivity, and changes in community structure. Although few measurements are available for interannual- and decadal-scale variability in primary and secondary productivity in this region, Northeast Pacific oceanic zooplankton samples collected in nets from 1956–1980 showed a 5-fold variation (Frost 1993).

A compelling example of biophysical coupling in the GOA and PWS is the analysis of the large-scale properties of the pelagic production cycle during both positive and negative phases of the PDO (Mantua et al. 1997). Those authors and Mantua (1998) showed that the dominant pattern of Pacific coast salmon production is driven by the low-frequency climate variability associated with the PDO, rather than the higher-frequency ENSO events. Brodeur and Ware (1995) showed that during the 1980s, net-captured zooplankton biomass in the GOA doubled under conditions of increased winter winds resulting from an intensified Aleutian Low (positive PDO). This sustained doubling of biomass was reflected at higher trophic levels in the offshore food web. It is hypothesized that this increase in production during the 1980s resulted from increased nutrient levels associated with greater upwelling in the Alaska Gyre. While these zooplankton samples were collected in the GOA outside PWS, they can be important sources for subsequent food web transfers within the
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PWS ecosystem, as the entrance to PWS is deep and shelf waters can readily enter the Sound from the GOA carrying entrained shelf zooplankton, particularly during the periods of greater allochthonous carbon. In addition, the density patterns of zooplankton stocks showed a marked areal expansion during periods of positive PDO and contraction during negative PDO cycles (Mundy 2005). Peterson and Schwing (2003) suggested that the 1998 climate-regime shift may have led to more cold-water zooplankton species at much lower abundance and a decline of salmon, cod, and other higher-trophic fish populations, along with other transformations of the ecosystem. Hollowed et al. (1998) discussed how the coupling of the PDO and ENSO events may interact and result in dramatic shifts in the abundance trends of marine fish stocks in the North Pacific, experienced in the late 1970s, in which the frequency of ENSO events increased coincidentally with a major shift to a positive PDO phase. Anderson and Piatt (1999) demonstrated that a significant community-level trophic reorganization occurred following that climate-regime shift. It is clear from these examples, among other studies, that the coupled climatic-oceanographic processes are a major driver in shaping the structure and controlling the spatial and temporal dynamics of the PWS ecosystem.

ECOLOGICAL CHARACTERISTICS OF PRINCE WILLIAM SOUND

We briefly describe the ecological characteristics of the PWS ecosystem, captured in the trophodynamic model that is presented here (Figure 2) and integrated into the CEM (discussed later), drawing on Steiner (2002), Mundy (2005), Spies (2007), and our own understanding of the ecosystem; more complete descriptions of the components and relationships in the PWS trophodynamic structure can be found in Steiner (2002), Cooney (2005), Peterson (2005), Springer (2005), Mundy and Hollowed (2005), and Lowry and Bodkin (2005), and a more detailed discussion of trophic levels of the PWS ecosystem is presented in Okey and Pauly (1999).

Primary and Secondary Producers

The PWS trophodynamic structure consists of two coupled components: the nearshore, benthic-based food web, and the open-water, pelagic-based food web (Figure 2). In the nearshore system (<20 m isopleth), the primary producers are dominated in the ITZ by Fucus gardneri, constituting more than 90% of the macroalgal biomass, and in the STZ by several species of kelp and by eelgrass (Zostera marina). It is estimated that these macrophytes constitute more than 800 tons km$^{-2}$ of total biomass (Steiner 2002). There is also a substantial input of organic material into the trophic web in the form of detritus, with an estimated $1 \times 10^6$ tons of organic carbon in PWS at any one time, 90% of which is in the sediments (Steiner 2002). Much of this organic material comes from pelagic community biodegradation or input from terrestrial sources, such as salmon carcasses and biogenic hydrocarbons. Salmon carcasses also play a major role in the nutrient dynamics of streams and lakes in the PWS watershed, coupling local productivity to the oceanographic dynamics of the GOA (Fujiwara and Highsmith 1997; Finney et al. 2000).

The infaunal and epifaunal micro- and macro-benthos are the secondary producers in the ITZ and STZ, feeding on nearshore benthic micro-and macro-phytes,
detritus, and pelagic primary producers. Because the shallow-water epibenthos is ~75% filter feeders (Steiner 2002), consuming phytoplankton and detritus particulates, it is a key coupling between the benthic and pelagic systems. The small epifaunal invertebrates include mussels, snails, chitons, amphipods, and crabs. Small benthic infauna are dominated by several species of clams, including at shallower depths into the sediments (≤10 cm) the littleneck clam (*Protothaeca staminea*) and cockles (*Clinocardium* sp.), and somewhat deeper into the sediments (≤35 cm) the butter clam (*Saxidomus giganteus*) and soft-shell clams (*Mya* spp); these are all filter feeders. Another small clam, *Macoma* sp., is a deposit-feeder, consuming demersal organic detritus. Small infauna biomass is estimated at 70–80 tons km$^{-2}$, whereas epibenthic biomass is estimated at 700 tons km$^{-2}$ (Steiner 2002). Macrobenthos are primarily epifaunal crustaceans and molluscs, feeding on the smaller benthic epi- and infauna. In deeper waters clam biomass is supplanted by crustaceans (*e.g.*, shrimp, larger crabs), primarily feeding on terrestrial and marine detritus or preying on other invertebrates. Several species of marine birds and mammals (*e.g.*, seaducks and sea otters) feed on ITZ and STZ benthic fauna or inshore detritus.

The pelagic system is based on phytoplankton productivity, dominated by diatoms in the spring and dinoflagellates in late summer and winter (Ward 1997). These are consumed by herbivorous zooplankton, including copepods, pteropods, and cladocerans, or by omnivorous zooplankton, including meroplankton (particularly

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**Figure 2.** The trophodynamic model of Prince William Sound, Alaska, showing the coupled benthic and pelagic systems. Circles indicate members of a group feed on other members of the same group. The major species constituting each labeled group are identified in the text and in Table 3.
larval fishes and larval decapods), euphausiids, and amphipods. The omnivorous zooplankton also feed on the smaller zooplankton, as do carnivorous jellyfish and ctenophores. The phytoplankton biomass is highly seasonal and is driven by the availability of nutrients and sunlight, making this critical component highly controlled by climatic and oceanographic processes as discussed previously. Zooplankton biomass is also highly variable spatially and seasonally, ranging from 5 tons km\(^{-2}\) in winter to >170 tons km\(^{-2}\) after the spring bloom and through the summer (Steiner 2002); the biomass is dominated by calanoid copepods. Benthic and pelagic secondary producers, as the circles indicate for these and other trophic components in Figure 2, also feed on other members of their own group.

Forage and Large Fish Species

Pelagic productivity continues through the marine food web via consumption by forage fish such as salmon fry, consisting in order of importance of pink salmon (Oncorhynchus gorbuscha), chum salmon (O. keta), sockeye salmon (O. nerka), coho or silver salmon (O. kisutch), and king or Chinook salmon (O. tshawytscha), as well as Pacific herring (Clupea pallasii), sand lance (Ammodytes sp.), capelin (Mallotus villosus), and other species.

Forage fish are a critical component of the ecosystem, providing the pathway for the variability in primary production to cascade through the PWS ecosystem. Pacific herring is a particularly important species in PWS ecologically and economically (Brown and Carls 1998). It has an especially high fat content, large abundance, and visibility and proximity to the surface, where it aggregates in very large schools to feed on dense patches of zooplankton and to spawn in nearshore subtidal and intertidal habitats. Thus, Pacific herring functions as a critical species in transferring pelagic primary productivity to upper trophic-level species, such as marine mammals (e.g., humpback whales, harbor seals), many seabirds (e.g., kittiwakes, murres), other fishes (e.g., haddock), and other species of concern (e.g., bald eagle) (Brown and Carls 1998).

The large-fish component consists of the adult salmon species listed previously, plus Alaska or Pacific cod (Gadus macrocephalus), pollock (Theragra chalcogramma), rockfishes (Sebastes sp.), halibut (Hippoglossus stenolepis), arrowtooth flounder (Atheresthes stomias), sablefish (Anoplopoma fimbria), various sharks (e.g., the salmon shark [Lamna ditropis], Pacific sleeper shark [Somniosus pacificus], and spiny dogfish shark [Squalus acanthias]), and other fish species. The large fish feed on forage fish, epibenthic invertebrates, and members of their own group. Nearshore bottom fish include sculpins (family Cottidae), greenling (Hexagrammos decagrammus), lingcod (Ophiodon elongatus), crescent gunnels (Pholis laeta), Alaska cod, and rockfish; these live primarily in kelp or eelgrass beds, feeding on small crabs and other epibenthos. Non-pelagic rockfish also inhabit deep rocky bays. Deeper habitats (400–800-m isopleth) are dominated by several species of sharks and sablefish, which prey on salmon and arrowtooth flounder, as well as forage fish. The arrowtooth flounder, considered the most abundant fish species in the GOA (Mundy and Hollowed 2005), feeds primarily on pollock. The salmon species are especially important in coupling the pelagic and nearshore systems, providing a major part of the detritus food base.
of the Sound and driving the nutrient dynamics of PWS watershed lakes (Finney et al. 2000).

Marine Birds

The forage fish, large fish, and other secondary producers support the many species of marine birds that occur in PWS and the GOA with a wide diversity of feeding habits in both the pelagic- and benthic-based systems. For instance, the harlequin duck (Histrionicus histrionicus) forages in intertidal and shallow subtidal habitats to a depth of 10–20 m; their diet consists of a large diversity of epibenthic invertebrates including crabs, amphipods, snails (Littorina and Lacuna), limpets (Lottia), and lesser amounts of two-dozen other taxa (Robertson and Goudie 1999; Patten et al. 2000). There are three species of cormorants in PWS: the double-crested cormorant (Phalacrocorax auritus) feeds on fish in shallow open waters over sandy bottoms, among rocks, or in seagrass or kelp beds (Hatch and Weseloh 1999); the pelagic cormorant (P. pelagicus) feeds in swirling riptides on non-schooling fish and benthic invertebrates (Hobson 1997); and the red-faced cormorant (P. urile) feeds by underwater pursuit of solitary fish and invertebrates near the bottom (Causey 2002). The common murre (Uria aalge) is one of the most numerous marine birds (Piatt et al. 1990), diving to 100 m to feed on fish and pelagic invertebrates such as euphausiids (krill) and cephalopods (Ainley et al. 2002). Black-legged kittiwakes (Rissa tridactyla) and many other species of tern- and gull-like birds are also quite common in PWS, including the glaucous-winged gull (Larus glaucescens) (Hatch 2002), mew gull (Larus canus) (Moskoff and Bevier 2002), Arctic tern (Sterna paradisaea) (Hayward and Verbeck 2008), and others. Black-legged kittiwakes feed in flocks, are surface feeders, and have a primarily piscivorous diet, particularly Pacific herring, Pacific sand lance, and capelin, supplemented by various invertebrate species (Hatch et al. 2009). Similarly, the marbled murrelet also feeds extensively on small schooling fish, including the Pacific sand lance, Pacific herring, and capelin, among other species, diving to pursue prey by flying underwater (Nelson 1997). Both kittiwakes and marbled murrelets also feed extensively on schooling out-migrations of pink salmon (Scheel and Hough 1997). The glaucous-winged gull is an omnivorous surface feeder, taking a wide variety of fish and invertebrate species, including an estimated one-fourth of the Pacific herring spawn in PWS in spring (Hayward and Verbeck 2008). Pigeon guillemots (Cephus columba) swim underwater to feed on fish or dive up to 40 m to feed on demersal or epibenthic prey (Ewins 1993). The black oystercatcher (Haematopus bachmani) is completely dependent on marine shorelines for feeding and nesting, foraging in the ITZ on invertebrates (Andres and Falxa 1995). The bald eagle (Haliaeetus leucocephalus) opportunistically forages on a diversity of prey, generally preferring fish, and often scavenges (i.e., feeds on the detritus category in the trophic model) (Buehler 2000). Additionally, the eelgrass communities, marshes, and freshwater ponds at the upper ends of various bays and fjords within the Sound and its watershed provide important habitat and feeding grounds in spring and fall for waterfowl and other migratory birds, including the Dusky Canada goose (Branta canadensis occidentalis), and, at its northernmost limit, the great blue heron (Ardea herodias) (Mickelson 1989; Butler 1992; McRoy and Bridges 1999; Mowbray et al. 2002).
These examples, among the many dozens of avian species that nest and/or feed in PWS and the GOA, illustrate the great diversity of feeding habits and the broad role of marine birds in feeding on virtually every component of the PWS pelagic and nearshore trophodynamic model. Because many marine birds in PWS and the GOA substantially depend on forage fish and other secondary producers as their food resource, which in turn are highly affected by the climate/physical oceanography of the region, many PWS and GOA bird populations are also driven by these physical processes, similar to other Pacific Northwest bird species (Parrish and Zador 2003).

Marine Mammals

Important marine mammals in PWS include the sea otter (*Enhydra lutris*), harbor seal (*Phoca vitulina*), Steller sea lion (*Eumetopias jubatus*), killer whale (*Orcinus orca*), Dall (*Phocoenoides dalli*) and harbor porpoises (*Phocoena phocoena*), and humpback (*Megaptera novaeangliae*) and sei whales (*Balaenoptera borealis*). Collectively, they feed on pelagic and benthic invertebrates such as euphausiids, decapods, and bivalves; forage fish, such as Pacific herring, capelin, and cod; large fish, such as salmon, pollock, and flounder; and other members of their own group, such as sea lions and harbor seals.

A total of 150 species of prey has been identified for sea otters (Riedman and Estes 1990), indicating an exceptional degree of dietary flexibility. In PWS, sea otters mostly feed on clams, mussels, sea urchins, snails, and crabs (Garshelis 1983; Bodkin and Ballachey 1997; Dean *et al.* 2002; Harwell *et al.* 2010). Their habitat is limited to a relatively narrow zone along the shorelines in PWS that is sufficiently shallow to reach the benthic communities, primarily within the 40-m isobath (Garshelis 1983; Bodkin and Ballachey 1997). Rather than rely on fat tissues for thermal protection, sea otters rely on a dense fur that traps layers of air, making them prime targets of extensive human exploitation from the 18th into the 20th centuries. In fact, sea otters were hunted almost to extinction by 1911, when protection through the International Fur Seal Treaty was implemented (Doroff *et al.* 2003). The population recovered from a few hundred at that time to more than 100,000 worldwide at present, about two-thirds of the pre-hunting population (Bodkin and Ballachey 1997). This recovery included a large and rapid areal expansion from the remnant Alaskan populations, such as those observed at Montague Island in 1936, into western PWS during the 1960s (Johnson and Garshelis 1995). The 1999 population in the Sound was estimated at more than 13,200 (NOAA 2002; Bodkin *et al.* 2003).

Broad-scale declines in sea otter populations have been reported in coastal Alaska during the 1990s, including a 70% decline in the Aleutians (Burn and Doroff 2005). The US Fish and Wildlife Service (USFWS 2005) estimated that the total southwest Alaska population was about 100,000 in 1976, but reduced to about 40,000 in 2004. As a consequence, the USFWS listed the northern sea otter as a threatened species in southwest Alaska from Attu Island to western Cook Inlet effective September 8, 2005 (USFWS 2005). To date the PWS population has not suffered this decline. Estes *et al.* (1998) concluded that the population declines in SW Alaska resulted from increased mortality caused by increased predation by transient killer whales. Those authors suggested that the increased predation was likely caused by changing prey...
availability because of population collapses of Steller sea lions and harbor seals across the North Pacific, in turn caused by reduced fish stocks (i.e., both a top-down and bottom-up cascading effect). Alternatively, the over-harvesting of great whales in the North Pacific in the 1950s and 1960s that depleted this important component of the transient killer whale diet, a phenomenon termed sequential megafaunal collapse, has also been hypothesized to explain the increased predation on sea otters (Springer 2003; Estes et al. 2009a,b). Although Wade et al. (2009) dispute this hypothesis, they did not contest the role of increased killer whale predation on the sea otter decline.

Other stressors also affect sea otters: for instance, human subsistence harvesting continues, especially in the Kodiak Archipelago, where currently 0.4–1.3% of the sea otter population is harvested per year. Nevertheless, the USFWS (2005) determined that subsistence harvesting is not responsible for the population decline. Biological stressors also exist: as one example, the phocine distemper virus has been found in sea otters in southcentral Alaska since 2000 (Goldstein et al. 2009) and recently in Kachemak Bay and Resurrection Bay, both of which are close to PWS. Thus, there is the potential for the virus to spread into PWS; however, since this virus was not detected in monitoring done prior to 2000, it is not a plausible explanation of the SW Alaska population decline, which primarily occurred in the 1980s and 1990s (Burn and Doroff 2005; USFWS 2005). Consequently, enhanced killer whale predation on sea otters as a result of a cascading effect mediated via the trophic structure seems to be the most likely explanation for the major decline in the sea otter population in coastal Alaska west of PWS (Estes et al. 1998, 2009a; USFWS 2005).

The harbor seal is one of the most common marine mammals in PWS, feeding in shallow, nearshore waters and diving for food at depths up to 100 m (Frost et al. 2001). Its primary food sources are pollock, octopus (Enteroctopus dofleini), capelin, Pacific cod, and herring; the species is predated on by killer whales, Steller sea lions, sharks, and humans (Frost 1997). The year-round population in the PWS and the GOA area was estimated at 125,000 in 1973, but more recent estimates showed significant declines in the population to about 21,000–34,000 by the 1990s (Frost 1997). Frost et al. (2001) reported a 60% decline in the harbor seal population since 1984, citing a possible cause of the decline as changes in the trophic structure and availability of food.

The Steller sea lion is another forage-fish feeder whose population has declined precipitously over the past few decades, losing more than 80% of its population in the GOA during the past 25 years. NRC (2003) offered two hypotheses for this decline in the Steller sea lion population, with similar implications for other marine mammals and birds that are predators on forage and large fish in the trophodynamic model: (a) reduced food supply from overfishing and a climate-regime shift in the 1970s, and pollutants (e.g., chronic exposures to PCBs and DDT-derivatives) reducing fecundity; or (b) increased predation from transient killer whales; incidental take by fishing activities; subsistence harvesting; poaching; and mortality from pollution or disease (NRC 2003; Hobson et al. 2004; Miller et al. 2005). A review by Trites et al. (2007) concluded that the climate-regime shift induces changes in the relative abundance of primary and secondary productivity that affect sea lion health and ultimately impacts population growth through altered birth and death rates. In addition to climate-regime shifts, resource availability, and predator optimization,
Trites et al. (2007) did not exclude other hypotheses, such as overfishing or killer whale predation, as contributory to population declines.

Humpback whales in Alaska feed principally on Pacific herring, other small schooling fish, and swarms of euphausiids (krill). More than 500 humpbacks may be present in SE Alaska during summer, including >100 in PWS (Zimmerman 1994). Humpbacks may be seen in PWS during any month, but most migrate to temperate or tropical areas during fall and winter for reproduction and birthing. Migrating humpbacks return to Alaska for the abundant forage fish and krill in the spring (Zimmerman 1994). They are preyed upon by transient killer whales and historically by humans until protected by the International Whaling Commission in 1966.

The top predator in the PWS ecosystem, the killer whale, is a highly charismatic, societally important species, the largest of the dolphin family, Delphinidae. There are two types of killer whales, resident and transient, each maintaining genetically and socially distinct populations (Matkin et al. 1999; Scheel et al. 2001). Resident killer whales are primarily fish-eating (in PWS primarily salmon and Pacific herring), occurring in much greater numbers than transients. Transient killer whales are primarily mammal-eating, feeding on Steller sea lions, harbor seals, sea otters, river otters (Lontra canadensis), and small cetaceans (porpoises and young whales, such as humpbacks during migration); they have also been documented feeding on marine birds (e.g., cormorants, seaducks) and cephalopods (Vos et al. 2006). The GOA population of resident killer whales is estimated at ~800, increasing by 2% per year, though the transient population may be in decline (Matkin and Saulitis 1997). During summer in PWS and Kenai Fjords, ~130 residents currently live in six pods (Matkin 2004), up from ~110 in 1989. However, one resident pod (named AB) has not yet recovered from the reduction of numbers that occurred soon after EVOS (discussed below), and the local transient pod (named AT1) has failed to recruit since five years before the oil spill, continuing to decline in numbers (Matkin et al. 2008).

EPISODIC EVENTS

In addition to the physical and ecological characteristics of the PWS–GOA ecosystem discussed earlier, two extraordinary episodic events occurred in recent decades: the Great Alaska Earthquake of 1964 and the Exxon Valdez oil spill in 1989, each of which at least for a period of time caused major changes to the structure and/or functioning of the ecosystem. These are briefly described and subsequently incorporated into the CEM.

The Great Alaska Earthquake of 1964

On March 27, 1964, the second strongest earthquake ever recorded struck the northwest corner of PWS (Figure 1), with an estimated magnitude of 9.2 on the Richter scale (AEIC 2002; USGS 2009), causing extensive destruction or relocation of coastal habitats for seabirds, shellfish, and salmon (Hanna 1971). An estimated 520,000 km² was involved in vertical displacement (USGS 2009), more extensive than any other known earthquake, with the dividing line between the subsidence and uplift areas occurring along the western shoreline of PWS down to Kodiak Island (State of Alaska 1964; Stanley 1968; NRC 1971; USGS 2009). The uplift covered wide...
areas of PWS, with an average shoreline uplift of 2 m and local shoreline uplift of up to 10 m at Montague Island; the uplift of the sea bottom off Montague Island exceeded 15 m (Hansen 1967; NRC 1971). A tectonic tsunami swept over PWS and the GOA, across the Pacific to coastal British Columbia, the U.S. Pacific Northwest, and Hawaii, and a wave height of more than 1 m was reported at the Palmer Peninsula of Antarctica (Hansen 1967; NRC 1971; TRG 2009). Major submarine landslides and marine slumps caused by spontaneous liquefaction of granular deltaic materials created additional tsunamis at many locations along the Alaskan coastline that caused extensive shoreline damage throughout PWS (Hansen 1967; TRG 2009). The maximum wave height of all the tsunamis (67 m) was recorded at Shoup Bay on Valdez Inlet (USGS 2009). Additionally, PWS moved laterally 3 m relative to adjacent areas (Hansen 1967), with Latouche Island moving 18 m (AEIC 2002).

The primary ecological effects of the earthquake were caused by the vertical displacements, the tsunamis, and associated alterations to PWS coastal habitats (NRC 1971). These caused extensive damage to PWS biota, including coastal forests, migratory-bird nesting grounds, salmon-spawning waters and gravels, and shellfish habitats, and caused long-term changes in littoral and stream morphology (NRC 1971).

Uplifted intertidal zones were suddenly raised well above any tidal influence, and exposed marine and intertidal communities were immediately obliterated; virtually all such beaches in PWS were stranded out of reach of the sea (Stanley 1968). In areas of subsidence, which included coastal western PWS, terrestrial communities suddenly became intertidal or even subtidal zones. Stream length in uplifted areas increased, and in subsidence areas, streams were shortened and stream mouths drowned, especially in low-gradient areas (Stanley 1968). On shorelines composed of sand and silt in areas of higher uplift, rapid gullying occurred at stream mouths, and on shingle and gravel beaches, some streams disappeared into the gravel (Stanley 1968). Estuarine habitats used as nesting areas suddenly became uplands or were completely submerged, in either case losing their functionality for the bird communities.

The effects of the tsunamis on stream mouths in the uplifted areas varied widely; in many cases, sand and silt were scoured from river and stream mouths and carried into upper reaches of the streams. Over time, those became sources for considerable silting on the stream channels and mouths, on occasion leading to damming of the stream (Stanley 1968). Substantial relocation of submarine sand bars was driven by seismic waves, changes comparable to many centuries of fluctuations in sea level (Stanley 1968). Submarine slides and tidal waves caused considerable (although largely undocumented) damage to marine benthic communities (NRC 1971).

At the time of the earthquake, most young salmon had hatched but remained in stream gravels, with widespread mortality from subsequent siltation. However, in other areas of PWS, subsidence led over time to creation of new salmon spawning habitat (NRC 1971). Spawning areas for the intertidal-spawners pink and chum salmon in particular experienced major damage (Hansen 1967). Of PWS’ 223 salmon-producing streams prior to the earthquake, 138 were uplifted 1–10 m, and 42 subsided up to 2 m, with the remaining 42 unchanged within ± 0.5 m (NRC
1971). Massive declines of salmon runs occurred in some areas; e.g., Montague Island salmon runs decreased from pre-earthquake levels of about 700,000 salmon to only 20,000 in 1969 (NRC 1971).

Direct mortality also occurred for thousands of large red rockfish and cod (Hansen 1967; NRC 1971), which were probably forced to the surface by violent water turbulence and, once surfaced, could not return to their deep-water habitats because of expanded air bladders (NRC 1971). Bivalve resources were severely affected, with estimates of 10–40% loss of the six clam species of economic importance (Baxter 1971), and 90% of the blue mussel (Mytilus edulis) population was destroyed, with similarly high mortalities for razor clams (Siliqua patula) and littleneck clams (Protothaca staminea). In some areas, the hardshell clam (S. giganteus) population was completely annihilated (NRC 1971). Much of the new potential habitat in uplifted zones in PWS was considered unsuitable for establishment of clams because it consisted of pre-earthquake subtidal silty-bottom material (Baxter 1971); however, new potential clam habitat in much of the subsidence areas could support larval clams (NRC 1971).

Salinity-vulnerable coastal freshwater lakes were inundated by the tsunamis, in some cases washing away their outlets (Hansen 1967; NRC 1971). The freshwater plankton in these lakes is strongly coupled to the production of juvenile sockeye salmon prior to their migration to the ocean (Finney et al. 2000). Within a year of the earthquake, some lakes were virtually sterile, the hypolimnion was severely depleted in dissolved oxygen, and the lakes were no longer suitable as sockeye nurseries (NRC 1971).

The long-term effects of the massive habitat alteration of intertidal and nearby communities throughout PWS from the earthquake have not been subject to extensive studies, so the record of ecological recovery is incomplete. This habitat alteration in most cases was irreversible because obviously the fundamental driver controlling intertidal habitats is elevation relative to the tidal regime, and that was permanently changed by the earthquake. However, other areas that previously had been submerged or elevated above tidal influence suddenly became the new physical ITZ, creating new habitat. Over time, on the order of years to a decade or more, the ecological community appropriate for the ITZ reestablished itself (Spies et al. 2007). For example, a study by one co-author (CPM) showed that the eelgrass (Z. marina) community was re-established within about 10 years in the new ITZ that developed in an area of 20-m uplift at Montague Island.

It is not possible to evaluate if the areal extent of the coastal habitats of PWS experienced a net change because of insufficient quantitative characterization of habitats prior to the earthquake. However, at particular locations, specific ecological functions were permanently lost, including some of the salmon runs on Montague Island (Spies et al. 2007). The PWS clam populations that experienced extensive effects may never recover to the pre-earthquake condition, in part because other stressors likely impede recovery (Spies et al. 2007). Because the diet of sea otters in PWS is ~50% to ~75% clams (ITZ and STZ, respectively; Harwell et al. 2010) and the sea otter population re-colonized PWS during the 1960s, 1970s, and 1980s (Johnson and Garshelis 1995), with a 17.6% annual rate of increase from 1975 to 1987 (Estes 1990), sea otter predation in particular contributed to lack of clam
recovery. Similarly, Spies et al. (2007) suggested that the earthquake effects are still cascading through the population of oystercatchers on Middleton Island. In an ongoing study by a co-author (KWC) on freshwater ponds newly created from an uplifted, tidally influenced marsh in the Copper River Delta, the ponds continue to experience changes in vegetative composition and many are shrinking in size. The linkages between particular plant species in the ponds, which grow in essentially monoculture patches, and their specific invertebrate assemblages are related to waterfowl use, raising concerns about the potential for the future production of waterfowl in these ponds.

In general, the immediate ecological effects of the 1964 earthquake were at least as consequential and spatially extensive as the immediate effects of the Exxon Valdez oil spill, discussed below. Unlike EVOS, the earthquake caused permanent habitat alteration throughout the coastal areas of PWS (Spies et al. 2007), and those specific areas that experienced habitat alteration will never return to the pre-earthquake condition. However, at the larger scale, the ecosystem largely recovered within years to a decade.

**Exxon Valdez Oil Spill**

One anthropogenic event that significantly affected the PWS ecosystem was the Exxon Valdez oil spill, which is instructive about the functioning of PWS and the potential for anthropogenic events to dominate a coastal ecosystem. EVOS released >250,000 barrels of North Slope crude oil into northeastern PWS (Figure 1) on 24 March 1989 (Galt et al. 1991; NOAA 1992; US Coast Guard 1993). The oil distributed along the shoreline and inter- and sub-tidal areas of central and western PWS, down the eastern Kenai Peninsula and the Shelikof Strait of the Alaska Peninsula, and as far southwest as Chignik Bay, 970 km from the spill site (Wolfe et al. 1994; Neff et al. 1995). Neff et al. (1995) reported that 783 km of PWS (∼16% of the shoreline) and 1315 km of the GOA (∼14% of the shoreline) were oiled. EVOS caused four types of stressors: (1) volatile organic chemicals (VOCs), which quickly dissipated but may have been an inhalation risk to some biota; (2) physical oiling, which caused loss of thermoregulation and most of the mortality to seabirds and sea otters in the cold PWS waters; (3) polycyclic aromatic hydrocarbons (PAHs), a longer-term toxicity risk; and (4) stressors from the oil clean-up activities. Most visible was the unprecedented loss of seabirds, with total bird mortality estimated up to 375,000 (Ford et al. 1996). For summaries of initial effects, see Loughlin (1994), Wells et al. (1995), Rice et al. (1996), Wiens et al. (1996), Paine et al. (1996), and Harwell and Gentile (2006). The spilled oil had a distinctive fingerprint of PAHs in the coastal environment (Page et al. 1995; Bence et al. 1996; Short et al. 1999); however, even immediately after the spill, seawater concentrations of PAHs were below acute toxicity levels for marine animals (Neff and Stubblefield 1995; Short and Harris 1996).

Massive clean-up operations were conducted during the summers of 1989 and 1990 (Harrison 1991; Owens et al. 1991; Teal 1991; Mearns 1996), with up to 11,000 people and 1400 boats engaged in cleaning more than 1600 km of shorelines and intertidal areas (Harrison 1991). Less-intrusive clean-up efforts were completed.
in summer 1991. The clean-up activities contributed additional stressors to shoreline and intertidal communities, including the physical effects of high-pressure, high-temperature water removal of oil, noise, and unprecedented human presence (Harrison 1991; Highsmith et al. 1996, 2000; Lees et al. 1996; Skalski et al. 2001).

Because PWS is such a highly dynamic system, residual oil on shore was greatly reduced in the first few years, and by 2001, remnant surface and subsurface oil residues had decreased by more than 99% (Short et al. 2004, 2006). The surface residues in a 2002 survey were limited to traces of asphalt or highly weathered tar splats in the upper-middle intertidal to supratidal zones, usually on cobble, boulder, and pebble beaches (Taylor and Reimer 2008). The mostly weathered subsurface residues were primarily buried under clean sediments beneath boulder/cobble armor in the middle and upper ITZ, that is, protected from waves and physical disturbance of the sediments (Hayes and Michel 1999; Short et al. 2006; Michel et al. 2006; Taylor and Reimer 2008). Boehm et al. (2007) concluded that any remaining toxicity risk from PAHs in the subsurface oil residues is low. Nevertheless, there has been some speculation that this risk is sufficient to cause effects on the subpopulation of sea otters at Northern Knight Island (NKI) (e.g., Bodkin et al. 2002; Peterson et al. 2003; Short et al. 2006). To examine this potential toxicological risk, Harwell et al. (2010) conducted a comprehensive quantitatively toxicological risk assessment and demonstrated that assimilated doses of PAHs for even for the 1-in-1000th most-exposed sea otters at NKI at present would be one or more orders of magnitude below thresholds of health effects, suggesting that no population-level effects could plausibly be caused by the remaining subsurface oil residues. All of the other three stressors from EVOS (VOCs, oiling, and clean-up activities) were virtually eliminated from PWS and GOA within months to a few years after the spill (Harwell and Gentile 2006).

**CONCEPTUALIZATION OF THE PRINCE WILLIAM SOUND ECOSYSTEM**

We next present a conceptual ecosystem model of the PWS ecosystem developed through consensus of scientists with experience in the Sound and expertise covering the range needed to address ecological (including plants, invertebrates, birds, mammals, and fish), oceanographic, toxicological, climate, and ecological risk issues. The purpose of the CEM is to: (a) provide a basis for scientific dialog concerning the current risks to PWS from natural and anthropogenic stressors; (b) advance the articulation of scientific hypotheses about the functioning of the coupled PWS-GOA ecosystem; and (c) integrate a trophodynamic model into a risk-based CEM to illustrate the potential for indirect and cascading effects. We have included discussion of the 1964 Great Alaska Earthquake and EVOS to illustrate how major episodic events, whether natural (e.g., earthquakes, with permanent alterations of the topography of the Sound) or anthropogenic (e.g., oil spills, with transient adverse effects on many species), may temporarily override the normal climate and oceanographic processes that predominately shape the PWS ecosystem. This approach also allows a qualitative assessment of the relative importance at present of EVOS-caused stressors compared to natural drivers and processes.
Conceptual Model of the Prince William Sound Ecosystem

Conceptual Ecosystem Model Development Process

There are many types of conceptual ecosystem models, including pictorial diagrams of ecosystem components, such as the visualization of PWS and GOA presented in Mundy (2005); hierarchical representations of ecosystem processes aimed variously at audiences from the general public to technical experts, such as the series of conceptual process models in the Coastal Louisiana Ecosystem Assessment and Restoration Program (CLEAR; http://www.clear.lsu.edu/conceptual_ecological_models); representations of trophic structures, such as the detailed trophic model of PWS presented in Okey and Pauly (1999); and toxicological models illustrating pathways of exposures to ecological components of concern, such as the pathways of PAH exposures to sea otters in PWS presented in Harwell et al. (2010), among many others.

The particular class of CEM developed here derives from the USEPA ecological risk assessment framework (USEPA 1992, 1998; Gentile et al. 1993). This risk-based CEM represents two essential characterizations: (a) the stressor (exposure) regime, where stressor is any physical, chemical, or biological agent that could adversely affect an ecological system; and (b) ecological effects from environmental stressors. The effects are evaluated on a set of ecological attributes termed valued ecosystem components (VECs), which are chosen to represent ecosystem attributes that are important ecologically and/or societally. Thus, the risk-based CEM is designed specifically to capture the natural and anthropogenic forces and associated stressors that can affect the PWS ecosystem, that is, the causal pathways by which a stressor can lead to ecological effects on particular attributes of the ecosystem.

The risk-based CEM graphically captures the direct relationships between the drivers and stressors and between stressors and ecological effects (Gentile et al. 2001). This serves as the basis for articulating testable hypotheses concerning how PWS functions and is shaped by variability of the natural drivers and stressors and by human activities. The particular graphical construct used here was initially developed by USEPA to illustrate methods for regional- or watershed-scale assessments, using the Big Darby Creek, Ohio, ecosystem as the test case (Cormier and Smith 1996) and subsequently applied to a series of case studies on other watersheds (e.g., Cormier et al. 2000; USEPA 2002). The risk-based CEM approach has been used for many habitats in support of the Comprehensive Everglades Restoration Program (e.g., Ogden et al. 2005), for support of ecosystem management of National Estuarine Research Reserves (Reiter et al. 2006), and for the highly contaminated Coeur d’Alene watershed (USEPA 2001), among many other cases.

To develop the CEM, we used a multi-step process that included: (a) conducting an exhaustive review of the literature on PWS and the GOA; (b) implementing a systematic approach to capturing information from a group of experts concerning the stress-effects relationships of the ecosystem based on the literature and their own knowledge of the ecosystem; (c) as a part of that process, applying a suite of criteria for determining ecological significance and the strength of the stress-effects relationships; and (d) following a specific construct for converting the information developed in the expert-judgment process into a risk-based graphical representation of the PWS ecosystem. The central purpose of this process was to characterize the driver-stressor-effects relationships that control the structure and functioning of the PWS ecosystem. The factors we considered when assigning the magnitude
of each driver-stressor and stressor-effects relationship were based on the criteria used to assess ecological significance that were developed for the USEPA Risk Assessment Forum (Gentile and Harwell 1998). These criteria included, among other factors, assessing: (a) the spatial extent and intensity of effects caused by a stressor; (b) the degree of reversibility versus irreversibility and the time-domain for recovery once a stressor is removed; (c) the redundancy of functionality and degree to which multiple components of a particular functionality would be affected by a stressor; (d) the effects of a stressor on keystone or other critical species or functions; and (e) the potential for ecosystem-level cascading effects to ensue from a stressor or from multiple stressors associated with a particular driver. Similar criteria were used in the USEPA Unfinished Business and Reducing Risk projects (Harwell and Kelly 1987; USEPA 1987; USEPA SAB 1990a,b; Harwell et al. 1992). The application and interpretation of these criteria were informed by the group’s scientific expertise, experience in PWS and similar ecosystems, and consensus professional judgment.

In developing the CEMs, the group sequentially followed these specific steps:

1. Identification of the natural drivers and processes and the anthropogenic drivers and human activities affecting the PWS ecosystem: This entailed the systematic consideration of physical, chemical, and biological processes that have occurred in the past, presently exist, or potentially could occur that could affect the PWS ecosystem, and, similarly, the systematic identification of the types of human activities that historically, currently, or prospectively could affect the PWS ecosystem. The outcome of this step is a list of natural and anthropogenic drivers, processes, and human activities relevant to the PWS ecosystem.

2. Identification of the environmental stressors affecting PWS that result from those drivers, processes, and human activities: This entailed the systematic consideration of each process, driver, and activity to identify the physical, chemical, and/or biological stressors that could ensue. The outcome of this step is a list of the environmental stressors affecting the PWS ecosystem.

3. Development of a matrix that links each natural driver/process to its resulting environmental stressors: This entailed systematically considering each natural driver/process and each of the listed environmental stressors to determine the relative strength of each driver-stressor relationship (i.e., how intensely a particular process is likely to be generated by a particular stressor). The outcome of this step is a matrix completely populated with the natural driver-stressor relationships, capturing a wealth of qualitative information about the system.

4. Development of a matrix that links each anthropogenic driver and associated human activities to their resulting environmental stressors: This followed the same approach, qualitatively assigning weights to the relative strength of each societal driver-human activity in generating each environmental stressor. The outcome of this step is a similar matrix populated with all anthropogenic driver/human activity-stressor relationships for the PWS ecosystem.

5. Identification of the important species and ecological attributes in the PWS ecosystem: This process began with the list of ecological attributes identified as being a concern in assessing effects from EVOS (EVOSTC 2009; Harwell and Gentile 2006) and systematically expanding that list to a more extensive set of
species and other ecological attributes of PWS that are important either ecologically and/or societally. Criteria used for selecting these ecological attributes are discussed in detail in Gentile et al. (2001). The outcome of this step is a comprehensive list of species and other ecological attributes representing the valued ecosystem components of concern.

6. Development of a coupled benthic and pelagic trophodynamic model: This entailed first aggregating the list of VECs from the previous step into the functional components of the PWS ecosystem and then characterizing the trophodynamic relationships among those components. The outcome of this process is a graphical trophodynamic model and a mapping of each important species and ecological attribute onto the trophic structure of PWS.

7. Assessing the magnitude of potential ecological effects from each natural stressor on each affected VEC: Using the matrix approach and the criteria described earlier, each natural stressor was systematically considered with respect to each VEC by qualitatively assigning the relative magnitude of the direct effect of that stressor on that VEC. The outcome of this step is a completed matrix capturing the stress–response relationships associated with the natural processes that affect the PWS ecosystem.

8. Assessing the magnitude of potential ecological effects from each anthropogenic stressor on each VEC: Similarly, a matrix was developed showing the direct effect of each anthropogenic stressor on each VEC; as with the driver-stressor matrices, these two sets of stressor-effects matrices capture a wealth of qualitative information about the ecosystem.

9. Converting the direct driver-stressor-effect information into a graphical CEM: Following the risk-based CEM construct discussed previously, the outcome of this step is the graphical representation of the information in the driver-stressor and stressor-effects matrices, visually highlighting the relative importance of each potential direct linkage.

10. Incorporating the trophodynamic model into the CEM: This integration extends the CEM to represent the indirect effects on VECs from the natural and anthropogenic stressors, particularly useful to identify important cascading effects that result from the dominant processes affecting PWS. The outcome of this step is the final graphical CEM for each natural process and each anthropogenic driver affecting the PWS ecosystem.

By systematically following this CEM-development process, the relative importance of the drivers and stressors that affect the PWS ecosystem are illuminated. Those factors that actually control and dominate the ecosystem become manifest and clearly distinguished from those factors of lesser ecological importance, based on a substantial literature detailing the critical stress-effects linkages, as discussed earlier. Although this qualitative assignment of information in the matrices was based on an expert-judgment process, assigning relative values, as done here, (e.g., matrix Cell A is High whereas matrix Cell B is Low) is much less uncertain than assigning absolute values (e.g., the magnitude of matrix Cell A is 8.3). Moreover, the scientific understanding of certain factors show that they are so clearly dominant in controlling the PWS ecosystem components and processes, whereas other factors are clearly not so controlling. By analogy, beachgoers can correctly conclude that a flying kite is
lower than a low-flying airplane, and that both are far below a jet airliner and its contrail, without knowing the altitudes of any of them. Consequently, we are confident that that the overall picture presented here would be replicated by a different group of experts familiar with the PWS ecosystem. By integrating the trophodynamical model into this risk-based CEM, the pathways by which indirect effects may propagate through the ecosystem can be visualized, including the potential for potentially important cascading effects. Again, those potentially cascading effects emerge clearly from this CEM-development process because of the dominance of certain processes.

**Stressor Regime: Processes, Drivers, and Stressors Affecting the PWS Ecosystem**

We identified five categories and many subcategories of natural drivers that shape the PWS ecosystem: (1) climatic processes; (2) physical/chemical oceanographic processes; (3) watershed/geomorphological processes; (4) atmospheric processes; and (5) biological processes. Listed in Table 1 are the natural drivers, the nine categories of environmental stressors they generate, and the matrix of the strength of relationships between a driver and each stressor, recorded as Dominant (XXXX), High (XXX), Medium (XX), Low (X), or No Linkage (–). The specific aspect of each driver that can generate each stressor is also identified, indicated by presence (+) or absence (–) of a relationship, but without characterizing their relative importance. For instance, oceanographic processes have a dominant role in determining the salinity, nutrient, and sedimentation regimes, involving, for example, the ACC, up- and downwelling, vertical mixing, and gyres, but the relative contribution of each subcategory varies and would require a more detailed analysis that would be beyond the scope of this paper.

PWS is also influenced by several anthropogenic factors (Table 2), including the historical commercial fur trade (*e.g.*, sea otter, harbor seals), subsistence and commercial whaling, recreational and commercial fishing within PWS and throughout the Pacific Ocean, logging, mining, tourism (particularly the rapidly expanding cruise ship industry), shipping of petroleum products, air pollution from regional and longer-range sources, habitat alteration for human development, and introduced exotic species (*e.g.*, foxes and hatchery-reared pink salmon) (*cf.*, Wooley 2002; NWF 2003; Harwell and Gentile 2006). These and other human activities were aggregated into four categories of anthropogenic drivers (development; resource harvesting; recreation/tourism; and marine transport) and were considered to generate eleven categories of stressors. We identified the strength of relationships between each human activity and each stressor, reporting a scale that is comparable between the two classes of drivers, natural and anthropogenic, allowing comparisons of relative importance across all drivers and stressors. We were able to assign these relative values at the human activity level; consequently, more specific information in each cell is shown in Table 2 than could be captured in Table 1. Note that the assignment shown at the driver scale (*e.g.*, for development or resource harvesting) reflects the magnitude of the highest entry among the human activities caused by that driver, rather than some combination of all the entries for that driver. Also note that for the driver marine transport, we differentiated the nature and magnitude of stressors immediately after a major oil spill versus the conditions that would exist.
| Natural Drivers | Salinity | Temperature | Nutrients | Contaminants | Suspended Sediments | Physical Disturbance | Pests (HAB) | Disease (VHS) | Introduced Species |
|-----------------|----------|-------------|-----------|--------------|---------------------|----------------------|-------------|--------------|------------------|
| Climates Processes | XXXX     | XXXX        | XXXX      | XX           | XXXX                | XXXX                 | XX          | XXX          | XXX              |
| • PDO            | −        | +           | +         |              | +                   | −                    | +           | +            | +                |
| • Aleutian LP    | +        | +           | +         |              | +                   | +                    | +           | +            | +                |
| • ENSO           | +        | +           | +         |              | +                   | +                    | +           | +            | +                |
| • Climate Change | +        | +           | +         |              | +                   | +                    | +           | +            | +                |
| • Storm Regime   | +        | +           | +         |              | +                   | +                    | +           | +            | +                |
| • Solar Cycle    | −        | +           | +         |              | +                   | −                    | −           | +            | +                |
| Physical/Chemical Oceanographic Processes | XXXX     | XXX         | XXXX      | XX           | XXXX                | XX                   | X           | XXX          | XXX              |
| • Alaska Coastal Current | +         | +           | +         | −            | −                   | +                    | −           | −            | +                |
| • Upwelling      | +        | +           | +         |              | +                   | −                    | +           | +            | +                |
| • Downwelling    | +        | +           | +         |              | +                   | −                    | −           | −            | +                |
| • Eddies/Gyres   | +        | +           | +         |              | +                   | −                    | +           | −            | +                |
| • Stratification | +        | +           | +         |              | +                   | −                    | +           | −            | −                |
| • Vertical Mixing | +        | +           | +         |              | +                   | −                    | +           | −            | +                |
| • Sea-Level Rise | +        | −           | −         |              | −                   | −                    | +           | −            | −                |
| • Light Transmissivity | −        | +           | +         | −            | +                   | −                    | +           | −            | −                |
| • Tides          | +        | −           | −         |              | +                   | +                    | −           | −            | +                |
| • Circulation    | +        | +           | +         |              | +                   | −                    | +           | +            | +                |
| • Waves          | +        | −           | −         |              | +                   | +                    | −           | −            | −                |

(Continued on next page)
Table 1. The strength of relationships between the natural drivers/processes and the stressors in PWS. (Continued)

| Natural Drivers | Stressors          | Salinity | Temperature | Nutrients | Contaminants | Suspended Sediments | Physical Disturbance | Pests (HAB) | Disease (VHS) | Introduced Species |
|-----------------|--------------------|----------|-------------|-----------|--------------|---------------------|----------------------|-------------|---------------|---------------------|
| Watershed/Geomorphological Processes | XXXX | XXX | XXX | XX | XXXX | XXXX | XX | − | X |
| • Runoff | + | + | + | + | + | + | + | − | + |
| • Erosion | − | − | + | + | + | + | + | − | − |
| • Sedimentation | − | − | + | + | + | − | + | − | − |
| • Earthquakes | − | − | − | + | + | + | + | − | − |
| • Glacial Melting | + | + | + | + | + | + | + | − | − |
| Atmospheric Processes | − | XXX | XXX | XXX | − | − | X | − | − |
| • Deposition | − | − | + | + | − | − | + | − | − |
| • Clouds | − | + | + | + | − | − | + | − | − |
| Biological Processes | − | − | XXX | XX | X | X | XXX | XXX | XXX | XXX |

Key: XXXX, dominant; XXX, high; XX, medium; X, low; −, none.

Note: The strength of relationships follows a common scale with that used for the anthropogenic drivers (Table 2). The + symbol indicates that subcategory is a component of the category that causes the stressor; the − symbol indicates that category or subcategory does not generate the stressor.
Table 2. The strength of relationship between the anthropogenic drivers/human activities and the stressors in PWS.

| Anthropogenic Drivers | Habitat Alteration | Harvesting | Nutrients | Chemical Contaminants | Biological Competition | Physical Disturbance | Noise | Disease | Introduced Species | Oiling | Solid Wastes |
|-----------------------|-------------------|------------|-----------|-----------------------|------------------------|----------------------|-------|---------|-------------------|--------|-------------|
| Development           | XXX               | XX         | XXX       | XX                    | −                      | X                    | X     | X       | X                 | XX     | XX          |
| Urbanization          | XXX               | XX         | XXX       | XX                    | −                      | X                    | X     | X       | X                 | XX     | XX          |
| Dredging              | XX                | X          | X         | X                     | −                      | X                    | X     | −       | −                 | X      | X           |
| Energy Industry       | XX                | −          | −         | XX                    | −                      | X                    | X     | −       | −                 | XX     | XX          |
| Transportation        | XX                | X          | X         | X                     | −                      | X                    | X     | X       | X                 | XX     | XX          |
| Air Pollution         | −                 | −          | −         | X                     | −                      | −                    | −     | −       | −                 | −      | −           |
| Construction          | XXX               | X          | XX        | X                     | −                      | X                    | X     | −       | −                 | X      | X           |
| Resource Harvesting   | XXX               | XXXX       | X         | X                     | XXX                   | XXX                 | X     | XX      | XX                | X      | X           |
| Commercial Fishery    | XX                | XXXX       | X         | −                     | X                     | X                    | X     | X       | XX                | XX     | X           |
| Hatchery/Aquaculture  | XX                | XXXX       | X         | X                     | XXX                   | X                   | −     | XX      | XX                | −      | −           |
| Recreational Fishing  | X                 | XXX        | X         | −                     | XXX                   | X                    | X     | X       | X                 | X      | X           |
| Subsistence Fishing,  | X                 | XX         | X         | −                     | X                     | −                   | X     | X       | xx                | X      | X           |
| Hunting               |                   |            |           |                       |                        |                      |       |         |                   |        |             |
| Logging               | XXX               | XX         | X         | X                     | −                      | XXX                 | X     | −       | −                 | X      | X           |
| Mining                | XXX               | −          | −         | X                     | −                      | XXX                 | X     | −       | −                 | X      | X           |
| Recreation/Tourism    | X                 | X          | X         | X                     | −                      | X                    | X     | −       | −                 | X      | X           |
| Cruise Vessel Traffic | X                 | −          | X         | X                     | −                      | X                    | X     | −       | −                 | X      | X           |
| Private Vessel Traffic| X                 | −          | X         | X                     | −                      | X                    | X     | −       | −                 | X      | X           |
| Air Traffic           | −                 | −          | −         | −                     | −                      | −                    | −     | −       | −                 | −      | −           |
| Presence of People    | X                 | X          | X         | −                     | −                      | X                    | X     | −       | −                 | −      | −           |

(Continued on next page)
Table 2. The strength of relationship between the anthropogenic drivers/human activities and the stressors in PWS.

(Continued)

| Drivers Human Activities | Habitat Alteration | Harvesting | Nutrients | Chemical Contaminants | Biological Competition | Physical Disturbance | Noise | Disease | Introduced Species | Oiling | Solid Wastes |
|--------------------------|-------------------|------------|-----------|-----------------------|------------------------|---------------------|-------|---------|-------------------|--------|-------------|
| Marine Transport         | XXX               | XXX        | X         | XXX                   | −                      | XXX                 | XXX   | XX      | XX                | XXX    | XXX         |
| Ballast                 | −                 | −          | −         | X                     | −                      | −                   | −     | X       | XX                | XX     | −           |
| Chemical Spills          | −                 | XXX        | −         | XXX                   | −                      | −                   | −     | X       | −                 | −      | −           |
| Commercial Vessel Traffic| X                 | −          | X         | X                     | −                      | X                   | X     | −       | X                 | X      | X           |

Oil Spills (immediate) XXXX XXXX X XXXX − − − X − XXXX −
Oil Spill Cleanup (immediate) XXXX − X X − XXXX XXX XX − X XXX

Oil Spills (long term) X X X X − − − X − X −

Key: XXXX, dominant; XXX, high; XX, medium; X, low; −, none.

Note the difference between immediate and long-term conditions following an oil spill, such as EVOS. The scale of relationships is common with that used for the natural processes (Table 1).
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prior to or several years after a spill. We used EVOS as the case example, but we would expect similar magnitudes of stressors from other major oil or chemical spills.

Effects Regime: Valued Ecosystem Components of the PWS Ecosystem

Valued ecosystem components are those ecological attributes that can be used to characterize effects from stressors across the hierarchy of ecological organization. The benefit of using VECs to assess effects is that if there is a significant change in one or more VEC, that would constitute a change in the condition (or “health”) of the ecological system, and conversely, if there is a change in the health of the ecosystem, that would be manifested in one or more VEC (see Gentile et al. 2001). For the CEM development, we began with a list of ecological attributes that have been the focus of injury and recovery assessments from EVOS (Harwell and Gentile 2006; Integral 2006; EVOSTC 2009) and expanded that to a more comprehensive list that includes important primary producers, filter feeders, fish and bird primary consumers, fish and bird top predators, a bird scavenger, mammalian primary consumers and top predators, biotic communities, ecosystem-level properties of trophodynamics and biogeochemical processes, and landscape-level properties of habitat mosaic and wilderness quality. We aggregated these into the benthic and pelagic trophic components and constructed the trophodynamic model (Figure 2) representing the functional ecological components of PWS, on which map the individual species monitored for recovery assessments and the other VECs (Table 3). This allows us to capture the effects of a stressor on the PWS ecosystem, including indirect or second-order effects that are mediated through the trophodynamic structure of the ecosystem.

PRINCE WILLIAM SOUND CONCEPTUAL ECOSYSTEM MODEL

The final step in the development of the PWS CEM was to assess the strength of the direct effect of each natural or anthropogenic stressor on each VEC if that stressor occurred at the magnitude and spatial extent that are appropriate to the PWS ecosystems or plausibly could occur in the future (Tables 4 and 5). We assigned levels of High (H), Medium (M), Low (L), or No (–) to these direct cause–effect linkages, following the criteria discussed previously. However, indirect effects clearly are also very important to the ecosystem, where an effect on one VEC is propagated via the trophic structure to effects on one or more other VECs. To capture the pathways for those indirect effects, the trophodynamic model (Figure 2) illustrates how a direct stress–effect relationship between a stressor and a VEC can cascade through the ecosystem to cause indirect effects on other VECs higher in the food web. For example, while a change in nutrients has a major influence on the productivity of phytoplankton, there is no direct effect on planktivores. However, the indirect effect on planktivores is very large: since the plankton producers are the food base of the planktivores, if plankton are depleted, then planktivores are as well. Thus, we integrated the trophodynamical model into the CEM as a new protocol for this class of CEMs (i.e., the risk-based, stress-response construct) to capture both the functionally important ecosystem attributes and the indirect effects of stressors on VECs.
| Trophic Categories | Watershed | Islands | Glacial Estuary < 1 km from shoreline | Soft Bottom < 1 km from shoreline | Rocky Intertidal & Subtidal < 1 km from shoreline | Epi-Pelagic > 1 km from shoreline | Pelagic > 1 km from shoreline |
|-------------------|-----------|---------|--------------------------------------|-----------------------------------|-----------------------------------------------|---------------------------------|--------------------------------|
| Plankton Producers | marsh plants | micro and macrophytes | seagrass, microalgae | micro & macroalgae; *Fucus; kelp* | phytoplankton | phytoplankton |
| Benthic Producers | | | | | | |
| Macrophyte Feeders | | | | | | |
| Secondary Producers | | | | | | |
| Benthic Invert Feeders | Harlequin Duck | Black Oystercatcher, Harlequin Duck; Sea Otter | Sea Otter | Black Oystercatcher, Harlequin Duck; Sea Otter | Sea Otter |
| Planktivores | Pink Salmon; Sockeye Salmon; Coho Salmon | Marbled Murrelet | dam; Pacific Herring | Mussels | Pacific Herring | Pacific Herring |
| Marine Bird Forage Fish Consumers | Marbled Murrelet | Pigeon Guillemot; Harbor Seal | Marbled Murrelet | Common Murre; Cormorants; Pigeon Guillemot; Kittiwakes | Common Murre; Cormorants; Pigeon Guillemot |
| Large Vertebrates (fish, mammals) | River Otter | Harbor Seal; Sea Otter; Steller sea lion | Halibut; Sea Otter | Sea Otter |
| Scavengers | Bald Eagle | | | | Bald Eagle |

Notes:
1. Location and habitat categories relate to all aspects of organisms' natural history: foraging, resting/loafing, breeding.
2. Habitat categories are relative to distance from shore.
Table 4. The strength of relationships between the natural stressors and the VEC categories in PWS.

| Natural Stressors | Chemical | Suspended | Physical | Pests | Disease | Introduced |
|-------------------|----------|-----------|----------|-------|---------|------------|
|                   | Salinity | Temperature | Nutrients | Contaminants | Sediments | Disturb. | (HAB) | (VHS) | Species |
| Plankton Producers | M        | M         | H        | M     | H       | –         | L-M   | L     | L-H     |
| Benthic Producers  | L        | L         | H        | L     | H       | H         | L-M   | L     | L-H     |
| Macrophyte Feeders | L-M      | L         | –        | L-M   | L       | M         | L     | L-H   | L-H     |
| Secondary Producers| L-M      | L         | –        | L-M   | L-M     | M         | L     | L-H   | L-H     |
| Benthic Invert Feeders | L-M    | L         | –        | L-M   | L       | L-H       | L     | L     | L-H     |
| Planktivores       | L        | M         | –        | M-H   | L-H     | –         | M-H   | H     | L-H     |
| Forage Fish Consumers | –       | –         | –        | L-M   | L       | –         | M-H   | L     | L-H     |
| Large Vertebrate Consumers | –   | –         | –        | L-H   | L       | L         | M-H   | L     | L-H     |
| (fish, birds, mammals) | | | | | | | | | |
| Scavengers         | L        | –         | –        | L-H   | –       | L         | M-H   | L     | L-H     |

Key: H, high; M, medium; L, low; –, none.

Comments:
Nutrients and suspended sediments are strongly associated with both plankton primary and benthic primary producers.
Physical disturbance is particularly important to benthic producers and feeders inhabiting the intertidal zone on the open shorelines.
The heading “pests” primarily refers to harmful algal blooms (HAB) which can have both direct and indirect effects on the resources of PWS.
Disease is always a potential problem but here the impact to planktivores refers specifically to the viral hemoragic septicemia of herring.
Table 5. The strength of relationships between the anthropogenic stressors and the VEC categories in PWS.

| VECs               | Habitat Alteration | Harvesting | Nutrients | Chemical Contaminants | Biological Competition | Physical Disturbance | Noise | Disease | Introduced Species | Oiling | Solid Wastes |
|-------------------|--------------------|------------|-----------|-----------------------|------------------------|----------------------|-------|---------|-------------------|--------|-------------|
| Plankton Producers| –                  | –          | H         | M                     | –                      | –                    | –     | –       | L-H               | L      | –           |
| Benthic Producers | H                  | L-H        | H         | L                     | –                      | H                    | –     | L       | L-H               | H      | –           |
| Macrophyte Feeders| L                  | L          | –         | L-M                   | –                      | M                    | L     | –       | L-H               | H      | L-M         |
| Secondary Producers| L-H                | M          | –         | L-M                   | –                      | L-H                  | L-M   | –       | L-H               | H      | L-M         |
| Benthic Invert Feeders| L-H              | M          | –         | L-M                   | –                      | L-H                  | L-M   | –       | L-H               | H      | L-M         |
| Planktivores      | L-H                | H          | –         | M-H                   | L-H                    | –                    | –     | –       | L-H               | L-H    | L-M         |
| Forage Fish Consumers| L-H               | H          | –         | L-M                   | L-H                    | –                    | L-M   | –       | L-H               | H      | L-M         |
| Large Vertebrate Consumers (fish, birds, mammals)| L-H | H | – | L-H | – | L | L-M | L-H | L-H | H | L-M |
| Scavengers        | L                  | L          | –         | L-H                   | –                      | L                    | L-M   | L-H     | H                 | L-M    |             |

Key: H, high; M, medium; L, low; –, none.

Comments:
Habitat alteration and physical disturbance are strongly related to benthic producers occupying the intertidal zone and may also be strongly associated with specific members of the category but not the category as a whole.
Harvesting is strongly associated with planktivores, forage fish consumers, and large invertebrates and to specific benthic producers.
Nutrients are strongly associated with plankton and benthic producers.
For the most part, the remaining stressors exhibit low to moderate association with VEC categories with some exceptions.
The L-H designations for disease and introduced species are used to denote that specific members of the VEC category may show a strong association while other members of the category do not.
The L-M designation for the solid wastes and noise relate differences between current conditions and those during spill clean-up activities.
We recognize that a combination of multiple anthropogenic and/or natural stressors might result in synergistic effects on the ecosystem. For example, a population or biological process might be marginally stressed by the influence of a single stressor. If, however, an additional stressor is added concurrently, the combined effects of both might have more significant consequences on the population. Thus, the effects of stressors might not be simply additive but combine nonlinearly. Any such synergistic effects by necessity are not captured in the matrices or the graphical conceptual models. Nevertheless, we believe the major direct and indirect effects of natural and anthropogenic stressors on the PWS ecosystem are represented in the conceptual models.

By describing the full suite of direct and indirect linkages from drivers to stressors to ecological effects, one can ascertain the relative importance of natural and anthropogenic processes in shaping the condition of the PWS ecosystem. These relationships are organized by driver category and captured graphically in Figures 3A–E and 4A–E. These CEMs are constructed with the upper tier (rectangles) representing natural or anthropogenic drivers. These lead to the environmental stressors (ovals) shown at the second tier in these figures. Note that for clarity of presentation, each individual human activity is not shown, with the exception of an oil spill and its clean-up activities; however, more complex and detailed CEMs could readily be developed based on the information in the tables.

Using the same CEM, these causal relationships could also be graphically represented by focusing on a particular stressor (i.e., showing all the drivers leading to a particular stressor and all the VECs it affects) or on a particular VEC (i.e., showing all the causal drivers and stressors that put a selected VEC at-risk). In general, for a selected process/driver, we show the resulting dominant stressors in bold red and high-level stressors in blue. Medium-strength relationships are shown in normal black font, and low or no relationships are shown in background.

Since these relationships are aggregated at the driver level, differences at the subcategory level of drivers or processes cannot be shown; within a category in the graphical model, we show the relationship for the highest of the subcategories. Also, to keep each graphic more manageable, we do not show the specific pathways of stressors to effects, other than indicating which effects are direct (normal font) and which are indirect (italicized font); however, those specific pathways can be discerned from the matrices (Tables 4 and 5) and could readily be shown in a more-detailed CEM.

Selecting the level of aggregation or detail to represent in a CEM is always challenging and relates to the targeted audience for the CEM. For the purposes of this CEM, we chose a middle-level of aggregation, aimed at both scientists and at decision-makers. The CEMs are sufficiently detailed to identify the major components of the PWS ecosystem, the types of stressors impinging on the ecosystem, and the direct and indirect linkages among these, and thereby to demonstrate to the scientific community that the CEMs are comprehensive and capture the important elements of the ecosystem. But the CEMs are not so detailed that the big picture of the relative importance of the various factors is lost, obscuring messages relevant to decision-makers. By accompanying the graphical CEMs with the somewhat more detailed matrices and, in particular, the much greater detailed discussion derived from the literature on how the PWS ecosystem works, this CEM should be useful for
a variety of audiences, and those desiring more in-depth understanding are led to information sources that can provide that detail. The CEM could be disaggregated to illustrate more-detailed linkages for a particular activity or process, or could show the details of each specific causal pathways by which a particular stressor causes a particular response in a VEC. A next step in development for a CEM aimed at

![Figure 3](image.png)

**Figure 3.** The graphical Conceptual Ecosystem Model (CEM) for Prince William Sound for the natural drivers. The information in the figure derives from Tables 1 and 4. The top tier (rectangular boxes) indicates the specific natural driver for the CEM. The middle tier (ovals) identifies the stressors associated with the natural drivers. For a particular driver, the resulting stressor that has a dominant role in causing ecological effects is highlighted in red bold; a stressor that has a high role in causing effects is indicated in dotted blue; medium stressors are identified in black; stressors with low or no effects are shown in background coloring. The third tier is the trophodynamical model from Figure 2, modified to show dominant (red), high (blue), medium (black), or no (background) trophic-structure-mediated effects for the particular natural driver. Direct pathways are shown in normal font; indirect pathways are shown in *italics*. Separate figures are shown for each natural driver: (A) Climate Processes; (B) Physical/Chemical Oceanographic Processes; (C) Watershed/Geomorphological Processes; (D) Atmospheric Processes; (E) Biological Processes. (Continued)
Figure 3. (Continued)
Figure 3. (Continued)
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multiple audiences like this would be to create a set of nested CEMs that could cover more of the aggregation-disaggregation continuum, similar to the nested or hierarchical approach used in the CLEARS conceptual models of coastal Louisiana ecosystems (http://www.clear.lsu.edu/conceptual_ecological_models).

Figure 4. The graphical Conceptual Ecosystem Model (CEM) for Prince William Sound for the anthropogenic drivers. The information in the figure derives from Tables 2 and 5. The top tier (rectangular boxes) indicates the specific anthropogenic driver for the CEM. The middle tier (ovals) identifies the stressors associated with the anthropogenic drivers. For a particular driver, the resulting stressor that has a dominant role in causing ecological effects is highlighted in red bold; a stressor that has a high role in causing effects is indicated in dotted blue; medium stressors are identified in black; stressors with low or no effects are shown in background coloring. The third tier is the trophodynamical model from Figure 2, modified to show dominant (red), high (blue), medium (black), or no (background) trophic-structure-mediated effects for the particular natural driver. Direct pathways are shown in normal font; indirect pathways are shown in italics. Separate figures are shown for each anthropogenic driver: (A) Development; (B) Resource Harvesting; (C) Recreation/Tourism; (D) Oil Spill and Cleanup (Immediate); (E) Oil Spill and Cleanup (Long-Term). (Continued)
Figure 4. (Continued)
Figure 4. (Continued)
Natural Drivers

As is clear from the previous discussion based on the literature, climate processes have a dominating role in determining the condition of the PWS ecosystem, especially by influencing the salinity, temperature, nutrient, and sediment regimes (see Figure 3A). Climate processes also have an important role in generating the stressors of physical disturbance, disease (e.g., viral hemorrhagic septicemia, VHS), and introduced species (e.g., species entering the system from warmer climates in response to global climate change). Nutrients especially control pelagic primary productivity, and nutrients in turn are significantly affected by winds and the salinity and temperature regimes through mechanisms such as upwelling, circulation, and vertical mixing, as discussed previously. Nutrients do not have a direct effect on secondary producers and other animals, but because of cascading effects, there is a dominant indirect effect throughout the pelagic trophic structure. Nutrients have an important role in affecting benthic primary productivity, but not as intensely as the control over the phytoplankton producers; consequently the right side of the trophodynamic model (benthic VECs) is shown in blue rather than the red of the pelagic system. Again, effects on benthic macrophytes lead to indirect effects on the rest of the benthic-based trophic structure. Suspended sediments affect the ecosystem significantly, through both reduction in sunlight available to the primary producers and impacts on filter feeders.

Physical/chemical oceanographic processes play a similar dominating role (Figure 3B), particularly as mediated through the nutrient regime (and hence salinity and mixing regime). As we have seen, the climatic and oceanographic processes are themselves tightly coupled, so Figures 3A and 3B are quite similar. Because of this coupling of climate and physical/chemical oceanographic processes and the importance of each to the structure and functioning of the PWS ecosystem, the regional physical processes of the North Pacific, including the GOA, operating over seasonal to interdecadal time scales, dominate the condition of the PWS ecosystem.

Watershed/geomorphological processes (Figure 3C) also have a dominating role for PWS, through runoff effects on salinity and suspended sediments, but less controlling than the climate and oceanographic drivers. The greatest impact of geomorphological processes on PWS during the past century was the 1964 Great Alaska Earthquake, discussed in detail earlier. The earthquake instantaneously altered virtually all coastal habitats throughout PWS, with profound effects on the coastal forests, migratory-bird nesting grounds, salmon-spawning waters and gravels, and shellfish habitats and populations of the Sound. During this phase, the structural and functional components of the PWS ecosystem were forced to realign to the new physical conditions. However, over a period of time, the coastal habitats and associated communities became reestablished, and the overall PWS ecosystem had essentially recovered after a period of years to a decade or more.

Atmospheric processes (Figure 3D) have an important but much more modest role in shaping the ecosystem, primarily through effects on nutrients and atmospheric deposition of chemical contaminants. These stressors directly or indirectly affect all of the pelagic and benthic trophic systems. Similarly, biological processes (Figure 3E) have an important but not dominating role affecting all of the ecosystem. Harmful algal blooms (HAB) and VHS have a particularly important role on the biota.
Introduced species is a difficult category to characterize because the vast majority of naturally occurring introduced species fail to become established, but in rare instances can change the system fundamentally (cf., Mooney et al. 2005).

Anthropogenic Drivers

Only two anthropogenic drivers have a dominant role in the PWS ecosystem: resource harvesting, particularly over-exploitation of fish populations, and the immediate aftermath of a major oil (or potentially a chemical) spill, clearly illustrated by EVOS and its clean-up activities. Other human activities and associated stressors have a relatively minor role in determining the condition of the ecosystem compared to natural processes.

Development (Figure 4A) primarily affects habitat alteration (e.g., replacement of coastal habitat with human settlements) and nutrients (e.g., release of nutrients from surface runoff in developed areas). These more modest stressors affect primary productivity of both benthic and pelagic producers, but the level of cascading effects through the ecosystem is much less than, for example, effects on primary productivity from oceanographic processes because the contribution of nutrients from this pathway is very small compared to natural sources. Development also leads to chemical contamination (e.g., from processing facilities), oiling (e.g., leaks from storage tanks), and solid wastes (e.g., Page et al. 1999).

Resource harvesting (Figure 4B), such as commercial fisheries and hatcheries, has a dominant role in affecting many marine ecosystems throughout the world (Jackson et al. 2001; Hilborn et al. 2003), and PWS is no exception. In this case resource harvesting directly affects the forage and large fish components and indirectly affects the marine birds and mammals that feed on them. For example, overfishing in the North Pacific may be a significant contributor to the reduction of some marine mammal populations like the Steller sea lion, as discussed previously (NRC 2003; Hobson et al. 2004; Miller et al. 2005). Other harvesting historically had a dominant role, particularly the direct effect of harvesting marine mammals (e.g., sea otters, whales) by commercial or subsistence harvesters. Resource harvesting also affects biological competition (e.g., release of genetically homogeneous hatchery-reared fish) (Hilborn and Eggers 2000) and physical disturbance (e.g., effects on benthic habitat from trawling) (Hilborn et al. 2003). Harvesting may significantly enhance disease, for example, the suspected role of herring confinement in the spawn-on-kelp fishery in enhancing the incidence of VHS (Marty et al. 1998; Hershberger et al. 1999). Harvesting also impacts a number of important benthic invertebrate species of commercial and subsistence interest such as king, Tanner, and Dungeness crabs, shrimp, and bivalves. All of the commercially harvested crab and shrimp species have experienced regulatory closures or limited harvests in the last 20–30 years (Berceli and Trowbridge 2006; Berceli et al. 2008). While overharvesting is thought to be involved, other factors such as environmental changes may also impact population levels or recovery failures.

Recreation/tourism (Figure 4C), while a source of chemical contamination, noise, habitat alteration, and so on, is presently at too small a scale to cause dominant-, high-, or even medium-level stressors; thus this figure shows no relationships attaining the level of importance seen for many of the natural and other anthropogenic
drivers. There is the potential for this conclusion to change, however, as recreational tourism in Alaska has increased rapidly in recent years. As one indicator, Colt (2001) reported that the number of summer visitors (May–September) arriving by air into Alaska increased between 1989 and 1998 from 150,000 to 450,000, and the number arriving by cruise ships doubled to ∼600,000. After the highway tunnel to Whittier was completed in 2000, the number of visitors to PWS increased dramatically, and NWF (2003) stated that 1.4 million people are expected to access PWS via Whittier by 2015. The EVOS Trustees reported 1.2 million visitors to PWS in 2001, double the number in 1989; the number of sportsfishers increased by 65% from 1989 to 1997 (EVOSTC 2005). If these trends continue, concomitant increases in anthropogenic stressors on the system can be expected.

The immediate aftermath of an oil spill of the magnitude of EVOS is an anthropogenic driver that has a truly dominant role in shaping the PWS ecosystem (Figure 4D). In addition to the four stressors and their immediate catastrophic effects, discussed previously, EVOS adversely affected harvesting through the complete shut-down of the salmon fishery. In essence, much of the entire western PWS ecosystem was fundamentally adversely affected by EVOS, particularly by the direct oiling stressor and perhaps by toxicological stressors. Thus, this anthropogenic driver rose to a level of importance during the months and few years after the oil spill that is comparable to the climate/oceanographic drivers. While there may have been some indirect effects on VECs via the trophic structure, the immediate effects were predominately direct.

By contrast, the normal oil spill-related stressors prior to or well after a major spill (Figure 4E) are substantially below levels that could cause even medium-level effects on the PWS VECs. While routine oil releases occur from boats and shipping, many petroleum storage facilities were breached by the 1964 earthquake (Kvenvolden et al. 1993) and continue to release PAHs into the PWS environment (Page et al. 1995), and remnant sources of EVOS oil remain in subsurface sediments (Short et al. 2006; Michel et al. 2006; Taylor and Reimer 2007; Harwell et al. 2010), the magnitude of the oiling, chemical contamination, and physical disturbance stressors caused by these sources are extremely low relative to their magnitude soon after the spill and relative to the various natural drivers/stressors associated with climate, oceanographic, and geomorphological processes, discussed above. In essence, other than in the months to few years after a major spill, oil spill-related stressors and effects are quite lost in the noise of natural variability in the climatic and physical oceanographic processes of the GOA and PWS and their associated effects on the biota.

SYNTHESIS AND SUMMARY

The dominance of natural drivers and processes in shaping the structure and functioning of the larger GOA and PWS ecosystems is an important conclusion from this ecosystem conceptualization. The CEMs presented here illustrate the dominant role of climatic and oceanographic processes compared to the other natural processes and the anthropogenic drivers and stressors affecting the PWS; this dynamic is more fully described in Stabeno et al. (2004), Mundy (2005), and Weingartner (2007).
Figures 5A–B provide a snapshot of the CEMs that allows ready comparison and characterization of relative importance across drivers/processes and, by so doing, achieves our primary objective for the CEM-development process. Clearly, physical processes and their natural variability dominate PWS ecological attributes in terms of abundance, productivity, composition, and variability. PWS is tightly coupled to the GOA and the larger North Pacific Ocean system. Climate and physical/chemical processes and their natural variability dominate PWS ecological attributes in terms of abundance, productivity, composition, and variability. PWS is tightly coupled to the GOA and the larger North Pacific Ocean system. Climate and physical/chemical processes and their natural variability dominate PWS ecological attributes in terms of abundance, productivity, composition, and variability. PWS is tightly coupled to the GOA and the larger North Pacific Ocean system.

**Figure 5.** Comparisons of the Conceptual Ecosystem Models across natural and anthropogenic drivers. Each of the natural or anthropogenic driver-specific CEMs is shown schematically, summarizing the information shown in the individual CEM. Figure 5A summarizes the information for natural drivers reported in Figures 3A–3E, and Figure 5B summarizes the information for anthropogenic drivers reported in Figures 4A–4E. The same construct is followed as in the CEMs, with the top tier of each graphic showing the driver, middle tier reflecting the stressors for that driver, and lower tier the components of the trophodynamical model. The location of each stressor and trophodynamical component is identical to the associated CEM. For example, in Figure 5A, Climate Processes (identified by the bold rectangle labeled “C”), the top left stressor is salinity, the next stressor to the right is temperature, and so on (derived from associated Figure 3A). Stressor and trophodynamical component symbols having dominant roles are filled with red; high stressors or trophodynamical components are filled with striped blue; medium stressors or components are filled with cross-hatching; and low or no stressors are open symbols. (Continued)
oceanographic processes, and to a lesser degree geomorphological processes, are all coupled, reinforcing and enhancing their importance to PWS. Natural intra- and inter-annual variability in these processes causes the high variability in the biological components.

As an example of how this comparative graphic can be used, consider the climate and oceanographic processes (Figures 3A and 3B): variability in nutrients, which is controlled by the salinity and temperature regimes, can cause high variability in pelagic primary productivity, which in turn can cascade throughout the pelagic-based trophic structure. Similarly, benthic primary productivity is most affected by the geomorphological driver (Figure 3C), especially via physical changes of the ITZ and STZ caused by earthquakes. By contrast, none of the anthropogenic drivers dominate primary productivity; for example, the magnitude of the stressor nutrients within the anthropogenic driver development does not rise to the level of the magnitude of the stressor nutrients that the climatic/oceanographic natural processes can cause, and the habitat alteration stressor from development does not rise to the level of the habitat alteration caused by the Great Earthquake. Indeed, in both cases, there would have to be tremendously greater magnitude of nutrient or habitat alteration stressors resulting from human activities to rise to those levels of importance, far beyond what is a reasonable expectation for human activities in PWS. Similarly, Figures 5A and 5B also help visualize how much of an increase in a stressor would be needed to trigger high- or dominant-level effects; for example, the immediate aftermath of EVOS rose to that level, but no other current or plausible future anthropogenic stressor would do so, with the sole exception of the potential...
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for over-harvesting of fisheries resources affecting the higher levels of the pelagic trophic system (Figure 4B).

In general, these graphical CEMs allow articulation of a diversity of hypotheses about the PWS ecosystem, each of which can be explored through further investigations in the literature, development of quantitative models that explore particular relationships identified in the CEM, or conducting new scientific investigations. For those cases in which a quantitative model is developed, the CEM can also provide very useful guidance in identifying the sensitivity analyses or specific model scenarios to conduct. An example of this application of a CEM is seen in the suite of scenarios and sensitivity analyses that were conducted in the toxicological risk assessment of PAHs and sea otters in PWS (Harwell et al. 2010). But a particular utility of the comparative graphics of Figures 5A and 5B is a synoptic view of what truly matters to the PWS ecosystem, versus what is only important, versus what is not at all that important to the ecosystem’s structure and functioning. This can be an effective communications tool for scientists and non-scientists alike, and should have particular utility for decision-makers, whether in assisting decisions about allocations of research resources, evaluating effects of human activities, or anticipating future management options.

A second important result from this CEM development is the integration of the trophodynamic model into this class of risk-based CEM. This integrated CEM illustrates how direct driver-stressor-effects on VECs can be propagated through indirect effects to other ecological attributes of the PWS ecosystem, highlighting the potential for bottom-up and top-down cascading effects for this ecosystem. This extension of the driver-stressor-effect conceptual model construct developed by USEPA (2002) should have significant utility for other CEM development activities.

Trophic relationships mediate the dominating influence that climatic and oceanographic processes have on the PWS and GOA ecosystems. Cascading effects in PWS are largely driven by bottom-up processes, in which major changes to the fundamental energetic base of the trophic structure are determined by climatic and/or oceanographic variability, which causes effects on the primary and secondary productivity of the Sound. These changes in trophic dynamics propagate or cascade throughout the ecosystem through major impacts on the planktivorous forage-fish populations (e.g., Pacific herring) and consequently on their predators, particularly the large fish, marine birds, and marine mammals. This dynamic is discussed more fully in Mundy (2005) and elsewhere (e.g., Mantua et al. 1977; Finney et al. 2000; Cooney et al. 2001a; Eslinger et al. 2001; Miller et al. 2005; Lees et al. 2006) but is captured here graphically in the CEM. The breadth of this bottom-up cascading effect exceeds the top-down cascades from loss of a top predator seen in other ecosystems (e.g., Paine 1980), because the fundamental bases of the entire trophic structure, the primary producers, are dominantly controlled throughout the PWS ecosystem by these coupled physical processes.

A third important result from the CEM development process is consensus that the initial impacts of the 1964 Great Alaska Earthquake and the Exxon Valdez oil spill and its clean-up activities rose to a level of importance comparable to that of the natural physical processes in affecting the overall condition of the PWS ecosystem. The extensive vertical displacements by the earthquake fundamentally caused massive habitat alteration of the coastal zones throughout PWS. In essence, the entire ITZ
was annihilated, and previously submerged or upland habitats suddenly became intertidal. Consequently, at the local scale, coastal habitats were permanently changed, but a new regime emerged after a period of a few years to a decade in which the overall PWS ecosystem essentially recovered. Likewise, for a similar period of time after the *Exxon Valdez* oil spill, anthropogenic factors were as dominant in controlling the ecosystem as natural variability is under more normal circumstances. However, following the spill-aftermath period, PWS also essentially recovered from EOVS, and anthropogenic factors again have considerably less influence on the PWS ecosystem than do natural processes. Nevertheless, as human presence in PWS is expected to continue to increase in the future, following the trends of the last two decades, the relative role of anthropogenic drivers on the health of the Prince William Sound ecosystem will likely grow in importance.

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