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Temporal Variability of Benthic Communities in
an Alaskan Glacial Fjord, 1971-2007

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ABSTRACT: Temporal trends of deep subtidal macrofauna in Port Valdez, Alaska, were assessed with respect to multiple environmental stressors. Effects from a magnitude 9.2 earthquake in Prince William Sound, Alaska, 1964, were reflected in recolonization of the basin of the fjord, increased abundance and number of taxa over time, and moderately increased variability in abundance through 1990, stabilizing 26 years after the earthquake. Long-term climatic variability and local physical processes were important sources of spatial and temporal variability. Correlative evidence suggests that indirect effects of juvenile salmon from a shoreline salmon hatchery and deposition of adult salmon carcasses moderately enhanced deep basin benthic communities. Effects on the deep benthos from a marine oil terminal were negligible. Overall, faunal trends deviated from the stability expected for benthic communities in other fjords. Physical characteristics of the fjord were important in mediating the effects of stressors and in delaying the readjustment process.

Keywords: Benthos; Earthquake; Port Valdez; Prince William Sound; Marine Oil Terminal; Multiple Stressors; Disturbance; Long-Term Monitoring; Climate Change.

1. Introduction

The coastal fringe is a multiple-use region where frequent environmental perturbations from natural and anthropogenic stressors can have large, long-lasting effects (Lindegarth and Hoskin, 2001). Human activities can result in temporally persistent changes and stress in coastal environments through disturbance as varied as nonindigenous species introductions, alteration of drainage patterns by industrial and

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urban development, dredging, and waste disposal (Nichols, 1985; Nichols and Thompson, 1985; Pearson and Barnett, 1987; Burd et al., 2000; Perus and Bonsdorff, 2004). Changes in nearshore environments often reflect increasing stress from urban growth and development with the direction of change towards greater habitat loss and long-term disturbance to marine communities (Schiff et al., 2000). In view of large-scale changes in the marine environment resulting from climate change, human activities, and landscape-scale changes, understanding how communities vary in response to stressors becomes critical.

Assessment of disturbance in marine communities is complicated by multiple stressors acting and interacting over varying spatial and temporal scales (Blanchard and Feder, 2003; Hewitt et al., 2005). Preferably, undisturbed community characteristics and information on natural sources and directions of change should be available prior to a disturbance (Nichols, 1985). This is difficult since marine communities are continually adjusting to long-term change from varied sources of stress such as nonindigenous species introductions, global climatic change, global spread of contaminants, urbanization, and increasing resource use (Steneck and Carlton, 2001; Dojiri et al., 2003; Hewitt et al., 2005). Small, localized disturbances from human activities can often be readily identified (Blanchard et al., 2002, 2003; Blanchard and Feder, 2003) whereas determination of community readjustment from perturbations large enough to impact whole marine ecosystems (Josefson and Rosenberg, 1988; Austen et al., 1991; Lay et al., 2005) is more difficult. Although the effects of stressors cannot always be predicted, long-term studies of disturbed systems provide a means to gain insights into the responses to stress and temporal variability of marine communities and long-term trends (Hawkins et al., 2002; Whomersley et al., 2007).

Physical and ecological characteristics of glacial fjords result in strong environmental sensitivity to natural and anthropogenic stressors. Deep basins in glacial fjords are sheltered environments with restricted exchange with oceanic water and are highly stratified with only seasonal mixing of deep water (Muench and Nebert, 1973; Jewett et al., 1996; Burd et al., 2000; Renaud et al., 2007). The restricted circulation and stratification in silled-fjords limits larval dispersion, nutrient exchange, and deep water renewal as well (Jewett et al., 1996; Josefson and Rosenberg, 1988; Burd et al., 2000;

Molinet et al., 2006; Renaud et al., 2007). The fine glacial sediments deposited in glacial fjords form unstable slopes, bury juvenile and adult macrofauna, and dilute particulate organic carbon (POC) (Görlich et al., 1987; Feder and Jewett, 1988; Holte et al., 1996; Wlodarska-Kowalczyk and Pearson, 2004; Renaud et al., 2007). Fluxes of organic carbon to deep basins of fjords may be on the order of $1-3 \text{ g C m}^{-2} \text{ year}^{-1}$, as in the Balsfjord in Norway and Port Valdez, Alaska, resulting in carbon-poor benthic systems with low infaunal abundance and biomass (Feder and Jewett, 1988; Wlodarska-Kowalczyk et al., 1998; Oug, 2000; Renaud et al., 2007). Spatial gradients in fauna and community structure may show little change on decadal scales but the sensitivity of fauna to long-term climatic change is unknown (Renaud et al., 2007). As a result of their physical and ecological characteristics, glacial fjords can be very sensitive to anthropogenic disturbance (Josefson and Rosenberg, 1988; Holte et al., 1996; Burd et al., 2000; Blanchard and Feder, 2003; Renaud et al., 2007). The restricted circulation and thus, isolation of deep basins of glacial fjords contributes to their importance as sites for monitoring long-term change (Josefson and Rosenberg, 1988; Holte et al., 1996; Renaud et al., 2007).

A 35-year investigation of the deep-subtidal macrofauna in Port Valdez, Alaska, provides the opportunity to examine the temporal variability of benthic organisms in a glacial fjord during a period with large environmental changes. Environmental perturbations in the study area include a major earthquake in 1964 and increasing anthropogenic stresses (1971-2005) (Feder and Jewett, 1988; McRoy, 1988; Wiegiers et al., 1998). Regional climatic variations have been identified as key factors for ecological processes in the Gulf of Alaska and Prince William Sound (PWS) ecosystems (Mundy and Spies, 2005) contributing to temporal variability of infaunal communities in Port Valdez and PWS. Additionally, limited responses of fauna to short-term increases in sediment hydrocarbons have been observed in shallow sediments adjacent to the marine oil terminal in Port Valdez (Blanchard et al., 2002). Objectives of this study were to examine the macrofaunal community in the deep basin of the fjord from 1971 to 2007 to determine if temporal variability represented biologically significant deviations from the stability expected of fjord-basin communities and to gain insights into the influences of climatic variability, natural gradients, and stressors on variability in community structure.

2. Study area

Sampling occurred in Port Valdez, a glacial outwash fjord in the northeastern corner of PWS (Hood et al., 1973; Colonell, 1980b; Shaw and Hameedi, 1988) (Figure 1). Port Valdez has two sills (at 120 and 200 m depth) and a relatively flat bottom in the deep basin varying between 230-250 m depth. In summer, positive estuarine circulation occurs within surface waters to about 15 m (Muench and Nebert, 1973; Sharma and Burbank, 1973; Colonell, 1980a). The counterclockwise movement of water is slow ($< 5 \text{ cm sec}^{-1}$) with a residence time estimated as 40 days. Deep-water layers below sills ($> 120 \text{ m}$) have little exchange with upper water layers in summer but are well mixed in winter (Colonell, 1980a). The sediment is dominated by silt and clay fractions carried to the fjord in glacial melt water from the surrounding mountains. Seasonal variations in sediment flux are large ranging from less than $5 \text{ mg cm}^{-2} \text{ day}^{-1}$ in winter up to $48 \text{ mg cm}^{-2} \text{ day}^{-1}$ in summer with highest sediment fluxes observed in the eastern end of the fjord (Feder and Matheke, 1980; Fig. 2). Annual sedimentation rate at the eastern end of the fjord was estimated to be 13.5 cm yr^{-1} but $< 1 \text{ cm yr}^{-1}$ at the western end (Naidu and Klein, 1988). Macrofaunal communities in the fjord's basin demonstrated relatively low numbers overall and moderate gradients in community structure associated with high sediment loads from glacial rivers (Feder and Matheke, 1980; Feder and Jewett, 1988). An east to west division of faunal communities was related to sedimentation of fine glacial sediments corresponding to the general position of the seasonal sediment plume from glacial runoff in the fjord (Fig. 1) (Feder and Matheke, 1980; Feder and Jewett, 1988).

A magnitude 9.2 earthquake in March, 1964, caused catastrophic disturbances to all marine communities in PWS (Haven, 1971; Hubbard, 1971; Stanley, 1968). The intertidal and subtidal benthic communities of the study area were impacted by scouring from the tsunamis and catastrophic sediment slumping (Coulter and Migliaccio, 1971; McRoy, 1988; Sharma and Burbank, 1973; Naidu and Klein, 1988). Displaced sediments were deposited in the basin of Port Valdez, directly impacting benthic organisms through burial.

Anthropogenic stresses on the marine environment in Port Valdez increased greatly over the 35-year investigation (McRoy, 1988). As the northernmost, ice-free port available for large vessel traffic, Port Valdez was selected to be the site of the marine oil terminal serving as the terminus for the Trans-Alaska pipeline which became operational in 1977. Discharge of treated ballast water from the oil terminal is a continuing stress to some shallow-water biological communities adjacent to the oil terminal (Blanchard et al., 2002, 2003). Oily ballast water is unloaded from tankers at the oil terminal, treated onshore to remove hydrocarbons, and discharged into the fjord through a diffuser pipe at 60m to 80 m depth. Discharges are decreasing due to the declining volume of oil transported (Blanchard et al., 2002; Richardson and Erickson, 2005). A salmon hatchery located on the south side of the fjord, downstream from the oil terminal, began commercial operations in 1982 with first returns in 1983. Over 200 million salmon fry are now raised and released every year with returns of more than 10 million adult fish (predominantly pink salmon *Oncorhynchus gorbuscha*) (White, 2008). There are too many returning adult salmon to fully harvest, so many salmon die in the fjord and their carcasses are deposited in the intertidal or settle on subtidal sediments. Growth of the City of Valdez and associated urban development altered nearshore habitats largely through urban development and industrialization such as construction of roads, docks, and a gas refinery (Wiegers et al., 1998; Blanchard and Feder 2003). Ecosystem stress in the fjord increased through various means including urban discharges and uncontrolled urban runoff, habitat alterations, increased marine vessel traffic, and continuing nearshore development (McRoy, 1988; Wiegers et al., 1998; Blanchard and Feder, 2003).

3. Methods

Subtidal fauna were first sampled in Port Valdez in 1971. Six stations sampled over the study period comprise a transect down the center of the fjord with three replicate samples collected at sites on the transect in September 1971 and generally five from late summer to fall in 1976-1977, 1980 to 1982, 1985, 1987 and annually since 1989 to 2007 (not all sites were sampled every year) (Fig. 1). This transect encompasses a gradient in sedimentation rates and environmental processes from the head of the fjord (where

glacial rivers enter the fjord and suspended sediments are highest) to the fjord mouth. Sediment for faunal samples was collected with a van Veen grab (0.1 m^2), washed over a 1.0 mm screen, and fauna preserved in 10% buffered formalin. Macrofauna (infaunal invertebrates retained on 1.0 mm mesh sieve) were identified to the lowest taxonomic level practical, mostly to genera or species, counted, and weighed. Faunal identifications were aggregated to the family level or higher for all analyses because of taxonomic uncertainties and changes in identifications from the early years of the study (1971-1980) to the present. While analysis of more detailed taxonomic information is preferable, the loss of information due to aggregation to family is not too great and ecologically relevant trends will still be apparent (Feder and Blanchard, 1998; Wlodarska-Kowalczyk and Kedra, 2007). Species identifications are noted in the text where possible. In 2002, field sampling also included occupation of many sites from the fjord-wide grid established in 1971 (Fig. 1).

Faunal measures calculated include average abundance (individuals m^{-2}), wet weight biomass (g m^{-2}), and total number of taxa (includes family or unique higher taxonomic categories). Average abundance and biomass for each year represent the averages for stations on the deep-basin transect for each year. The tabulated statistic total number of taxa was calculated as the number of taxa found within a year (over all stations combined) whereas geostatistical modeling relied on the number of taxa per station per year.

Nonmetric multidimensional scaling (MDS) was used to elucidate community-level changes in family abundance estimates over time. To assess the changes in the faunal relationships, surveys from 1971, 1976, 1981, 1985, 1990, 1995, 2000, and 2005 were analyzed. Bray-Curtis similarity coefficients (Bray and Curtis, 1957) were calculated between the individual stations for each year using $\ln(X+1)$ -transformed mean family abundance. MDS was applied to the resulting similarity matrices using the PRIMER software package to assess similarities of stations between years (Clarke and Gorley, 2001). The ANOSIM routine tested for differences between years and the eastern and western stations (as determined by Feder and Matheke, 1980). The SIMPER routine of PRIMER was used to determine contributions of individual taxon categories to year groups.

Inclusion of the fjord-wide sites sampled in 1971 and 2002 allowed for direct comparisons to be made in the abundance and distribution of selected families. Bubble plots and bar charts of the abundance with 95% confidence intervals of the selected fauna were generated to assess changes in the distributions of fauna. Two-way ANOVA was used to assess differences between years and eastern and western fjord stations.

Spatio-temporal modeling was applied to assess changes over space and time in macrofauna abundance, biomass and the number of taxa (Stein et al., 1998). The statistical program R (www.r-project.org) and the spatial tools in the library GeoR (Ribeiro and Diggle, 2001; <http://cran.r-project.org/>) were used to perform geostatistical analysis of the biotic variables. The data were average abundance, biomass, and number of taxa for each station by year. Only those stations on the transect along the center of the fjord were used for spatio-temporal modeling (Fig. 1). The suite of stations sampled over time represents a one-dimensional measure of distance so distance and time were used to model changes in faunal parameters. The correlation structures of the variables were modeled with the spherical model (Cressie, 1993). Abundance values were $\ln(X+1)$ -transformed and biomass $\ln(X)$ -transformed to meet the assumption of normal errors and all data were detrended by modeling trends as a polynomial functions of distance and year. Contour plots of back-transformed predicted values from the spatial models are presented.

Spearman's nonparametric correlation coefficient was used to determine associations between biotic variables and measures of anthropogenic stress, weather variables, and a climatic index. Biological indices used include average abundance and biomass, and total number of taxa per year. Available measures of anthropogenic stress were salmon fry releases (1982-2007), adult salmon returns (1983-2007), and average total aromatics (PAH: 1976, 1977 (different deep stations for 1976 and 1977 but also representing a transect down the fjord), 1980-1982, 1985, 1989-2007). The data on salmon fry releases and adult returns were from annual reports to the State of Alaska (Alaska salmon enhancement program annual reports available through Alaska Dept. Fish and Game, Juneau, AK; e.g., White, 2008) and data for PAH (the sum of 18 polycyclic aromatic hydrocarbons) were from the long-term monitoring study in Port Valdez (Blanchard et al., 2002) (Table 1). Measures of weather and regional climatic

variability include average annual temperature, total precipitation, and annual snowfall from the Valdez weather station (<http://climate.gi.alaska.edu/>) and the yearly average of the Pacific Decadal Oscillation index (PDO) (www.aoss.org). The PDO reflects anomalies in sea surface temperature (with positive anomalies representing warmer water) and is a measure of climatic variability strongly associated with ecological processes and faunal changes in the northern Pacific ocean (Mundy and Spies, 2005; Pinchuk et al., 2008).

4. Results

A total of 11 phyla encompassing 77 families were identified. Polychaetes and bivalves comprised 64% and 22% of the total numbers of individuals, respectively, for all years combined. The highest abundance occurred in 1987 with an average of 589 ind. m⁻², the highest biomass value was in 2005 with 33.79 g m⁻², and the highest total number of taxa (family or greater) across the transect occurred in 1997 with 52 taxon categories followed by 1976 with 51 categories recorded (Table 1). The lowest abundance was in 1980 with 156 ind. m⁻², lowest biomass was in 1985 with 7.02 g m⁻², and the lowest number of taxa was in 1971 with 29 taxon categories identified.

The MDS ordination suggested a high level of similarity among years and sampling locations (Fig. 3). Nevertheless, separations by year were apparent as sampling locations for 1971 and 1976 grouped by year while stations for 1981 and 1985 were mixed together forming a separate group, as was also true for 1990 to 2005. ANOSIM indicated that the year groupings were significant as the overall $R = 0.563$ ($p = 0.001$). The multiple comparisons supported the observed groupings with $R = 0.159$ ($p = 0.084$) for the comparison between 1981 and 1985 suggesting weak differences at most, $R \leq 0.169$ ($p \geq 0.212$) for comparisons between the years 1990 to 2005 indicating no differences between years, and $R \geq 0.426$ ($p \leq 0.036$) indicating highly significant differences for all other comparisons. The MDS ordination also supported an additional separation of eastern and western fjord stations (as subgroups) as the ANOSIM overall $R = 0.583$ ($p = 0.001$) for an overall comparison of east vs. west stations (see Fig. 1 for definition of division boundaries). Support from multiple comparisons was weaker due to sample size limitations. For the east vs. west comparison by year, $R = 0.583$ for 1971

(small sample with too few permutations for accurate determination of the p-value), $R = 0.583$ for 1976 (small sample), $R = 0.319$ ($p = 0.011$) for 1981 to 1985, and $R = 0.248$ ($p = 0.033$) for 1990 to 2005.

Numerically dominant families determined by SIMPER for the multivariate year groupings demonstrated large temporal changes. In 1971, dominant species in the fjord included the polychaete family Capitellidae (frequently *Heteromastus filiformis*), a family known for opportunistic behavior, which comprised 21% and 34% of overall abundance in 1971 and 1976, respectively, with abundance dropping to 6% of total abundance in 1981 and 1985 and 7% in 1990 to 2005 (1990, 1995, 2000, and 2005) (Fig. 3). The polychaete family Spionidae was moderately abundant in 1971 comprising 12% of overall abundance but was infrequent in later years as abundance was 1% or less of total abundance in 1976 and later. Cumaceans of family Leuconidae (largely *Eudorella emarginata*) comprised 11% of abundance in 1971, 7% in 1976, and 2% from 1981 to 2005. The abundance of polychaetes of family Lumbrineridae (*Lumbrineris* spp. and *Ninoe gemmea*) was moderate in 1971 comprising 9% of total abundance, higher in 1976 at 11% of total abundance but declined to 4% in 1981 and 1985 and 6% in 1990 to 2005. Bivalves of family Thyasiridae (*Adontorhina cyclia*, *Axinopsida serricata*, and infrequently, *Thyasira flexuosa*) were not abundant in 1971 comprising only 2% of abundance but increased to 7% in 1976, 24% in 1981 and 1985, and 18% in 1990 to 2005. The polychaetes Oweniidae (primarily *Galathowenia oculata*) and Trichobranchidae (mostly *Terebellides stroemi*) were absent from the survey transect in 1971. Oweniid polychaetes were also absent in 1976 but present in 1981 and 1985 with 4% of total abundance and 6% in 1990 to 2005. Polychaetes of family Trichobranchidae were 4% of total abundance in 1976, 8% in 1981 and 1985, but only 2% in 1990 to 2005. The polychaete family Nephtyidae (numerically dominated by *Nephtys punctata*) was present all years in moderate abundance comprising 10% of total abundance in 1971, 4% abundance in 1976, 4% of total abundance in 1981 and 1985, and 6% total abundance in 1990 to 2005.

Changes in abundance and distributions of selected macrofauna families demonstrated significant changes over time between the stations sampled over the whole of the fjord in 1971 and 2002. Bubble plots of abundance demonstrate that the

polychaetes Maldanidae, Paraonidae, and Trichobranchidae were sparse in the fjord in 1971 but abundant and distributed throughout the fjord in 2002 (Fig. 4). The bivalves Thyasiridae occurred throughout the fjord in 1971 but in low abundance, as compared to 2002. The change in abundance for these taxon groups represents a 15-fold increase in abundance from 1971 to 2002 for Maldanidae and 8-fold, 13-fold, and an 8-fold increases for Paraonidae, Trichobranchidae, and Thyasiridae, respectively. Two-way ANOVA indicated significantly lower abundance values in 1971 than in 2002 for Maldanidae, Trichobranchidae, and Thyasiridae (Fig. 4). Average abundance of Paraonidae was significantly lower for the western stations than for the eastern sites and in 1971 as compared to 2002. The cumacean family Leuconidae (mostly *Eudorella emarginata*) was abundant in most of the fjord in 1971 with lower abundance in the eastern fjord but in 2002, the cumaceans were more abundant along the margins of the fjord than in the basin (Fig. 4). Leuconidae abundance in 1971 was 2 times that of the abundance found in 2002 with significantly higher abundance at the western stations in 1971 as compared to the other categories. Ophiuroids (mostly *Ophiura sarsi*) were common in 1971 in the western deep basin but were absent in 2002 (Fig. 4). In both years, the ophiuroid family Amphiuridae was moderately abundant at a few sites and particularly abundant adjacent to a small, outwash delta on the southern edge of the fjord. One polychaete family, Oweniidae (largely *G. oculata*) demonstrated particularly dramatic temporal changes in distribution. Although oweniid polychaetes were absent from the deep basin of the fjord in 1971, they occurred in very low abundance at one site in Valdez Arm just outside the fjord (Fig. 5). Comparisons of rank-transformed abundance indicated significant differences between 1971 and 2002. Oweniid polychaetes were still relatively uncommon in 1976, more common in 1982, and by 2002, they were a dominant member of the benthic community.

Spatio-temporal modeling demonstrated significant trends in abundance, biomass, and the number of taxa from 1971 to 2007. The kriging plot (the graphic summary of the spatio-temporal model) for abundance indicated increasing abundance over time and with distance from the west (station 50 near the mouth of the fjord: 0 km) to the east (station 11 near the head of the fjord: 14 km) with low abundance indicated in the lower left of the plot by orange and yellow and high values in the upper right corner shown in

blue and purple (Fig. 6). The whisker plot by year demonstrated more variable abundance through 1990 ($SD = 139.1 \text{ ind. m}^{-2}$ based on overall means; Table 1), as compared to 1991 to 2007 ($SD = 77.1 \text{ ind. m}^{-2}$), with significantly lower values (shown by the non-overlapping confidence intervals) generally occurring from 1971 to 1990 and an overall trend of increasing abundance. The whisker plot by distance indicates significantly lower abundance mid-fjord and significantly higher abundance at distances $> 11 \text{ km}$. The kriging plot and the whisker plot by distance for biomass demonstrated decreasing values with increasing distance from the west end of the fjord (Fig. 7). The whisker plot of biomass grouped by year showed a negligible increase in biomass over time and negligible differences in variance from 1971 through 1990 ($SD = 7.4 \text{ ind. m}^{-2}$) compared to 1991 to 2007 ($SD = 5.3 \text{ ind. m}^{-2}$). For the number of taxa, the kriging and whisker plots demonstrated increasing number of taxa over time, with a sharp increase in the number of taxa from 1985 through 2007, and decreasing values with distance west to east (Fig. 8). The difference in variability in the number of taxa was negligible from 1971 to 1990 ($SD = 8.0 \text{ ind. m}^{-2}$), as compared to later years ($SD = 6.6 \text{ ind. m}^{-2}$).

Correlation analysis indicated moderate relationships between faunal measures and indices of environmental change. Moderate correlations were observed between biomass and salmon fry releases and adult returns ($\rho = 0.350$ and 0.399 , respectively) and the average PDO and abundance and biomass ($\rho = 0.377$ and -0.311 , respectively; Table 2 and Fig. 9). Negligible to small correlations were observed between releases and returns and abundance ($\rho = 0.229$ and 0.119 , respectively) and the number of taxa ($\rho = -0.269$ and -0.244 , respectively). Correlations between PAH and the biological variables were also negligible to small ($\rho = 0.049$ to 0.292). Correlations between local climatic measures were small for average precipitation and biomass ($\rho = -0.280$), average temperature and abundance ($\rho = 0.250$), and total snowfall and biomass ($\rho = 0.257$).

5. Discussion

5.1 Influences of Environmental Gradients in Fjords and Climatic Variability

The macrofauna assemblage in the deep basin of Port Valdez is characteristic of fauna found in glacial fjords worldwide. Deposit-feeding polychaetes are dominant in

the study area, as found in glacial fjords elsewhere, including the surface-deposit feeding
 owenid polychaete *Galathowenia oculata*, spionid polychaetes (*Polydora* spp. and
Prionospio spp.), and subsurface-deposit feeding polychaetes *Heteromastus filiformis*
 (family Capitellidae) and family Maldanidae (Gulliksen et al., 1985; Holte, 1998;
 Wlodarska-Kowalczyk et al., 1998; Feder and Blanchard, 1998, Burd et al., 2000; Hoberg
 and Feder, 2002; Ríos et al., 2005). Deposit-feeding bivalves found in Port Valdez are
 also common in northern-hemisphere glacial fjords including the families Nuculanidae
 (*Megayoldia/Yoldia* spp. and *Nuculana* sp.) and Thyasiridae (*Axinospida* spp. and
Thyasira spp.) (Holte, 1998). The dominance of deposit-feeding animals is the result of
 the inability of most surface-dwelling fauna to adjust to the reduced availability of carbon
 fluxing to the bottom and high sedimentation rates (Görlich et al., 1987; Holte et al.,
 1996; Wlodarska-Kowalczyk and Pearson, 2004; Renaud et al., 2007). The combined
 influence of seasonal stratification, seasonality of production, early consumption of
 water-column primary production by zooplankton, and dilution of food by glacial
 sediments contribute to the paucity of carbon in benthic systems of glacial fjords (Sargent
 et al., 1983; Cooney and Coyle, 1988; Oug, 2000). Lack of carbon reaching the benthos
 in Port Valdez was evident in the low estimate for annual macrofaunal production (0.3 to
 1.7 g m⁻² yr⁻¹) (Feder and Jewett, 1988) and low abundance and biomass (Table 1).

Macrofauna in glacial fjords are stressed by high sedimentation rates resulting in
 strong gradients in community structure (Holte and Gulliksen, 1998; Wlodarska-
 Kowalczyk et al., 2005). A common trend of increasing abundance and diversity with
 lower biomass towards the head of a fjord reflects the increased proportions of small
 disturbance-tolerant organisms and the greater stress found near sources of glacial
 sediments (Holte and Gulliksen, 1998; Wlodarska-Kowalczyk and Pearson, 2004;
 Wlodarska-Kowalczyk et al., 2005). The general spatial trend associated with
 sedimentation rates and fine sediments was observed in prior studies of Port Valdez
 (Feder et al., 1973; Feder and Jewett, 1988; Naidu and Klein, 1988) where, as also
 indicated by spatio-temporal modeling in the present study, communities in the western
 end had higher number of taxa and biomass and lower abundance compared to the faunal
 assemblage of the eastern end (closest to the major sources for glacial sediments). The
 major faunal trend in van Mijenfjord, a silled fjord in Spitsbergen, reflected disturbance

from fine sediments, and gradients in faunal communities were similar between 1980 and 2001 (Wlodarska-Kowalczyk et al., 2005; Renaud, et al., 2007). Like van Mijenfjord, little temporal change in community structure was reported for Balsfjord, Norway although minor increases in abundance were noted, possibly a result of changes in the composition of pelagic fauna and grazing rates (Oug, 2000). In general, the physical characteristics and sediment gradients in glacial fjords result in the temporal and spatial persistence of gradients in benthic faunal community structure as well.

The Pacific decadal oscillation (PDO) is an index of climate variability associated with ecologically-important changes in physical processes of the North Pacific Ocean and nearshore coastal waters. The PDO contrasts sea surface temperatures between the Central and Northeast Pacific such that when the PDO is positive, sea surface temperatures are elevated in the coastal Northeast Pacific (Royer et al., 2001). The warmer waters of a positive PDO leads to increased rainfall and greater coastal freshwater flow along the Northeast Pacific which may have a number of effects on the ecosystem including strengthening of stratification in the water column in summer (Neal et al., 2002; Mundy and Cooney, 1995; Weingartner et al., 2005). Increased stratification of the water column will initially result in greater primary production but may prevent mixing of nutrients upward from deep water later (Royer et al., 2001). Shifts in ecological processes associated with the PDO variations may influence benthic fauna in Prince William Sound (PWS) and Port Valdez through changes in the timing and volume of annual primary production, grazer availability, grazing rates, flux of nutrients to the benthos, and processes influencing larval survival (Mundy and Cooney, 1995; Beuchel et al., 2006).

Fauna in the deep basin (>150 m) of Port Valdez appear to be sensitive to decadal-scale climatic variability although the pathways through which the PDO may have influenced fauna are unknown. Relationships between the PDO and macrofauna are suggested by the moderate associations of faunal summary measures and the PDO index in Port Valdez ($\rho = 0.38$ and -0.31 , for abundance and biomass, respectively; Table 2). The association between abundance and the PDO index were strongest from 1987 to 2007 with less apparent association from 1971 to 1987 when the benthos was recovering from the 1964 earthquake (Fig. 9) (see discussion below). Most primary production of

Alaskan glacial fjords reaches deep sediments through undigested matter in zooplankton fecal pellets with most production occurring in the spring before glacial melt waters reduce visibility (Cooney and Coyle, 1988; Burrell, 1983). This provides one potential pathway for climatic variability to affect benthic communities as greater rainfall associated with positive PDO values may result in a greater snowpack in surrounding mountains. The increased spring runoff may then enhance stratification resulting in greater spring primary production (Mundy and Cooney, 1995; Royer et al., 2001) and consumption of the increased production by zooplankton and fall of fecal pellets to the bottom would then enhance survival of new recruits in the benthos. Benthic community structure may also be directly influenced by interactions between water temperature and survival of pelagic larvae (Barnett and Watson, 1986; Pearson et al., 1986).

The temporal stability of community structure in a protected, silled-fjord in Spitsbergen (with tidewater glaciers) suggested that benthic fauna were largely influenced by interactions between local hydrography, physical characteristics, and faunal life-history traits and may be resistant to decadal-scale environmental variability (Renaud et al., 2007). Like the macrofauna of Spitsbergen (with tidewater glaciers), the overall community structure of macrofauna in the basin of Port Valdez has not shown great change since 1990 (see discussion below) since overall faunal composition is controlled by the ecological characteristics of the fjord. However, the present study does suggest that fauna in deep basins can be responsive to regional environmental trends through changes in other facets of community composition (abundance and biomass). The increased volume of glacial melt waters and runoff in warmer years from the large watershed in the Chugach Mountains surrounding Port Valdez (a glacial outwash fjord) (which would be absent or reduced in fjords with tidewater glaciers) is likely the source for effects on benthic fauna at depth (>150 m). Thus, sensitivity to climatic change in nearshore communities may be dependent on landscape-scale factors of surrounding watersheds rather than just interactions of oceanographic and biological features within a fjord.

5.2 Effects of the Great Alaska Earthquake in 1964

The greatest perturbation in Port Valdez in recent history was a magnitude 9.2 earthquake in PWS March, 1964. The earthquake was so great as to have impacted every marine community in PWS by topographic changes, scouring by tsunamis, and sediment slumping and resuspension (Coulter and Migliaccio, 1971; NRC, 1971). The deep benthos in Port Valdez was disrupted by the mass sediment slumping triggered by the earthquake and deposition of sediments over the bottom (Coulter and Migliaccio, 1971; Sharma and Burbank, 1973; Feder and Jewett, 1988; Naidu and Klein, 1988). Effects of the catastrophic disturbance in Port Valdez were reflected in differences of community structure among years in the multivariate analyses, the temporal changes in abundance and distributions of fauna, and spatio-temporal modeling (Fig. 3). Additionally, moderately increased variability in abundance (a symptom of disturbance) was apparent for Port Valdez from 1971 to 1989 as also occurred following cessation of sewage-sludge disposal in Liverpool Bay, UK (Fig. 6) (Warwick and Clarke, 1993; Whomersley et al., 2007). The much weaker association of faunal abundance to the PDO index from 1971 to 1989 is additional evidence for the presence of a strong, ecological process in the benthos related to faunal readjustment from the earthquake rather than climate effects (Fig. 9). Since there are no published studies of long-term trends in benthic fauna following a physical disturbance of a magnitude or scale comparable to the 1964 earthquake in PWS, it is difficult to discern to what extent physical characteristics of Port Valdez contributed to delayed recruitment. However, interactions between fauna and physical factors can be expected to influence temporal trends of faunal assemblages since readjustment is determined to varying degrees by hydrodynamics, circulation patterns or restrictions, and other physical features (e.g., Hall, 1994; Molinet et al., 2006).

Faunal readjustment from large disturbances can be a lengthy process in glacial fjords. The benthic community in disturbed sediments in Alice Arm, a silled fjord in British Columbia disturbed by mining activities, was dominated by disturbance-tolerant species until disturbance abated (Burd et al., 2000). Although considerable faunal readjustment occurred three years after cessation of tailing disposal, up to 18 years was required for biota to return to the ambient faunal community in Alice Arm. Faunal changes included introductions of numerous species into disturbed locations where they became dominant members of the macrofaunal assemblage. Initial colonizers responded

quickly to cessation of disturbance but recruitment of stress-intolerant species was delayed (Burd et al., 2000). The temporal trends in Port Valdez were similar in scope to readjustment patterns of fauna in Alice Arm suggesting that large-scale recolonization occurred, as would be expected following a very large earthquake. In the present study, the absence or low abundances of Maldanidae, Oweniidae, Paraonidae and Thyasiridae in 1971 and subsequent redistributions were striking since these organisms are common in muddy sediments in Prince William Sound (PWS) (Figs. 4 and 5) (Feder and Blanchard, 1998; Hoberg and Feder, 2002). Additionally, spatio-temporal modeling indicated that the number of taxa and abundance increased over time, as would be expected following disturbance (Figs. 6 and 8) (Boesch and Rosenberg, 1981; Burd et al., 2000). Disturbance to the faunal assemblage was also suggested by the relative dominance of Capitellidae, a disturbance-tolerant, opportunistic polychaete family, in 1971 and 1976 (Fig. 3). Evidence from faunal trends and spatio-temporal modeling indicates that the macrofaunal assemblage in the basin of Port Valdez reached a point of stability in 1990, 26 years after the 1964 earthquake.

Temporal persistence of effects from physical disturbance on benthic systems is dependent on the scale of disturbance, larval and adult recruit supplies, pre and post-settlement processes for recruits, and other factors (Hall, 1994). Recovery can be rapid when new recruits and adults are readily available even when disturbance is large (Boesch and Rosenberg, 1981; Snelgrove and Butman, 1994; Reise, 2002; Gimenez, 2004). In fjords, however, seasonal stratification of the water column and restriction of deep-water movement by sills in fjords may contribute to the slow recolonization of benthic organisms. The sills of glacial fjords like Port Valdez interfere with larval transport and recruitment, thereby preventing some larvae from reaching the deep basin while sluggish water movement may slow their dispersal within the basin (Muench and Nebert, 1973; Colonell, 1980a; Burd et al., 2000; Molinet et al., 2006). As a result, it can be difficult to predict recovery processes or the time frame required for benthic communities to return to prior environmental conditions and ambient faunal assemblages in fjords. Interactions between fauna, climate variations, and physical characteristics may be even more important when mature fauna are unavailable for larval production and larvae must come from distant sources as might occur with a very large, landscape-scale

perturbation. Such a large reduction of mature, reproducing macrofauna populations may have occurred in PWS following the 1964 earthquake, as suggested by the reduced abundance of fauna in 1971 and delayed recruitment of some otherwise ubiquitous polychaetes in Port Valdez.

5.3 Anthropogenic Stressors

Migratory salmon are an important link between oceans, estuaries, and watersheds wherever they occur (Kline et al., 1990, 1993; Finney et al., 2000; Naiman et al., 2002; Ray, 2005). Evidence for a fjord-wide influence of salmon released from a shoreline hatchery in Port Valdez includes the positive correlations of salmon releases and returns with macrofauna biomass shown in this study ($p=0.35$ and 0.40 , respectively) and the ubiquitous presence of fish bones and otoliths in sediment from the deep benthos (Table 2; A. L. Blanchard, personal observations). The large number of juveniles released into Port Valdez undoubtedly influence benthic systems by feeding on zooplankton thereby altering pathways of energy exchange between ecosystem components with unknown effects on the benthic components of marine ecosystems. Carcasses of adult salmon may directly influence benthic communities by providing an immediate food source for scavenging macrofauna but most carcasses are likely deposited intertidally or in the shallow subtidal with fewer reaching the deep benthos so the pathways through which carcasses may influence fauna in the basin of a fjord are not entirely clear. In freshwater systems, nutrients from salmon carcasses (dissolved or particulate marine-derived nutrients) are dispersed through numerous ecosystem components and multiple pathways (Naiman, 2002; Ray, 2005). Similarly, dissolved nutrients and particulates released by decomposing salmon from the intertidal and shallow subtidal are likely to be dispersed throughout a fjord. Particulate organics and dissolved nutrients indirectly reaching the benthos (e.g., transfers of particulates through water layers as opposed to direct carcass falls) would be available to deposit-feeding organisms in the basin of Port Valdez and the lack of scavenging organisms in the deep benthos suggests that such indirect transfers may be greatest. While the exact pathways for energy and nutrient flow of salmon carcass decomposition products to the deep basin are unknown for Port Valdez, the evidence

1 suggest that a moderate flow (likely through multiple, indirect pathways) is present, as
2 shown from studies of freshwater systems (Naiman, 2002; Ray, 2005).

3 The correlative evidence for associations between faunal measures from the deep
4 basin of Port Valdez and salmon releases and returns suggests small effects at most rather
5 than large changes like the gross organic enrichment caused by fish farming and
6 eutrophication elsewhere (Josefson and Rosenberg, 1988; Muslow et al., 2006).

7 Dominance by opportunistic species or complete loss of species resulting from organic
8 enrichment was not observed in the deep basin of Port Valdez, although deposition of
9 fish wastes from a processing plant adjacent to the City of Valdez led to such conditions
10 in a limited shallow subtidal area (Blanchard and Feder, 2003). Given the tendency for
11 increasing stress in coastal waters (Schiff et al., 2000), effects from hatchery salmon fry
12 releases (~200 million annually) and returns (~10 million annually) (White, 2008) in Port
13 Valdez could lead to large interactions in the future with other stressors and potentially
14 stronger, negative effects.

15 Effects from discharge of treated tanker ballast water from a treatment plant at the
16 marine oil terminal in Port Valdez were not observed in the deep basin. In the present
17 study, average sediment PAH concentrations in the deep basin were low and below
18 concentrations expected to result in alterations of faunal communities (Leung et al.,
19 2005). Hydrocarbon accumulations and associated effects on fauna of Port Valdez are
20 limited as most hydrocarbons are diluted within the water column due largely to the steep
21 slope where hydrocarbons are discharged, depth of the fjord, oceanography, and low
22 quantities of organics in sediment to which hydrocarbons may adsorb (Shaw, 1988).
23 Spatially and temporally limited effects associated with increased PAH were observed in
24 shallower waters within a few hundred meters of the point of discharge of treated ballast
25 water but similar trends in fauna (e.g., increases or gradients in hydrocarbon-tolerant
26 species near the oil terminal) were not noted for deep basin communities (Shaw, 1988;
27 Blanchard et al., 2002, 2003). As indicated by Wake (2002), interactions between
28 effluents and the physical environment are important in the fate of hydrocarbons
29 discharged into the marine environment and with adequate treatment, residual
30 hydrocarbons have very limited effects. Effects of hydrocarbons on fauna in Sullom
31 Voe, Shetland Islands, were strongly influenced by interactions with environmental

gradients and effects were reduced where accumulations were prevented by hydrodynamics (although hydrocarbon deposition and associated effects increased at sites with greater organics) (May and Pearson, 1995). The lack of effects from hydrocarbons in the deep basin of Port Valdez was likewise due to a combination of physical characteristics, oceanography, and treatment of wastes at the ballast-water treatment facility (Shaw, 1988).

6. Conclusions

Trends observed in Port Valdez from 1971 to 2007 suggest an ecosystem in flux. Although the macrofaunal assemblage in the deep basin was generally similar to that of glacial fjords elsewhere, trends in faunal abundance and community structure deviated significantly from the stability expected for glacial fjords. Natural factors were the strongest drivers of spatial and temporal change. Effects on biotic communities from the catastrophic disturbance of the 9.2 magnitude earthquake in 1964 were large and faunal readjustment was the dominant source of variability in the deep benthos from 1971 to 1989. The readjustment process was demonstrated through introductions and subsequent dispersal of macrofauna families in the basin and trends in the spatio-temporal models. Following readjustment from the earthquake, long-term climatic trends were important sources of variability for benthic fauna from 1989 to 2007. Spatial trends in faunal indices were associated with the sediment gradient from the head to the mouth of the fjord as well. Physical characteristics of the fjord (e.g., the sills, basin depth, limited water movement in the basin, and sedimentation rate) were important structuring factors of faunal communities spatially and temporally during the period of faunal readjustment. Releases of juvenile salmon at the hatchery since 1982 and returns of adult salmon were positively associated with macrofaunal biomass suggesting enhancement of the deep benthic fauna. The Valdez marine oil terminal does not measurably contribute to faunal variations in the deep basin largely due to the fjord's physical and oceanographic characteristics. Overall, benthic communities in the deep basin were in a state of flux up to 1990 while a state of greater stability was reached in 1990 that more closely reflected the stability observed in fjord-basin fauna of undisturbed fjords elsewhere.

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Table 1

Table 1. Summary measures from Port Valdez, Alaska 1971-2007. #Stat = number of stations per transect, abund. = abundance, PDO = average annual pacific decadal oscillation index, temp = annual temperature (C), snowfall = total annual snowfall (m), precip = total annual precipitation (m), and N/A = not available. Units for the variables are ind. m⁻² for abundance, g m⁻² for biomass, ng g⁻¹ for PAH, and millions yr⁻¹ for salmon releases and returns.

Year	#Stat	Abun.	SD	Biomass	SD	Total Taxa	PAH	SD	Salmon Rels.	Salmon Ret.	PDO	Temp	Snowfall	Precip
1971	5	207	54	15.99	7.79	29	N/A	N/A	N/A	N/A	-1.29	N/A	N/A	N/A
1976	5	494	245	16.79	4.56	51	6.9	12.15	N/A	N/A	0.01	3.39	1.98	8.92
1977	5	327	171	21.24	15.50	30	2.8	0.36	N/A	N/A	0.23	3.78	1.59	9.63
1980	5	156	29	31.33	22.61	35	5.8	3.26	N/A	N/A	0.60	3.44	1.76	7.66
1981	6	215	74	11.83	6.98	48	6.4	4.51	N/A	N/A	0.92	4.28	2.37	6.11
1982	6	353	174	14.66	10.31	46	2.3	3.62	8	N/A	0.11	2.67	1.56	6.54
1985	6	212	50	7.02	8.85	37	5.9	1.15	54	0.6	0.45	2.72	1.94	8.61
1987	3	589	287	7.28	1.08	41	N/A	N/A	63	5.6	1.82	4.39	1.95	9.77
1989	5	231	72	9.61	6.76	43	120.2	76.7	132	3.5	-0.18	3.50	2.19	7.95
1990	6	274	71	20.07	27.52	50	235.6	127.7	126	11.1	-0.36	3.17	1.71	13.99
1991	6	355	31	22.51	28.33	50	66.1	37.2	134	6.1	-0.42	4.11	1.72	8.31
1992	5	476	149	21.05	18.25	43	56.8	29.3	91	2.2	0.93	3.56	2.16	13.10
1993	5	450	53	18.27	11.48	49	30.0	13.1	160	1.8	1.42	4.83	2.16	8.72
1994	5	354	37	18.51	12.64	45	39.8	18.5	156	13.3	-0.15	3.61	1.76	8.68
1995	5	387	87	24.50	22.87	48	39.8	18.5	208	6.8	0.64	4.06	1.41	10.08
1996	5	404	42	15.89	11.21	49	29.0	11.7	225	7.8	0.64	3.39	1.29	6.79
1997	5	459	143	14.36	4.19	52	24.7	13.4	190	7.1	1.46	4.89	1.73	5.86
1998	5	337	76	13.28	6.27	41	25.2	12.4	197	4.7	0.25	4.22	1.46	7.05
1999	5	313	41	20.03	9.62	44	22.1	7.1	216	14.6	-1.06	3.33	1.84	8.66
2000	5	260	47	26.16	13.59	44	22.9	7.2	197	12.4	-0.59	4.33	1.58	9.58
2001	5	429	105	20.58	14.42	48	25.9	9.5	204	16.0	-0.56	3.83	1.77	9.94
2002	6	365	69	21.81	20.07	47	22.3	7.7	204	5.2	0.22	4.61	2.14	8.56
2003	3	534	286	13.62	8.79	36	38.2	28.7	208	16.4	0.97	4.72	1.65	6.36
2004	3	381	139	14.04	8.85	37	38.5	26.7	224	11.3	0.35	4.56	1.77	8.98
2005	3	334	85	33.79	20.22	32	41.5	26.5	224	18.4	0.38	4.67	1.90	7.82
2006	3	529	146	18.95	12.45	31	50.3	28.0	218	12.3	0.19	3.11	1.81	6.03
2007	3	481	143	24.40	17.92	35	31.7	14.8	222	14.3	-0.20	3.50	1.20	6.99

Table 2. Spearman correlations (ρ) of benthic indices, measures of anthropogenic stress, and climatic variables, from Port Valdez, Alaska 1982-2007. Values in bold are significant at $\alpha = 0.10$.

Variables	PAH	Releases	Returns	PDO	Temperature	Snowfall	Precipitation
Abundance	0.29	0.23	0.12	0.38	0.25	-0.02	-0.05
Biomass	0.12	0.35	0.40	-0.31	0.03	0.26	-0.28
# Taxa	0.05	-0.27	-0.24	0.06	0.07	0.13	0.06

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Figure 1. Sites sampled for benthic fauna in Port Valdez, Alaska, 1971-2007. The 1971 and 2002 grid sites are shown with the 1971-2007 transect sites identified by their station numbers. The dotted line represents the division between eastern and western stations as described by Feder and Matheke (1980).

Figure 2. Sediment flux in Port Valdez, 1976 To 1978.

Figure 3. MDS ordination of abundance data for the benthos transect sites from Port Valdez, 1971, 1976, 1981, 1985, 1990, 1995, 2000, and 2005. Data are $\ln(X+1)$ -transformed average abundance of infaunal families (ind. m^{-2}). Circles on the MDS plot represent year groupings. Average abundance and percent of total group abundance of dominant fauna, as suggested by SIMPER rankings, are presented for each year grouping.

Figure 4. Bubble and bar plots of the abundance (ind. m^{-2}) of selected fauna from Port Valdez, 1971 and 2002. Bar plots include 95% confidence intervals of average abundance (ind. m^{-2}). The dashed lines in the plots represent the division between eastern and western stations. P-values from ANOVA are given following the comparisons for year (Y), location (L), and the interaction (YxL)

Figure 5. Bubble plot of the abundance (ind. m^{-2}) of the polychaete *Galathowenia oculata* of the family Oweniidae in Port Valdez, 1971 to 2002. The thin dashed lines represent the boundaries for sampling in each year. Abundance data were rank-transformed prior to ANOVA. See legend of Figure 4 for further details.

Figure 6. Spatio-temporal model and whisker plots of abundance (ind. m^{-2}) for deep stations from Port Valdez, 1971-2007. Distances are from station 50 (0 km) in the west near the mouth to station 11 (14 km) in the east near the head of the fjord. Whisker plots are mean abundance with 95% confidence intervals. The dotted lines in the whisker plots are the grand means and the solid lines are estimated curve lines to show the general trends.

Figure 7. Spatio-temporal model and whisker plots of biomass (g m^{-2}) for deep stations from Port Valdez, 1971-2007. See legend of Figure 6 for details.

Figure 8. Spatio-temporal model and whisker plots of the number of taxa for deep stations from Port Valdez, 1971-2007. See legend of Figure 6 for details.

Figure 9. Plot of mean abundance (ind. m^{-2}) for the deep-basin station transect from Port Valdez and the annual mean pacific decadal oscillation index (PDO), 1971-2007. The dashed line indicates 0 for the PDO index. PDO values above the line indicate warm years and values below the line cold years. Major events occurring in the fjord are listed and indicated on the horizontal axis of the plot by an asterisk.

Figure 1

Figure 2

Figure 3

Figure 5

$Y < 0.001$; $1971 < 2002$
 $L = 0.233$
 $Y \times L = 0.233$

Figure 6

Figure 7

ACCEPTED MANUSCRIPT

Figure 8

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Figure 9

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