Exxon Valdez Oil Spill
Gulf Ecosystem Monitoring and Research Project Final Report

Synthesis of Natural Variability in the Nearshore:
Can We Detect Change?

Gulf Ecosystem Monitoring and Research Project 040702
Final Report

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Study History: This project directly addresses the first priority in the Gulf Ecosystem Monitoring Science Plan: detection of change. Implementation of Gulf Ecosystem Monitoring will be guided by the sequence of the goals of the program: to first, attain the ability to detect changes in the environment, then to understand the origin of those changes, to inform about changes and their origins, to use the information to solve problems created by changes, and lastly to predict changes. The ability to detect changes in the environment necessarily relies on the ability to separate natural variability from human-induced changes. This nearshore synthesis project builds on the Science Plan and the design work of Gulf Ecosystem Monitoring and Research Projects 040687 and 030687 “Monitoring in the Nearshore: A Process for Making Reasoned Decisions” and 02395 “Workshop on Nearshore/Intertidal Monitoring”.

Abstract: One of the primary goals of any monitoring program is to detect anthropogenic changes; however natural variability can be so high that it prevents detection of human-induced effects. This project synthesized existing data to identify patterns of temporal variation within nearshore marine habitats in the Gulf of Alaska. I collected 786 time series that were greater than two years in length and from unimpacted (control) sites for 226 species. I compared variability among time series for different taxonomic groups, measures of abundance, tidal height, and substrate type. Temporal variability (CV) of marine populations in the Gulf of Alaska varied widely from 1 to 447% and averaged 89% of the mean, which indicates that detecting human-induced change will be difficult. Differences in variability among taxonomic groups, time series of different lengths, metrics of abundance, most habitats, and life histories, were not detectable indicating no simple directive for the design of a monitoring program. The monitoring program should make efforts to reduce sampling error through stratified and other designs that minimize variability and use preliminary information to establish sample sizes in an effort to increase power to detect change. Understanding variability is a difficult task, but until we tackle it, we will likely not understand or have predictive capabilities in ecological populations and communities.

Key Words: anthropogenic effects, CV, Gulf of Alaska, intertidal, marine, monitoring, natural variability, substrate, time series

Project Data: No new data were collected as a part of this project.

Citation:

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EXECUTIVE SUMMARY

One of the primary goals of the Gulf Ecosystem Monitoring (GEM) program is to detect anthropogenic changes within the four focal habitats in the Gulf of Alaska; however natural variability in these systems can be so high that it prevents detection of human-induced effects. The best indicators of change are ones that are sensitive, but not too sensitive, to change, and have low natural variability. This project investigates which species or environments should demonstrate the lowest variability in order to establish predictions as to which kinds of species or environments should serve as a signal of human-induced change. The results will inform future monitoring activities in the Gulf of Alaska.

Long-term time series data from Gulf of Alaska nearshore populations were collected using datasets and literature identified by Bodkin and Dean in GEM Project # 030687, titled, “Monitoring in the Nearshore: A Process for Making Reasoned Decisions”. Of the 1,104 reports and articles identified by Bodkin and Dean that I surveyed, only 31 included time series with greater than 2 years of data from unimpacted populations and were appropriate for this project. At the time of this report, 786 Gulf of Alaska time series from 226 species were collected and used in analyses. Targeted species include marine mammals, birds, intertidal and benthic subtidal fishes, algae and invertebrates. Life history and natural history information were collected from the literature for the species for which time series were available. For each time series, I calculated proportional variability using the CV and then used this value as the response variable in an analysis of variance (ANOVA) comparing fluctuations among character traits. I compared variability among time series for different taxonomic groups, measures of abundance, tidal height, and substrate type.

Variability in time series differs significantly among taxonomic groups; however, this relationship disappears when only time series that are sampled at intervals close to one year are included. This result suggests that no single taxonomic group has notably high or low variability, and any can be considered when designing a monitoring program. Temporal variability of invertebrates and algae were not significantly different for populations whether abundance was measured as biomass, percent cover or density. Therefore, in designing a sampling program, any of these metrics may be used. Variability in time series differs significantly among tidal heights for algae, with greatest variability in subtidal algae and lowest variability in high intertidal algae. Such a pattern of increasing variability with depth does not occur for invertebrates; however time series from invertebrates in the low intertidal have greater variability than those in the high or mid intertidal or subtidal.

Sheltered and exposed rocky shores, wave-cut platforms, and beaches with varying mixtures of sediments, sand, gravel, cobble, and boulders are the dominant habitats in the Gulf of Alaska region. For algae, there was no difference in temporal variability of populations on either cobble or bedrock substrates. For invertebrates, populations on bedrock substrates had greater temporal variability than those on cobble or soft sediment substrates. Further studies are needed to elucidate the processes that may result in greater variability in bedrock habitats. One factor that may cause differences in temporal population variability among populations is wave exposure. However, I was not able to explore this factor, because authors do not report wave exposure in a

manner that allows for comparisons across studies. Because of the lack of detectable differences among substrates observed in this study, the optimal sampling design for a monitoring program in the Gulf of Alaska may be to sample habitats in proportion to their abundance.

Variability in time series varies substantially within a single species. Time series information is often only available for a single species from a single study and location; however, for a handful of species, many time series are available. *Fucus gardneri* is represented by 106 different time series, and the CV of these time series varies from 3 to 224. Harlequin ducks are represented in 33 different time series, with a range in CV from 26 to 231. Within the invertebrates, *Tectura persona*, *Semibalanus cariosus*, *Lottia pelta*, *Littorina sitkana*, and *Mytilus trossulus* are represented by 15 or more time series with the difference between the maximum and minimum CV ranging from 110 to 282. Harbor seals, sea otters, and Steller sea lions are represented by 22, 24 and 39 time series, with range in CV from 17 to 156, 1 to 203, and 26 to 191, respectively. Therefore, it is unlikely to designate any single species as having high or low variability, as variability seems highly context specific.

Future monitoring programs should be based on stratified and other sampling designs that minimize sampling error and provide consistency across space and time. The CVs found in this study, which ranged from 1 to 447% and were on average around 89%, suggest that probability of detecting human impacts is low. Population variability is the sum of variation due to sampling error within a site and the true temporal variation. Reducing sampling error through rigorous sampling designs can therefore improve the probability to detect change. Because we know so little about population variation and how it changes in response to environmental conditions, monitoring programs should be designed based on preliminary information collected on the species of interest at the locations of interest. Understanding variability is a difficult task, but until we tackle it, we will likely not understand or have predictive capabilities in ecological populations and communities.

INTRODUCTION

“Perhaps the most insidious problem associated with detecting effects stems from the natural variability of biotic assemblages” (Paine et al. 1996).

One of the primary goals of the Gulf Ecosystem Monitoring (GEM) program is to detect anthropogenic changes within the four focal habitats in the Gulf of Alaska; however natural variability in these systems can be so high that it prevents detection of human-induced effects. Distinguishing human-induced effects from natural variability is a difficult and challenging task (Thrush et al. 1994, Paine et al. 1996, Wiens 1996, Marsh 2001, Peterson et al. 2001). The goal of this project is to synthesize existing data to identify, within the nearshore habitat, the environments and species that have less natural variability so that these variables can be included in the monitoring plan. It is not intended that these species and environments would be the only ones included in the final monitoring plan, because other characteristics may necessitate the inclusion of certain environments or species. However, inclusion of environments and species that have less natural variability greatly increases the power to detect anthropogenic influences. This synthesis effort builds on the proposed monitoring structure (Schoch et al. 2002, Bodkin and Dean 2003) and uses existing data within the nearshore in the Gulf of Alaska to identify general characteristics that predict lower levels of natural variability in nearshore marine populations. Such an analysis will be informative not only to GEM, but also to other monitoring programs and the ecological community in general.

Designing a monitoring program requires, in essence, the ability to see into the future, because the data to be collected will be analyzed to examine the consequences of activities in the future. Some activities can be predicted, such as fishing, forestry, and other human uses of resources. However, the timing and location of some events cannot be predicted, such as the *Exxon Valdez* oil spill. In both cases, it is useful to have a baseline of information about the ecosystem and how it functioned before the event in question. In practice, baselines will concentrate on two categories of species: those that people care about and those that are reliable indicators of change (Paine et al. 1996). Selecting the former group of species is relatively easy, because people tend to care about a handful of charismatic and/or commercially important species. In contrast, selecting the latter group of species, those that are reliable indicators of change, can be difficult.

Indicators of change

A knowledge of when and where variances are small would allow for design of powerful monitoring programs (Benedetti-Cecchi 2001), however the range of variance is quite high and unpredictable (Carey and Keough 2002). Natural variability is often viewed as noise, with the non-natural inducer of change viewed as signal. What is desired is a high signal to noise ratio. Individual attributes (such as growth) and indicator metrics relying on the number of taxa (taxon richness, diversity, etc.) have greater power to detect change than population attributes (such as density) or physical-chemical attributes (such as hydrocarbon concentration) (Osenberg et al. 1994, Johnson 1998). Therefore, one immediate lesson is that the GEM monitoring plan should include individual parameters and higher level indicator metrics, but that is not to say that population parameters should not be monitored. Population attributes are often used in monitoring programs because they reflect the ecological consequences of the disturbance and are features of fundamental concern to resource managers and regulatory agencies. The low power of population attributes, compared to individual attributes, is due to their high natural variability. Marsh (2001) demonstrates that the probability to detect a 10% decline in a population of 1000 individuals increases from 0.32 to 1.00 as the variability (coefficient of variation) decreases from 99 to 20. Therefore, a decrease in the variability of the population results in an increase in the ability to detect changes in that population. Osenberg et al. (1994) note that while the average power for population parameters is low, some species will have greater power than others. The goal, in designing a monitoring program, is to identify these species and environments for which population parameters have greater power.

There is much dogma, but little direct evidence, in the scientific literature for which species are the best indicators of change in the nearshore. Paine et al. (1996) recommend focusing on species with local dispersal; however Eckert (2003) demonstrates that marine intertidal and shallow benthic subtidal species with no larval dispersal have greater population variability than species with larval dispersal. Eckert's (2003) study synthesizes 570 time series from 170 species and is unique in the large amount of data that are used to study the relationship between life history characteristics and temporal variability in marine species. More studies like this one would yield predictive information on the range of natural variation for different environments or species that could be used in designing monitoring programs. Paine et al. (1996) also recommend focusing on long-lived species; however there is little information to evaluate this recommendation.

One of the retrospective outcomes of the research on the effects of the Exxon Valdez oil spill in Prince William Sound was that good baseline data and better estimates of spatial and temporal variability may have helped to better quantify effects of the spill on natural populations (Paine et al. 1996). For many species it was unclear whether populations were smaller after the spill compared to before the spill, despite the clear evidence that a great amount of mortality had occurred (Wiens 1996). In the case of sea otters, a survey of otters after the spill showed higher densities than a survey taken in 1985 (Johnson and Garshelis 1995, Garshelis and Johnson 2001). In the case of some seabird species, populations appeared to be larger after the spill than before the spill, providing resounding evidence that spatial and temporal variability in pre- and post-spill surveys was large enough to swamp any effect, even one of such large magnitude as the *Exxon Valdez* oil spill (Wiens 1996). Knowledge of normal rates of annual change can be used to detect if population changes after an impact are greater or less than normal (Boersma et al. 1995). In a review of the future research needs within the field marine ecology, Estes and Peterson (2000) identified understanding spatial and temporal variability as is one of the most pressing topics.

OBJECTIVES

The overall objective of this project is to quantify and compare natural variability in order to establish predictions as to which kinds of species or environments demonstrate the lowest variability and yet serve as a signal of human-induced change. The results will inform future monitoring activities in the Gulf of Alaska. Specific objectives are described below.

1. Collect time series data of Gulf of Alaska nearshore populations.

2. Collect life history and natural history information for the species for which time series information is available (see Objective 1).

3. Quantify and compare natural variability in populations from different environments, including different substrates, exposure regimes, and tidal heights.

4. Quantify and compare natural variability in populations with different life history characteristics, such as life span, trophic level, and development mode.

5. Identify individual species that have low natural variability and could serve as good indicators of change for GEM.

6. Disseminate results of project through presentation at a professional conference and preparation of manuscript to be submitted to a peer-reviewed journal.

METHODS

This project is a data synthesis project. It therefore has two major components: data collection and data analysis. The data collection methods in Objectives 1-2 are described first (*Data Collection*), while the data analysis and methods for Objectives 3-5 are described in the following section (*Data Analysis and Statistical Methods*.)

Data Collection

Long-term time series data from Gulf of Alaska nearshore populations were collected using datasets and literature identified by Bodkin and Dean in GEM Project # 030687, titled, "Monitoring in the Nearshore: A Process for Making Reasoned Decisions". Of the 1,104 reports and articles identified by Bodkin and Dean that I surveyed, only 31 included time series with greater than 2 years of data from unimpacted populations and were appropriate for this project. At the time of this report, 786 Gulf of Alaska time series from 226 species were collected and used in analyses. Data from the literature in graph form was graphically digitized using image analysis software, and tables were entered directly. Each time series is contained in its own text data file and is referenced to a master file, like in a relational database. Data processing and integration were conducted using SAS (v. 9.1). Targeted species include marine mammals, birds, intertidal and benthic subtidal fishes, algae and invertebrates. As a small subset of the total, it is possible that the set of papers used may be biased. Some species and or habitats may be more likely to be monitored than others. The species and habitats therein may not be representative; however, this data set is the best currently available until more time series are generated, and no bias is evidently apparent. As many monitoring programs within the Gulf of Alaska are in their first few years (Kachemak Bay) or still in development (National Park Service), they were not used in this analysis.

Life history and natural history information were collected from the literature for the species for which time series were available. A primary source of information was a relational database that contains taxonomic information as well as information on geographic range, body size, distribution, habitat type, feeding mode, reproductive mode and season, development time, and several other life history characteristics for over 800 marine invertebrate species found on the west coast of North America (Eckert 1999). Literature searches were conducted to find natural history and life history information for many Gulf of Alaska species that were not in the relational database.

Data Analysis and Statistical Methods

Calculation of Variability

Variability is a measure of dispersion about the mean. When making comparisons among different populations across space, time, and different sampling methods, proportional variability is a more appropriate measure of variability than absolute variability because it scales variability relative to the mean. Take a simplified example—two populations have the same standard deviation, 4.23, and two different means, 61.67 and 11.67. The standard deviation and variance do not reflect the dispersion about the mean, whereas the coefficient of variation (CV) ([standard deviation/ mean]·100) does: for the large population it is 7.5 and for the small population it is 39. Another common proportional measure, the standard deviation of logarithm-transformed observations (SD log N), gives similar results to the CV, but cannot be used when the data contains zeros (McArdle and Gaston 1993, 1995). For each time series, I calculated proportional variability using the CV and then used this value as the response variable in an analysis of variance (ANOVA) comparing fluctuations among character traits. The sample size in ANOVA was the number of time series. I conducted a Levene's test (Levene 1960) to evaluate the assumption of homogeneity of variances (Zar 1996), and when this result was significant, I report Welch ANOVA (Welch 1951). Welch's ANOVA uses a highly conservative estimate of degrees of freedom to adjust for this assumption. Post-hoc Tukey tests were used when there were significant differences among greater than two character traits in ANOVA. All means are reported with standard error (SE). These methods were the same as used in the analysis of variability among populations with different developmental modes by Eckert (2003). When information on a character was not available for a time series, the time series was not used in the statistical comparison for that character.

Taxonomic Group

Each time series was categorized by organism type (marine mammals, birds, intertidal and benthic subtidal fishes, algae and invertebrates), and then variability was compared among these groups.

Metric of Abundance

Each time series was categorized by how abundance was quantified over time (percent cover, density, count, biomass). Marine mammal, bird, and fish abundance were predominantly quantified by a single measure of abundance (typically counts), and therefore, were not included in the analysis. However, algae and invertebrate abundance were frequently quantified using diverse measures of abundance that included percent cover, density, and biomass, and the variability of these different measures was compared. One species (*Fucus gardneri*) was represented with many time series using different measures of abundance, which made it possible to compare variability among these measures of abundance within a single species.

Habitat

Information was obtained from the published study or sampling program to determine the habitat in which each time series was collected. Substrate was classified as bedrock, cobble, or soft-sediment. Exposure was classified as exposed or sheltered. Habitat was classified as vegetated (macroalgae, kelp, eelgrass) or unvegetated. Tidal height was classified as high, mid or low intertidal or shallow subtidal (<20 m).

Life History

Life history information was obtained from the literature for each species for which a time series was collected. Life span information was collected as continuous rather than categorical data. Trophic level was classified as basal, intermediate or top. Basal species include autotrophs. Intermediate species include detritivores, suspension feeders, and herbivores. Top species include carnivores and omnivores. Development mode was classified for each species as no planktonic period, short planktonic period, or long planktonic period using the criteria outlined in Eckert (2003).

Species

The CV of all time series for a particular species was pooled, and variability was reported by species within a taxonomic group.

Statistical caveats

Comparing variability is a difficult task (McArdle and Gaston 1992, 1993, 1995). The CV and other measures of variability incorporate natural variability with process noise and observation error (Gerrodette 1987). Ideally, we would separate these error sources; however, because time series are usually unreplicated, that is difficult (Marsh 2001). Time series were assumed to be independent, although they may not be. The CV is estimated with low precision and therefore has low confidence itself because it the ratio of the square root of a variance to a mean and both are estimated with error. Nevertheless, a crude analysis like the one presented here can be a useful tool to identify potential monitoring strategies. Understanding variability is a difficult task, but until we tackle it, we will likely not understand or have predictive capabilities in ecological populations and communities.

Presentation of Project Results

Results of this project were presented at three scientific conferences. Feedback from each was instrumental in project development and completion. I presented a poster at the Alaska Marine Science Symposium, Anchorage, Alaska in January 2005, titled “A synthesis of natural variability in the nearshore: Can we detect change?” I made a presentation at Evolution 2005, a joint meeting of the Society for the Study of Evolution, the Society for Systematic Biologists, and the American Society of Naturalists, Fairbanks, Alaska in June 2005, titled “Assessing natural variability in Gulf of Alaska populations”. I made a presentation at the Western Society of Naturalists meeting in Monterey, California in November 2005, titled “Variability in nearshore Gulf of Alaska populations”.

RESULTS

Taxonomic Groups

Variability in time series differs significantly among taxonomic groups (Figure 1A; Welch ANOVA, df = 4/188.1, f = 15.29, $p < 0.0001$); however, this relationship disappears when only time series that are sampled at intervals close to one year are included (Figure 1B; Welch

ANOVA, df = 4/145.6, f = 1.06, p = 0.3786). Comparing Figures 1A and 1B, the CV decreases for birds and decreases a small amount for invertebrates when only time series sampled at intervals close to one year are included. The high CVs for birds and invertebrates in Figure 1A compared to Figure 1B may be the result of more frequent sampling for birds and invertebrates combined with high population variability at shorter intervals. In contrast, the number of algal time series decreases from 184 to 78 from Figure 1A to 1B; however, the CV is quite similar, indicating that the shorter sampling intervals have similar population variability as the longer ones for this taxon. Using the longer sampling interval (Figure 1B), we can conclude that variability is not statistically different among taxonomic groups.

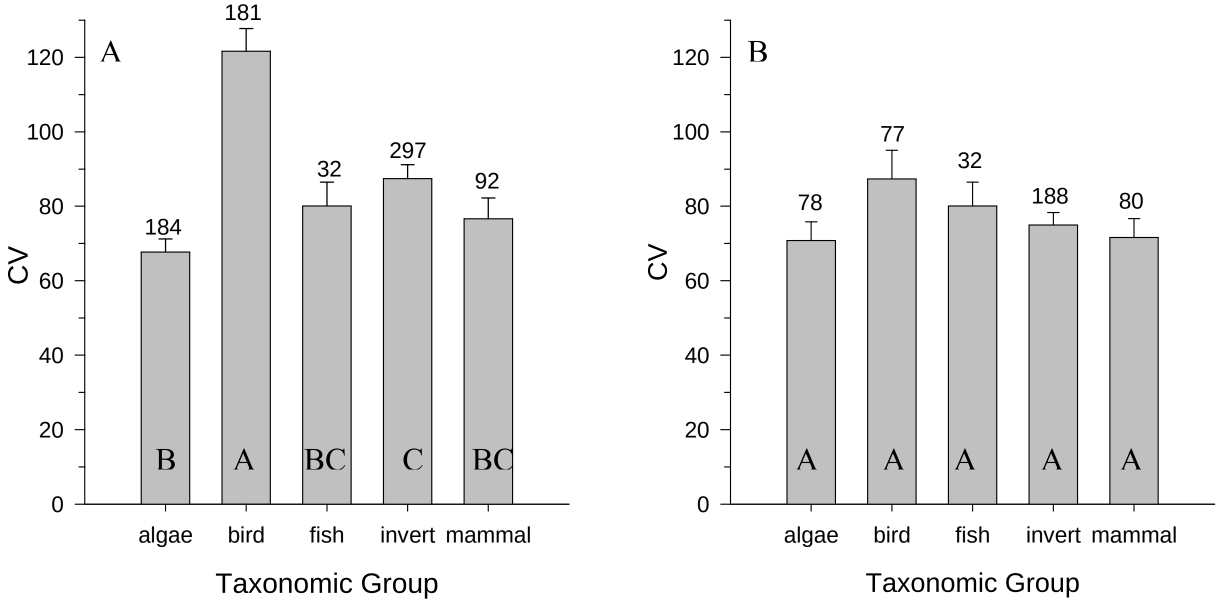

Figure 1. Variability among time series of different taxonomic groups
A) All time series included. B) Time series with intervals close to one year. Numbers above bar indicate numbers of time series, and letters on bars indicate significant differences ($p = 0.05$ Tukey test).

Time series variability was not explained by time series length (number of years sampled) (Figure 2A; Regression slope = 0.2122, $p = 0.6895$). The CV generally increased with a greater number of censuses; however, number of censuses explained just 5% of the variation in CV (Figure 2B; Regression slope = 2.1852, $r^2 = 0.0565$, $p < 0.0001$). The CV generally increased with greater number of censuses per year; however, the number of censuses per year explained just 7% of the variation in CV (Figure 2C; Regression slope = 8.628, $r^2 = 0.0731$, $p < 0.0001$).

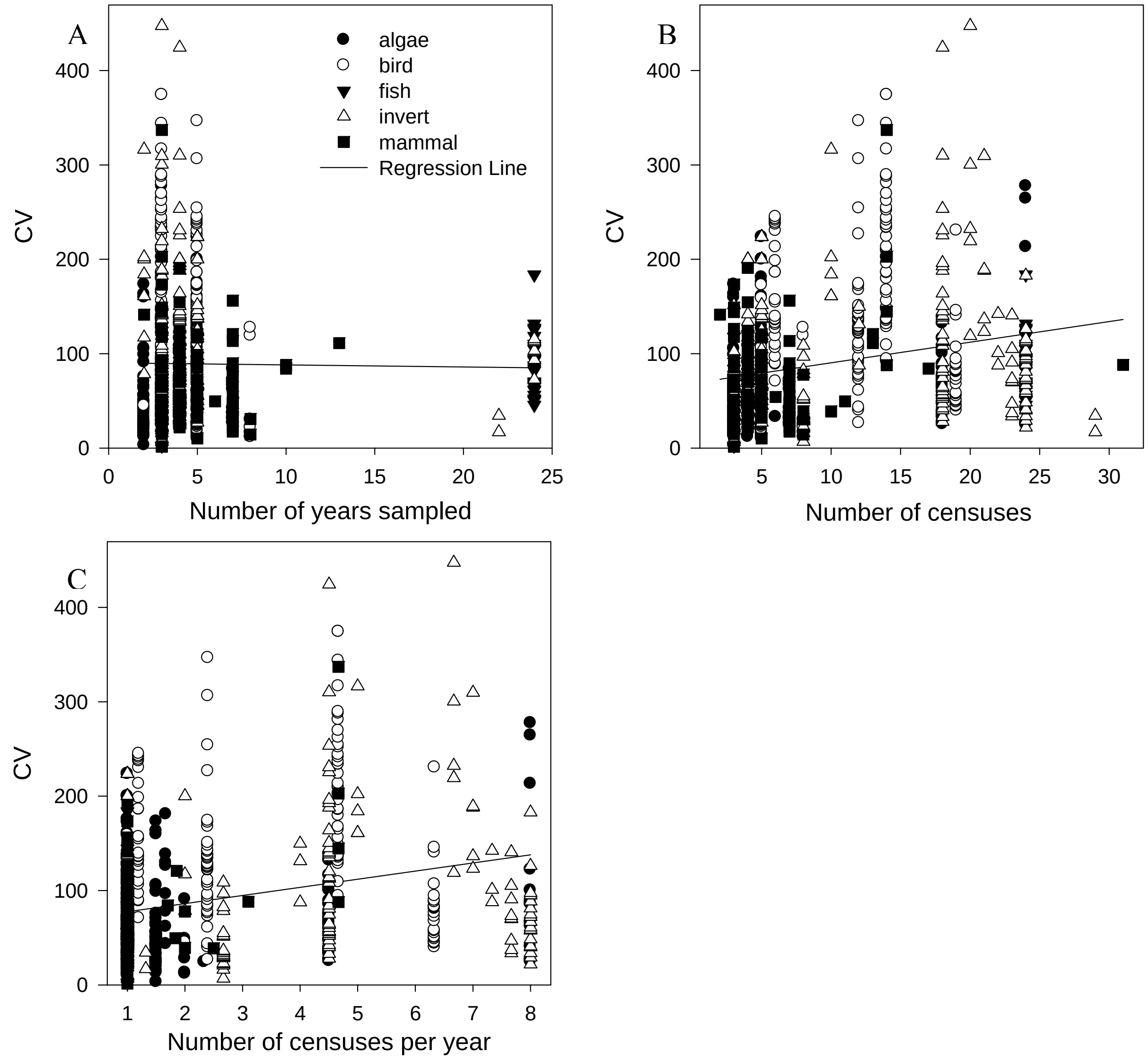

Figure 2. Relationship between temporal variability in time series (CV) and A) number of years sampled, B) number of censuses, and C) number of censuses per year
Taxonomic groups are represented by symbols as designated by the legend in A.

Metric of Abundance

The variability of time series does not differ significantly among metrics of abundance (biomass, percent cover, density) for algae (Figure 3A; ANOVA, df = 2/181, f = 0.24, p = 0.7899), invertebrates (Figure 3B; ANOVA, df = 2/294, f = 0.15, p = 0.8623)), or within a single species (*Fucus gardneri*, Figure 3C; ANOVA, df = 2/103, f = 0.88, p = 0.4172).

Habitat - Substrate

Variability in time series does not differ significantly between cobble and bedrock substrates for algae (Figure 4A; ANOVA, df = 1/127, f = 0.01, p = 0.9283. Time series for algae on soft sediment substrates are rarely available. Invertebrates on bedrock have significantly greater variability than those on cobble or soft sediment substrates (Figure 4B; ANOVA, df = 2/211, f =

7.08, $p < 0.0011$). When examining variability among time series for the same species found on cobble and bedrock, a lack of statistical power due to low sample size precludes conclusion for most species (Figure 5, Appendix 1). For *Fucus gardneri*, a species for which many time series are available on cobble and bedrock, there is no significant difference, even with large sample sizes (Figure 5; ANOVA, df = 1/99, f = 0.34, $p = 0.5637$). It is interesting to note the trends (Figure 5, *Mytilus trossulus* and *Tectura persona,* nonsignificant with $p \sim 0.06$, Appendix 1) of greater variability for populations on bedrock than on cobble are in the same direction as the overall pattern for invertebrates (Figure 4B).

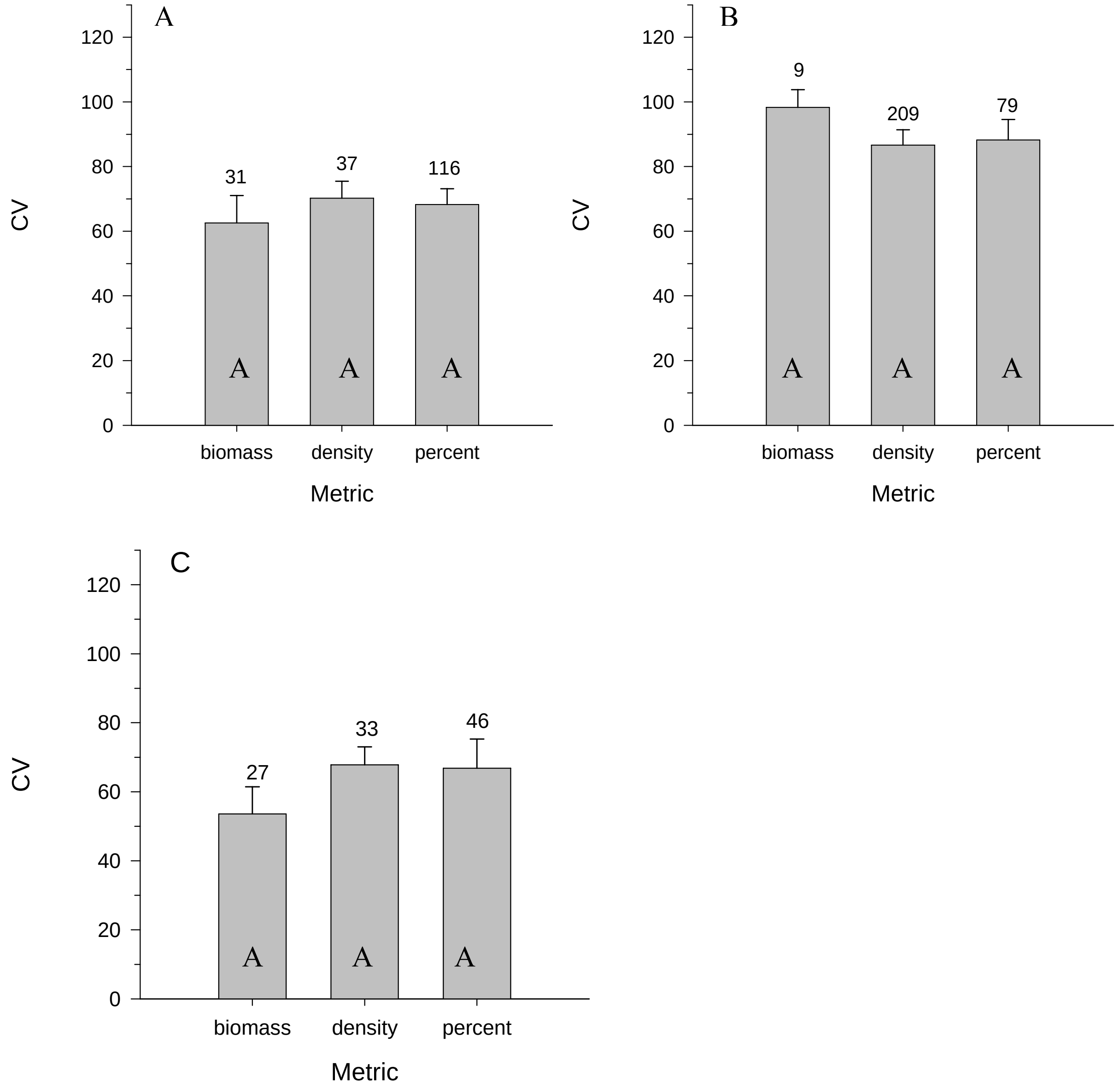

Figure 3. Variability among time series data for different metrics of abundance for A) algae and B) invertebrates, and C) Fucus gardneri
Numbers above bar indicate numbers of time series, and letters on bars indicate significant differences ($p = 0.05$ Tukey test).

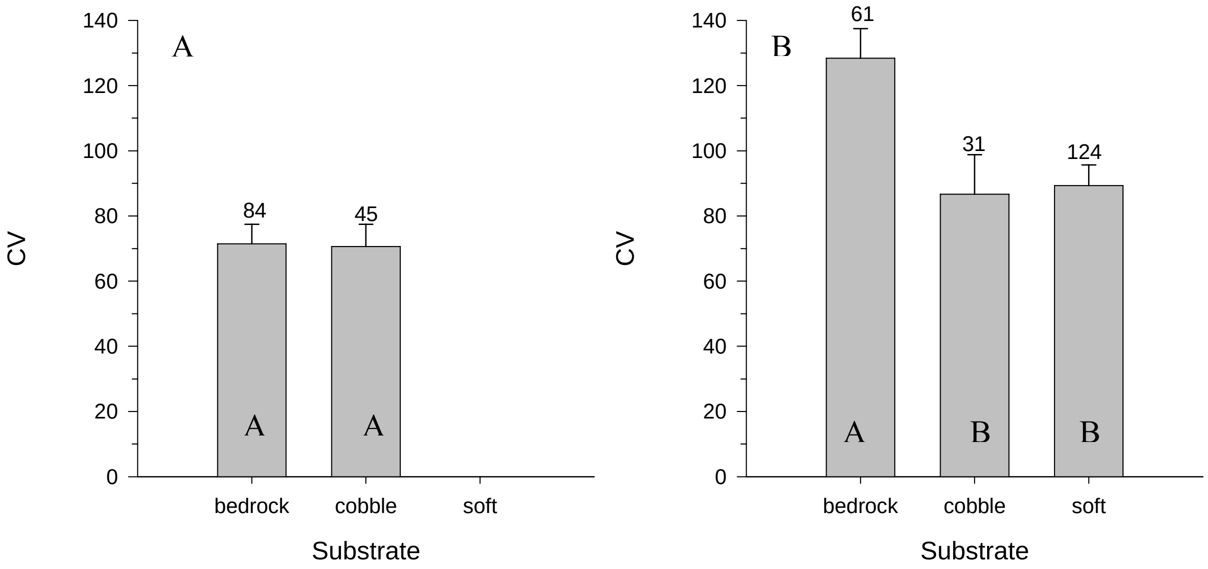

Figure 4. Variability among time series data for different substrates for A) algae and B) invertebrates
Numbers above bar indicate numbers of time series, and letters on bars indicate significant differences (p = 0.05 Tukey test).

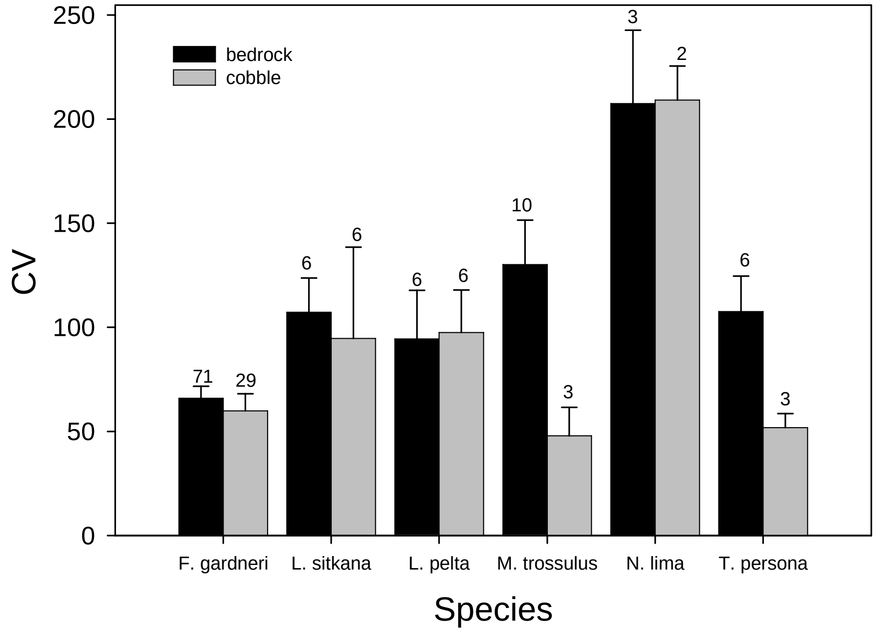

Figure 5. Variability among time series data for different substrates for species which have greater than two time series in bedrock and cobble substrates
Variability was not significantly different for any within species comparisons. Numbers above bar indicate numbers of time series.

Habitat - Tidal Height

Variability in time series differs significantly among tidal heights for algae (Figure 6A; ANOVA, df = 3/180, f = 3.70, p = 0.0128) with greatest variability in subtidal algae and lowest variability in high intertidal algae. Such a pattern of increasing variability with depth does not occur for invertebrates; however, time series from invertebrates in the low intertidal have greater variability than those in the high or mid intertidal or subtidal (Figure 6B; Welch ANOVA, df = 3/125.1, f = 11.41, p < 0.0001).

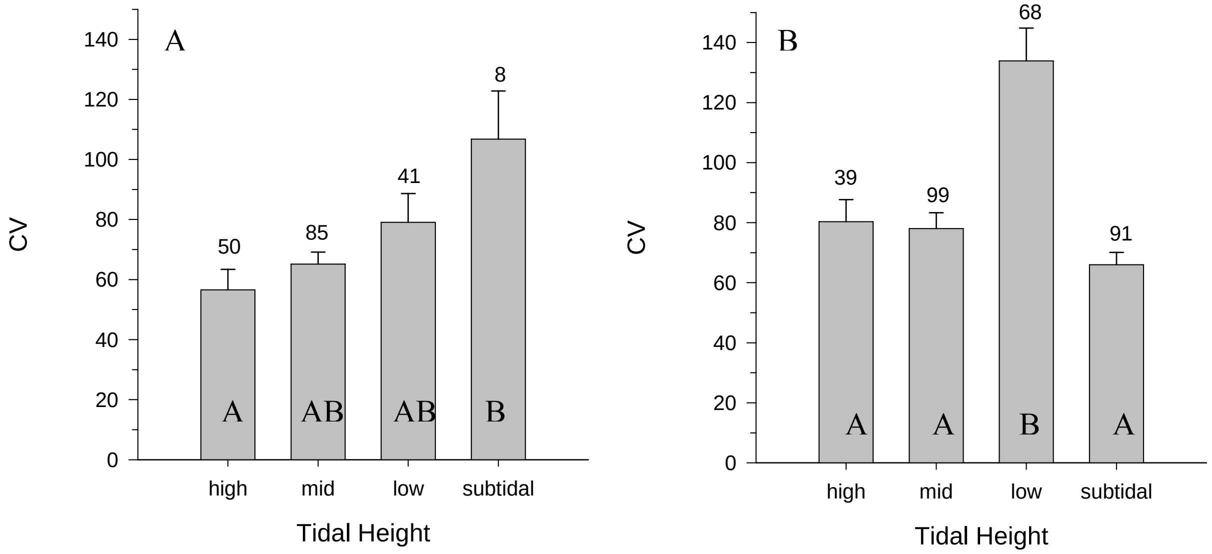

Figure 6. Variability among time series data collected at different tidal heights for A) algae and B) invertebrates

Numbers above bar indicate numbers of time series, and letters on bars indicate significant differences (p = 0.05 Tukey test).

Life History

Life span and trophic mode were not sufficiently available to warrant analysis. The analysis of development mode for invertebrates was the only life history analysis that was possible. Variability in time series does not differ significantly among development modes for invertebrates (Figure 7A; Welch ANOVA, df = 2/75.4, f = 2.09, p = 0.1306).

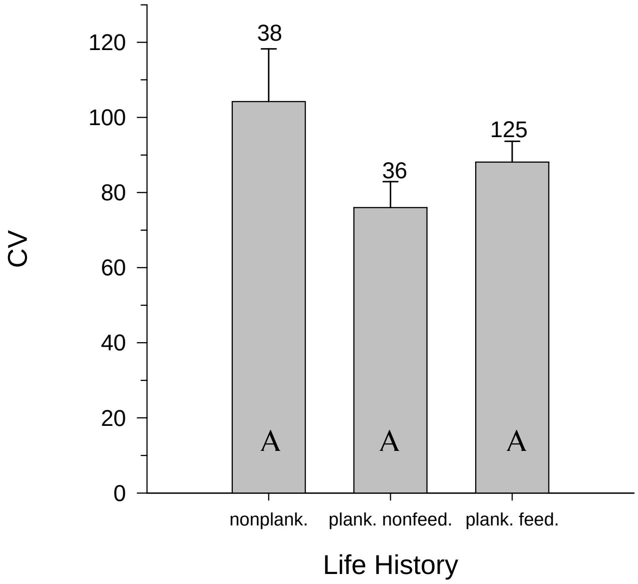

Figure 7. Variability among time series for different invertebrate life histories
Numbers above bar indicate numbers of time series, and letters on bars indicate significant differences (p = 0.05 Tukey test).

Species
Some monitoring programs necessarily lump information for species groups or complexes. Variability does not differ, in general, among time series of groups of species versus individual species time series (Figure 8A; ANOVA, df = 1/719, f = 2.13, p = 0.1449). When only datasets that contain both individual species and species groups were used, the result was similar (Figure 8B; ANOVA, df = 1/306, f = 1.07, p = 0.3008).

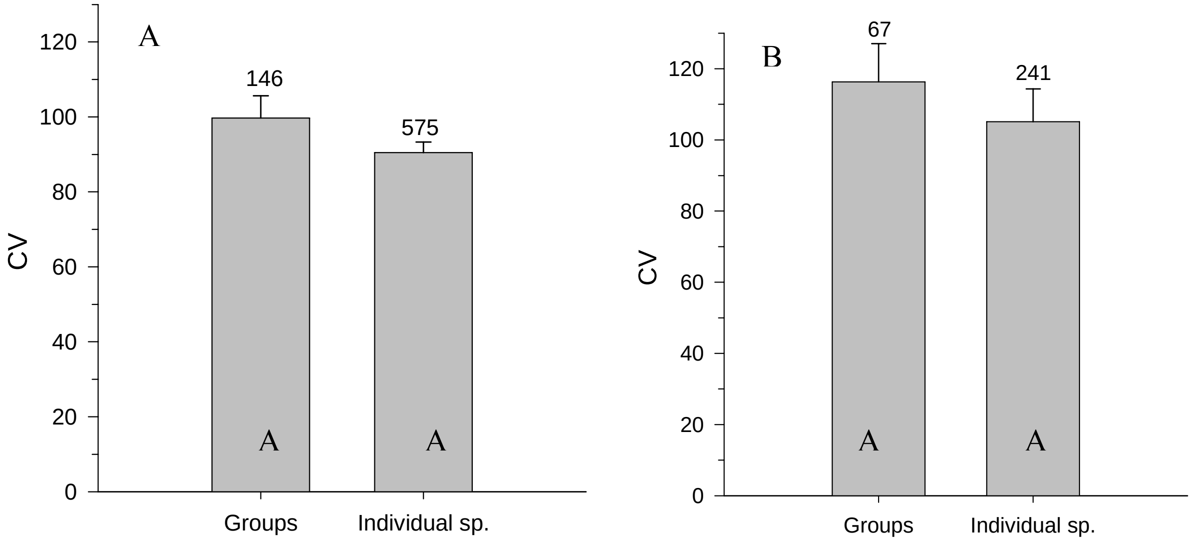

Figure 8. Variability between time series of species complexes (groups) and individual species A) All time series included. B) Time series only from datasets with species complexes (groups) and individual species. Numbers above bar indicate number of time series.

Variability in time series varies substantially within a single species (Appendix 2). Time series information is often only available for a single species from a single study and location; however, for a handful of species, many time series are available. *Fucus gardneri* is represented by 106 different time series, and the CV of these time series varies from 3 to 224 (Appendix 2). Harlequin ducks are represented in 33 different time series, with a range in CV from 26 to 231 (Appendix 2). Within the invertebrates, *Tectura persona*, *Semibalanus cariosus*, *Lottia pelta*, *Littorina sitkana*, and *Mytilus trossulus* are represented by 15 or more time series with the difference between the maximum and minimum CV ranging from 110 to 282 (Appendix 2). Harbor seals, sea otters, and Steller sea lions are represented by 22, 24 and 39 time series, with range in CV from 17 to 156, 1 to 203, and 26 to 191, respectively. Therefore, it is unlikely to designate any single species as having high or low variability, as variability seems highly context specific.

DISCUSSION

Taxonomic Groups and Sampling Frequency

Temporal variability was not significantly different among marine populations of birds, mammals, fish, algae and invertebrates from the Gulf of Alaska. This result is surprising, given the differences in movement patterns, survey methods, life histories, and so forth, among these groups. Gerrodette (1987) suggests that CV will contain less natural variability for species with reproduction spread over many age classes (longer-lived mammals, birds, fish), however such a pattern is not evident from my results. Insect populations have greater variability than mammals (Hanski 1990), presumably because they have shorter generation times and smaller ranges (McArdle and Gaston 1992). I did not find an analogous result in this marine ecosystem, potentially because marine invertebrates (analogous to insects) do not necessarily have small ranges or short generation times. My result suggests that any taxonomic groups can be considered when designing a monitoring program because no single group has more or less temporal variability than the others.

I did not detect a difference in variability among time series with a greater number of years sampled. However, the range of variability found here, from near 0 to over 400% of the mean for time series less than 5 years, precluded detection of an effect. The range of variability for time series of greater than 20 years is still quite broad, from near 50 to almost 200% of the mean. Cyr (1997) found only very small increases in variability (0.1 units over 25 years) for 70 populations of freshwater fish, zooplankton and phytoplankton sampled between 10 and 51 years. Any environmental change, such as a regime shift or temperature increase, over time might be expected to cause greater variability if the time series incorporates the time period with the environmental change. I did find an increase in variability for time series that were sampled more frequently; however only 5% of this variability was explained by sampling frequency. Seasonal variation, expressed as number of samples per year, also explained a small amount of the variation in temporal variability.

Metric of Abundance

Temporal variability of invertebrates and algae were not significantly different for populations with abundance measured as biomass, percent cover or density. Therefore, in designing a sampling program, any of these metrics may be used.

Population variability in different environments

Sheltered and exposed rocky shores, wave-cut platforms, and beaches with varying mixtures of sediments, sand, gravel, cobble, and boulders are the dominant habitats in the Gulf of Alaska region (Page et al. 1995, Sundberg et al. 1996). I had expected that population variability would differ among different substrates in the nearshore habitat due to the interaction between and relative importance of natural disturbance and ecological interactions such as competition and predation. Disturbance and competition are likely causes of variability based on previous studies in boulder habitats, where the frequency of disturbance and the intensity of competition interact to result in intermediate levels of diversity (Connell 1978, Sousa 1979a, 1979b). However, competition is not a structuring force in soft sediment substrates (Peterson 1979), and the effect of disturbance varies in different substrates. The results of this study show that, for algae, there was no significant difference in temporal variability of populations on either cobble or bedrock substrates. For invertebrates, populations on bedrock substrates had greater temporal variability than those on cobble or soft sediment substrates. Further studies are needed to elucidate the processes that may result in greater variability in bedrock habitats. When analyses were conducted for individual species that were found in different substrates, there were not significant differences in variability between populations on cobble and bedrock habitats; however these comparisons suffered from low sample size. One factor that may cause differences in temporal population variability among substrates is wave exposure. However, I was not able to explore this factor, because authors do not report wave exposure in a manner that allows for comparisons across studies. Bedrock habitats in the Gulf of Alaska may have greater wave exposure and therefore greater possible disturbance than cobble or soft sediment habitats, which could explain the higher population variability there.

Environmental sensitivity may vary among these different substrates. Sensitivity is presumed to be lower in high-energy environments, where oil or other pollutants are more likely to be removed by wave action and where vertebrate consumers are less able to forage (Teal & Howarth 1984, National Research Council 1986). Estuarine soft sediment marshes are thought to be highly sensitive to human impact (Teal & Howarth 1984). However, sensitivity is little more than an informed guess (Peterson et al. 2001). Ideally, necessarily limited resources should not be squandered either by devoting extensive effort to sampling abundant habitats with low sensitivity or by oversampling rare but sensitive habitats in hopes of detecting small but biologically unimportant differences (Peterson et al. 2001). Because of the lack of differences among substrates observed in this study, the optimal sampling design for a monitoring program in the Gulf of Alaska may be to sample habitats in proportion to their abundance.

Variability among populations at different tidal heights was not consistent across invertebrates and algae, although both invertebrates and algae show higher variability in low intertidal habitat compared to high intertidal habitat. Such high variability in the low intertidal is curious, because environmental conditions are probably less harsh there than higher in the intertidal. The low intertidal may have higher variability because of the combination of intense biological interactions (e.g. predation, herbivory, competition) and varying environmental conditions that all have relative importance here, whereas each has less importance in the other zones (Menge and Sutherland 1987). The high variability observed in algal populations in subtidal habitat could be the result of small number of algal populations observed in this habitat. For invertebrates, where 91 populations were observed in the subtidal, variability was not significantly different from mid and high intertidal habitats.

Life History

Few life history data were available for Gulf of Alaska populations. I was only able to determine development mode for marine invertebrates for a small data set. This data set showed no significant difference in temporal variability with development mode; however, the trend coincided with the pattern reported for a larger data set by Eckert (2003) in that time series for species with no planktonic period (larval dispersal) had greater temporal variability than time series for species with a planktonic period, either planktonic feeding or planktonic nonfeeding development

Species

I did not find a difference in temporal variability among populations that were classified as species complexes compared to those classified by species, even when only datasets that contained both species complexes and individual species were used. The use of species complexes or higher level taxonomy has gained support because of the increased number of samples that can be examined per unit effort (Beattie and Oliver 1994), but doing so should be evaluated on a case-by-case basis and only done when biodiversity has been well described (Quijon and Snelgrove 2006). Using higher taxonomic levels precludes further analyses that depend on species-level traits. It is possible that only a single species is represented by a species complex because fine classification is difficult in the field. In other cases, multiple species may be lumped together. Whenever possible, monitoring programs should identify taxa to their lowest possible unit unless lumping species has been shown in that program to be effective.

For species in which multiple time series were available, estimates of temporal variability varied widely across studies, sites, and time periods. This result is similar to that found for terrestrial and aquatic species by Connell and Sousa (1983). A future study could replicate time series over space using a repeated measures design to elucidate patterns for variability within a study. Additionally, one could examine the variability of different species at the same site to examine if species are changing in concert or along similar trajectories. Given these results, I am unable to recommend any individual species that are more suitable than others for a monitoring program.

The average CV for all 786 time series in this study is 89% of the mean, with the range from 1 to 447%. Few other studies have examined time series variability for comparison. In Eckert (2003), the average CV of adult populations ranged from 88 to 134% for the different development modes of marine species.

Data limitations

Although I was able to collect 786 time series for this project, data sets for the Gulf of Alaska are sparse. For 43% of species (97/226), only one time series was available. The number of time series available for analysis was limited in many cases. Natural history and life history information are lacking for Gulf of Alaska marine species. The power of many of the statistical tests reported here is low, as evidenced by low F-statisitics and high p-values in statistical tests (Hoenig and Heisey 2001). This lack of power results from the broad range of CVs within a category, resulting in low confidence about the mean CVs. Increasing sample size may, in some cases, provide greater confidence. Connell and Sousa (1983) observed the same result in that the range of observed variabilities was broad. Post-hoc power tests are not recommended (Hoenig and Heisey 2001), because they simply demonstrate what the statistical result already indicates. For the purposes of the GEM program, the lack of statistical difference among CVs for taxa, measures, some substrates, some tidal heights and life histories indicates that, at this point, where no difference was found, no single approach can simply be predicted to result in less variability in a monitoring program. As detailed below, monitoring programs should have the goal of designing sampling schema to minimize variability.

Recommendations for GEM monitoring

1) Reduce sampling error

Future monitoring programs should be based on sampling designs that minimize sampling error and provide consistency across space and time. The CVs found in this study, which were on average around 89%, suggest that probability of detecting human impacts is low (Marsh 2001). Population variability is the sum of variation due to sampling error within a site and the true temporal variation. Reducing sampling error by more intensive sampling can improve the probability to detect change, to a point. Osenberg et al. (1994) estimate that increasing sampling intensity can only reduce observed variation by ≈ 50%. Designs that stratify by environmental and habitat conditions or include covariates can effectively reduce sampling error. Monitoring by GEM should include a statistically rigorous sampling scheme that minimizes sampling error (as designated in the GEM Science Plan). It is possible that sampling error varies among species and sampling methodologies. For example, seabird surveys that sample resting birds on shore may have a high variability due to sampling because the number of resting birds may not be consistent from time to time (Boersma et al. 1995). In contrast, it is possible that barnacles, because they are affixed to the rock, may be sampled with less error. Strategies for sampling and reducing sampling error, therefore, may need to be approached on a species by species basis.

2) Get preliminary information on temporal and spatial variance

Because most species that were represented here by more than one time series exhibited a wide range of variability, with CVs ranging from only a few percent to well over 400%, we can not simply suggest that certain species vary inherently more or less than others. Therefore, monitoring programs should collect preliminary information on temporal and spatial variance in order to evaluate what sample sizes are appropriate in that site for that species. Because we know so little about population variation and how it changes in response to environmental conditions, monitoring programs should be designed based on preliminary information collected on the species of interest at the locations of interest (Benedetii-Cecci 2001, Carey and Keough 2002).

CONCLUSIONS

Temporal variability for marine populations in the Gulf of Alaska indicates that detecting human-induced change will be difficult. Variability was not significantly different among taxonomic groups, time series of different lengths, metrics of abundance, most habitats, and life histories, indicating no clear directive for the design of a monitoring program. The monitoring program should make efforts to reduce sampling error and use preliminary information to establish sample sizes in an effort to increase power to detect change. More life history and natural history information is needed for marine populations in the Gulf of Alaska and studies are needed to examine why temporal variability has such a wide range for a single species.

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APPENDICES

Appendix 1. ANOVA Tables

Taxonomic groups – Figure 1

Complete Dataset

```
                 Levene's Test for Homogeneity of covar Variance
                   ANOVA of Squared Deviations from Group Means

                              Sum of        Mean
           Source        DF     Squares      Square    F Value    Pr > F

           taxa           4    2.2278E9    5.5696E8       6.15    <.0001
           Error        781    7.072E10    90546925


                             Welch's ANOVA for covar

                      Source          DF    F Value    Pr > F

                      taxa        4.0000      15.29    <.0001
                      Error        188.1
```

Data sampled at intervals close to one year

```
                 Levene's Test for Homogeneity of covar Variance
                   ANOVA of Squared Deviations from Group Means

                              Sum of        Mean
           Source        DF     Squares      Square    F Value    Pr > F

           taxa           4    4.3712E8    1.0928E8       5.25    0.0004
           Error        450    9.3704E9    20823197


                             Welch's ANOVA for covar

                      Source          DF    F Value    Pr > F

                      taxa        4.0000       1.06    0.3786
                      Error        145.6
```

Metric of abundance – Figure 3

Algae

```
                                                Sum of
      Source                        DF         Squares     Mean Square    F Value    Pr > F

      Model                          2       1087.0747        543.5374       0.24    0.7899

      Error                        181     416577.6126       2301.5338
```

Inverts

```
      Source                        DF         Squares     Mean Square    F Value    Pr > F

      Model                          2        1237.622         618.811       0.15    0.8623

      Error                        294     1227462.898        4175.044
```

Fucus gardneri

```
      Source                        DF         Squares     Mean Square    F Value    Pr > F

      Model                          2       3775.2741       1887.6370       0.88    0.4172

      Error                        103     220554.9241       2141.3099
```

Substrate – Figure 4

Algae

```
                                         Sum of
Source                    DF            Squares     Mean Square    F Value    Pr > F

Model                      1            21.6862         21.6862       0.01    0.9283

Error                    127        338796.1315       2667.6861
```

Inverts

```
Source                    DF            Squares     Mean Square    F Value    Pr > F

Model                      2          68563.908       34281.954       7.08    0.0011

Error                    211        1022104.251        4844.096
```

Substrate – Figure 5

F. gardneri

```
Source                    DF            Squares     Mean Square    F Value    Pr > F

Model                      1           763.1410        763.1410       0.34    0.5637

Error                     98        222846.9321       2273.9483
```

L. sitkana

```
Source                    DF            Squares     Mean Square    F Value    Pr > F

Model                      1          475.92983       475.92983       0.07    0.7938

Error                     10        66011.14089      6601.11409
```

L. pelta

```
Source                    DF            Squares     Mean Square    F Value    Pr > F

Model                      1           29.76902        29.76902       0.01    0.9212

Error                     10        28904.21009      2890.42101
```

M. trossulus

```
Source                    DF            Squares     Mean Square    F Value    Pr > F

Model                      1        15616.09551     15616.09551       4.08    0.0684

Error                     11        42074.76750      3824.97886
```

N. lima

```
Source                    DF            Squares     Mean Square    F Value    Pr > F

Model                      1           3.194757        3.194757       0.00    0.9745

Error                      3        7967.318407     2655.772802
```

T. persona

```
Source                    DF            Squares     Mean Square    F Value    Pr > F

Model                      1         6213.17212      6213.17212       4.83    0.0640

Error                      7         9010.19027      1287.17004
```

Tidal Height – Figure 6

Algae

```
Source                      DF         Squares     Mean Square    F Value    Pr > F

Model                        3      24273.9306       8091.3102       3.70    0.0128

Error                      180     393390.7567       2185.5042
```

Inverts

```
           Levene's Test for Homogeneity of covar Variance
             ANOVA of Squared Deviations from Group Means

                                Sum of        Mean
Source              DF       Squares      Square    F Value    Pr > F

tidalheight          3      1.8395E9    6.1317E8       7.97    <.0001
Error              293      2.255E10    76960917


                     Welch's ANOVA for covar

           Source               DF    F Value    Pr > F

           tidalheight      3.0000      11.41    <.0001
           Error             125.1
```

Life History – Figure 7

```
       Levene's Test for Homogeneity of covar Variance
         ANOVA of Squared Deviations from Group Means

                            Sum of        Mean
Source           DF       Squares      Square    F Value    Pr > F

Dev_Mode          2      5.8927E8    2.9463E8       3.11    0.0468
Error           190      1.798E10    94652982


                    Welch's ANOVA for covar

           Source             DF    F Value    Pr > F

           Dev_Mode       2.0000       2.09    0.1306
           Error         75.4121
```

Species – Figure 8

Complete Dataset

```
Source                      DF         Squares     Mean Square    F Value    Pr > F

Model                        1        9904.226        9904.226       2.13    0.1449

Error                      719     3343439.344        4650.124
```

Datasets for which both individual species and species groups were used

```
Source                      DF         Squares     Mean Square    F Value    Pr > F

Model                        1        6621.959        6621.959       1.07    0.3008

Error                      306     1885921.779        6163.143
```

Appendix 2. Coefficient of variation (CV) of time series used in this study, arranged by species

Species	n	mean	se	min	max	References
Algae						
Agarum cribrosum	2	78.88	17.24	61.64	96.12	Rosenthal 1978
Cladophora sericea	2	45.50	1.69	43.81	47.19	Coats et al. unpublished
Diatoms	1	213.08				Feder & Keiser 1980
Elachista fucicola	1	58.44				Coats et al. unpublished
Endocladia muricata	2	45.76	12.68	33.09	58.44	Coats et al. unpublished
Endozoic green algae	5	55.29	4.62	43.81	71.20	Coats et al. unpublished
Enteromorpha intestinalis	1	122.18				Feder & Keiser 1980
Fucus distichus	3	30.75	4.96	24.92	40.62	Feder & Keiser 1980
Fucus gardneri	106	63.76	4.49	3.04	223.61	Carroll 1994, vanTamelen & Stekoll 1996, Stekoll & Deysher 2000, Coats et al. unpublished
Fucus gardneri (germlings)	7	50.65	3.34	33.09	58.44	Coats et al. unpublished
Gloiopeltis furcata	4	57.06	5.25	47.19	71.20	Coats et al. unpublished
Halosaccion glandiforme	1	58.44				Coats et al. unpublished
Hildenbrandia rubra	4	63.79	3.05	58.44	71.20	Coats et al. unpublished
Laminaria groenlandica	2	155.27	25.67	129.60	180.94	Rosenthal 1978
Laminaria saccharina	2	60.48	17.16	43.32	77.65	Rosenthal 1978
Laminaria yezoensis	2	132.31	6.02	126.30	138.33	Rosenthal 1978
Leathesia difformis	1	35.12				Coats et al. unpublished
Mastocarpus papillatus	1	58.44				Coats et al. unpublished
Monostroma spp	3	150.05	57.29	85.77	264.33	Feder & Keiser 1980
Neorhodomela larix	1	41.74				Coats et al. unpublished
Neorhodomela oregona	4	51.77	2.39	47.19	58.44	Coats et al. unpublished
Other algae	11	92.87	16.21	27.01	223.61	Carroll 1994
Palmaria callophylloides	1	58.44				Coats et al. unpublished
Petrocelis spp.	1	33.83				Coats et al. unpublished
Pilayella littoralis	3	47.30	6.41	36.25	58.44	Coats et al. unpublished
Polysiphonia/Pterosiphonia spp	2	42.59	7.47	35.12	50.06	Coats et al. unpublished
Pterosiphonia bipinnata	1	66.38				Feder & Keiser 1980
Pylaiella littoralis	2	182.48	94.99	87.49	277.48	Feder & Keiser 1980
Soranthera ulvoidea	3	58.60	7.64	43.81	69.32	Coats et al. unpublished
Ulothrix flacca	1	62.30				Feder & Keiser 1980
Ulva/Ulvaria spp.	1	35.12				Coats et al. unpublished
Verrucaria spp.	3	55.15	4.76	46.36	62.72	Coats et al. unpublished
Birds						
Aleutian tern	1	195.78				Nishimoto 1988
American widgeon	1	238.58				Forsell & Gould 1980
Arctic tern	2	169.83	32.51	137.32	202.35	Nishimoto 1988, Laing 1991
Bald eagle	3	91.03	59.55	26.61	209.99	Nishimoto 1988, Laing 1991, Stephensen et al. 2001
Barrow's and common goldeneyes	2	30.10	3.43	26.68	33.53	Zwiefelhofer & Forsell 1989
Barrow's goldeneye	1	185.74				Forsell & Gould 1980
Black oystercatcher	1	75.77				Laing 1991

Black scoters	4	104.43	47.03	24.92	223.76	Forsell & Gould 1980, Nishimoto 1988, Zwiefelhofer & Forsell 1989
Black-legged kittiwake	5	106.58	24.92	22.07	172.64	Nysewander et al. 1986, Nishimoto 1988, Zwiefelhofer & Forsell 1989, Laing 1991
Bonaparte's gull	1	147.57				Laing 1991
Brachycamphus marbled murelet	1	131.29				Nishimoto 1988
Brachyramphus murrelets	4	79.97	29.36	15.31	148.33	Nishimoto 1988, Zwiefelhofer & Forsell 1989, Laing 1991
Bufflehead	3	122.23	40.07	42.32	167.52	Forsell & Gould 1980, Laing 1991, Stephensen et al. 2001
Canada goose	1	128.37				Laing 1991
Common eider	2	231.67	1.69	229.97	233.36	Forsell & Gould 1980, Nishimoto 1988
Common goldeneye	1	236.90				Forsell & Gould 1980
Common loon	1	136.94				Nishimoto 1988
Common merganser	1	96.73				Forsell & Gould 1980
Common murre	1	108.91				Nishimoto 1988
Cormorants	5	53.62	22.54	10.31	121.95	Nishimoto 1988, Zwiefelhofer & Forsell 1989, Laing 1991, Stephensen et al. 2001
Crested aukelets	2	112.57	25.33	87.23	137.90	Zwiefelhofer & Forsell 1989
Duck unknown	1	186.02				Nishimoto 1988
Eider	2	203.44	5.39	198.05	208.83	Forsell & Gould 1980, Nishimoto 1988
Emperor goose	1	130.45				Forsell & Gould 1980
Fork-tailed storm-petrel	2	193.06	68.96	124.11	262.02	Nishimoto 1988, Laing 1991
Gadwall	1	242.50				Forsell & Gould 1980
Glaucous gull	7	107.25	33.94	30.21	287.40	Nysewander et al. 1986, Nishimoto 1988, Zwiefelhofer & Forsell 1989, Laing 1991, Stephensen et al. 2001
Goldeneye	3	96.11	32.25	32.52	137.19	Forsell & Gould 1980, Laing 1991, Stephensen et al. 2001
Grebe	2	180.65	52.97	127.68	233.62	Laing 1991, Nishimoto 1988
Green-winged teal	2	188.33	52.67	135.66	241.00	Laing 1991, Forsell & Gould 1980
Gulls	2	131.49	53.72	77.77	185.21	Laing 1991, Nishimoto 1988
Harlequin duck	33	74.48	7.40	25.87	230.54	Forsell & Gould 1980, Nishimoto 1988, Zwiefelhofer & Forsell 1989, Rosenberg & Petrula 1998, Patten et al. 1998, Stephensen et al. 2001
Herring gull	2	211.71	39.99	171.72	251.70	Nishimoto 1988, Laing 1991
Horned grebes	2	89.92	16.39	73.53	106.31	Zwiefelhofer & Forsell 1989
Horned puffin	1	140.99				Laing 1991
King eiders	4	102.30	49.49	17.89	212.92	Forsell & Gould 1980, Nishimoto 1988, Zwiefelhofer & Forsell 1989
Kittlitz's murrelet	1	212.88				Nishimoto 1988
Long-tailed jaeger	1	226.39				Laing 1991

Loons	5	74.61	23.87	24.06	164.38	Nishimoto 1988, Zwiefelhofer & Forsell 1989, Laing 1991, Stephensen et al. 2001
Mallard	2	136.41	2.63	133.77	139.04	Forsell & Gould 1980, Laing 1991
Merganser	3	103.26	43.22	40.05	185.93	Forsell & Gould 1980, Laing 1991, Stephensen et al. 2001
Mew gull	5	77.15	16.27	40.39	136.21	Nishimoto 1988, Zwiefelhofer & Forsell 1989, Laing 1991, Stephensen et al. 2001
Murres	5	88.87	51.84	16.53	289.24	Nysewander et al. 1986, Nishimoto 1988, Zwiefelhofer & Forsell 1989, Laing 1991
Northern fulmar	1	280.87				Nishimoto 1988
Northern pintail	1	253.92				Laing 1991
Northwestern crow	1	37.62				Stephensen et al. 2001
Oldsquaw	5	129.08	42.00	47.82	269.27	Forsell & Gould 1980, Nishimoto 1988, Zwiefelhofer & Forsell 1989, Laing 1991
Parakeet auklet	1	134.13				Laing 1991
Parasitic jaeger	2	242.52	131.65	110.87	374.17	Laing 1991, Nishimoto 1988
Pelagic cormorant	2	127.71	115.87	11.84	243.57	Nysewander et al. 1986, Nishimoto 1988
Pigeon guillemot	4	56.26	21.66	17.89	94.21	Nishimoto 1988, Zwiefelhofer & Forsell 1989, Laing 1991
Pintail	1	154.24				Forsell & Gould 1980
Pomarine jaeger	1	142.68				Laing 1991
Red-breasted and Common mergansers	2	57.60	3.77	53.83	61.38	Zwiefelhofer & Forsell 1989
Red-breasted merganser	1	126.29				Forsell & Gould 1980
Red-faced cormorant	1	119.04				Nysewander et al. 1986
Red-necked grebe	3	95.11	53.63	33.63	201.96	Nishimoto 1988, Zwiefelhofer & Forsell 1989
Red-necked phalarope	2	181.18	59.94	121.24	241.12	Nishimoto 1988, Laing 1991
Red-throated loon	1	374.17				Nishimoto 1988
Rock sandpiper	1	306.13				Laing 1991
Sabine's gull	1	346.41				Laing 1991
Scaup	3	191.49	62.48	125.78	316.40	Forsell & Gould 1980, Nishimoto 1988, Laing 1991
Scoter	4	125.27	39.21	69.57	236.50	Forsell & Gould 1980, Nishimoto 1988, Laing 1991, Stephensen et al. 2001
Shorebirds	1	84.86				Laing 1991
Steller's eider	2	195.17	59.08	136.09	254.25	Forsell & Gould 1980, Nishimoto 1988
Surf scoter	2	138.35	28.81	109.53	167.16	Forsell & Gould 1980, Nishimoto 1988
Surfbird	1	150.55				Laing 1991
Swan	1	244.95				Forsell & Gould 1980
Tern	1	343.48				Nishimoto 1988
Tufted puffin	3	134.15	24.39	95.70	179.36	Nysewander et al. 1986, Nishimoto 1988, Laing 1991
White-winged scoter	2	108.43	19.79	88.64	128.22	Forsell & Gould 1980, Nishimoto 1988

Fish						
Alaska plaice	1	131.62				Anderson & Piatt 1999
Arrow tooth flounder	1	70.16				Anderson & Piatt 1999
Atka mackerel	1	183.68				Anderson & Piatt 1999
Bigmouth sculpin	1	68.15				Anderson & Piatt 1999
Capelin	1	125.45				Anderson & Piatt 1999
Eulachon	1	56.28				Anderson & Piatt 1999
Flathead sole	6	53.67	17.60	2.44	117.85	Armstrong et al. 1995
Greenlings	1	118.61				Anderson & Piatt 1999
Halibut	1	84.25				Anderson & Piatt 1999
Herring	1	110.30				Anderson & Piatt 1999
Longsnout prickleback	1	104.71				Anderson & Piatt 1999
Myoxocephalus sculpins	1	61.25				Anderson & Piatt 1999
Pacific cod	1	52.19				Anderson & Piatt 1999
Prowfish	1	69.53				Anderson & Piatt 1999
Rock sole	1	87.40				Anderson & Piatt 1999
Rockfishes	1	70.35				Anderson & Piatt 1999
Sandfish	1	65.26				Anderson & Piatt 1999
Shortfin eelpout	1	45.62				Anderson & Piatt 1999
Skates	1	50.84				Anderson & Piatt 1999
Spiny dogfish	1	92.91				Anderson & Piatt 1999
Starry flounder	1	61.96				Anderson & Piatt 1999
Sturgeon poacher	1	66.87				Anderson & Piatt 1999
Tomcod	1	127.30				Anderson & Piatt 1999
Walleye pollock	1	50.34				Anderson & Piatt 1999
Wattled eelpout	1	107.54				Anderson & Piatt 1999
Yellow fin sole	1	82.11				Anderson & Piatt 1999
Yellow irish lord	1	94.51				Anderson & Piatt 1999
Invertebrates						
Aricidea lupezi	1	54.83				Feder & Matheke 1980
Axinopsida viridis	2	80.38	1.97	78.42	82.35	Feder & Matheke 1980
Balanus crenatus	1	60.88				Feder & Keiser 1980
Balanus glandula	6	50.23	3.67	33.09	58.44	Coats et al. unpublished
Balanus glandula and Semibalanus balanoides	13	109.84	12.83	45.42	200.00	Carroll 1994
Balanus spp adults	3	34.55	7.72	21.63	48.32	Feder & Keiser 1980
Balanus spp spat	3	106.21	9.99	95.11	126.14	Feder & Keiser 1980
Balanus/Semibalanus spp. (dead)	6	58.50	6.55	41.74	81.16	Coats et al. unpublished
Balanus/Semibalanus spp. (set)	5	60.23	6.80	43.81	84.47	Coats et al. unpublished
Caecidae	1	200.00				Jewett et al. 1999
Capitella	3	265.40	91.24	161.02	447.21	Feder et al. 1976
Caprellidae	1	56.86				Jewett et al. 1999
Cephalopods	1	101.36				Anderson & Piatt 1999
Chaetoderma robusta	2	18.28	2.24	16.04	20.52	Feder & Matheke 1980
Chionoecetes bairdi	6	43.18	12.09	6.52	81.91	Armstrong et al. 1995
Chthamalus dalli	5	55.66	4.30	47.19	71.20	Coats et al. unpublished
Copepods	2	60.02	13.08	46.94	73.09	Feder & Paul 1980
Dermasterias imbricata	2	30.45	11.77	18.69	42.22	Dean et al. 1996

Epifaunal amphipoda	2	64.39	13.86	50.53	78.25	Jewett et al. 1999
Epifaunal bivalvia	2	85.79	28.05	57.74	113.84	Jewett et al. 1999
Epifaunal echinodermata	2	83.07	44.58	38.49	127.66	Jewett et al. 1999
Epifaunal gastropoda	2	73.09	25.95	47.14	99.03	Jewett et al. 1999
Epifaunal other crustacea	2	61.41	20.58	40.82	81.99	Jewett et al. 1999
Epifaunal polychaeta	2	104.47	29.51	74.96	133.97	Jewett et al. 1999
Eudorella emarginata	2	102.71	5.87	96.84	108.58	Feder & Matheke 1980
Exogone	3	141.95	21.09	118.70	184.04	Feder et al. 1976
Goniada annulata	2	32.33	3.06	29.28	35.39	Feder & Matheke 1980
Halectinosoma gothiceps	4	95.71	7.17	87.49	117.10	Feder et al. 1976
Harpacticus uniremis	4	112.68	14.26	78.32	140.58	Feder et al. 1976
Heterolaophonte sp.	4	149.26	19.55	104.98	200.00	Feder et al. 1976
Heteromastus filiformis	2	29.48	6.70	22.77	36.18	Feder & Matheke 1980
Infaunal amphipoda	2	50.29	1.70	48.59	51.99	Jewett et al. 1999
Infaunal bivalvia	2	26.49	2.53	23.96	29.02	Jewett et al. 1999
Infaunal echinodermata	2	50.06	10.06	40.00	60.11	Jewett et al. 1999
Infaunal gastropoda	2	60.78	0.54	60.24	61.32	Jewett et al. 1999
Infaunal other crustacea	2	60.77	15.40	45.37	76.16	Jewett et al. 1999
Infaunal polychaeta	2	66.74	13.42	53.32	80.16	Jewett et al. 1999
Isaeidae	2	69.07	17.59	51.48	86.67	Jewett et al. 1999
Ischyroceridae	1	125.60				Jewett et al. 1999
Lacunidae	1	68.87				Jewett et al. 1999
Leptasterias hexactis	2	287.39	136.88	150.51	424.26	Hooten & Highsmith 1996
Littorina scutulata	9	69.03	14.43	46.36	182.67	Feder & Keiser 1980, Coats et al. unpublished
Littorina sitkana	19	83.80	14.96	27.79	310.08	Feder & Keiser 1980, Hooten & Highsmith 1996, Coats et al. unpublished
Lottia pelta	17	84.09	11.35	32.93	196.08	Feder & Keiser 1980, Hooten & Highsmith 1996, Coats et al. unpublished
Lottiidae (juv.)	4	51.77	2.39	47.19	58.44	Coats et al. unpublished
Lucinidae	1	54.38				Jewett et al. 1999
Lumbrineridae	1	30.47				Jewett et al. 1999
Lumbrineris sp.	2	26.84	4.78	22.06	31.62	Feder & Matheke 1980
Macoma balthica	5	172.61	62.99	16.77	309.49	Feder et al. 1976, Naidu et al. 1992
Meiofauna	2	51.58	18.08	33.50	69.66	Feder & Paul 1980
Monticutidae	1	80.46				Jewett et al. 1999
Mytilidae	1	200.00				Jewett et al. 1999
Mytilus trossulus	19	93.13	14.46	29.06	223.61	Feder & Keiser 1980, Carroll 1994, Coats et al. unpublished
Nematodes	2	53.74	16.67	37.07	70.40	Feder & Paul 1980
Nephtys punctata	2	31.00	2.70	28.30	33.70	Feder & Matheke 1980
Nereidae	1	71.53				Jewett et al. 1999
Nucella lamellosa	6	74.93	7.56	58.44	108.44	Feder & Keiser 1980, Hooten & Highsmith 1996, Coats et al. unpublished
Nucella lima	6	180.40	32.17	41.74	253.49	Hooten & Highsmith 1996, Coats et al. unpublished
Opheliidae	1	112.14				Jewett et al. 1999
Pagurus hirsutiusculus	3	55.93	4.52	50.06	64.82	Coats et al. unpublished

Pandalus borealis	1	113.19				Anderson & Piatt 1999
Pandalus dispar	1	102.02				Anderson & Piatt 1999
Pandalus eous juv	4	51.24	21.28	8.48	98.58	Armstrong et al. 1995
Pandalus goniurus	1	112.01				Anderson & Piatt 1999
Pandalus hypsinotus	1	93.32				Anderson & Piatt 1999
Paralithodes camtschatica	1	115.37				Anderson & Piatt 1999
Phoxocephalidae	2	39.24	13.14	26.10	52.38	Jewett et al. 1999
Polydora	3	172.19	24.53	136.41	219.14	Feder et al. 1976
Praxillella gracillis	2	18.44	11.77	6.67	30.21	Feder & Matheke 1980
Protothaca staminea	1	26.99				Bechtol & Gustafson 1998
Pycnopodia helianthoides	2	43.20	0.80	42.40	43.99	Dean et al. 1996
Pycnopodia helianthoides juv.	2	126.56	24.64	101.92	151.21	Dean et al. 1996
Scyphozoa	1	72.48				Anderson & Piatt 1999
Semibalanus balanoides	5	57.60	4.86	46.36	71.20	Coats et al. unpublished
Semibalanus balanoides (set)	2	52.60	5.40	47.19	58.00	Coats et al. unpublished
Semibalanus cariosus	15	132.87	19.14	41.74	223.61	Carroll 1994, Coats et al. unpublished
Siphonaria thersites	2	51.13	7.31	43.81	58.44	Coats et al. unpublished
Spionidae	2	68.53	30.98	37.55	99.51	Jewett et al. 1999
Spirorbidae	1	141.74				Jewett et al. 1999
Starfish	1	103.17				Anderson & Piatt 1999
Sternaspis scutata	1	29.52				Feder & Matheke 1980
Syllidae	2	85.77	2.06	83.71	87.83	Jewett et al. 1999
Tectura persona	15	73.57	10.06	35.12	144.87	Hooten & Highsmith 1996, Coats et al. unpublished
Tectura scutum	4	50.44	7.33	33.83	69.32	Coats et al. unpublished
Tellinidae	1	25.95				Jewett et al. 1999
Telmessus cheiragonus	2	71.75	5.70	66.04	77.45	Dean et al. 1996
Terebellides stroemi	2	51.62	0.58	51.04	52.21	Feder & Matheke 1980
Tharyx	3	245.79	37.37	188.93	316.23	Feder et al. 1976
Thyasiridae	1	49.41				Jewett et al. 1999
Mammals						
Dall porpoise	2	79.41	5.85	73.57	85.26	Zwiefelhofer & Forsell 1989
Harbor porpoise	3	71.26	37.38	21.82	144.56	Nishimoto 1988, Zwiefelhofer & Forsell 1989, Laing 1991
Harbor seal	22	60.17	7.42	17.27	156.13	Nishimoto 1988, Zwiefelhofer & Forsell 1989, Frost et al. 1994
Humpback whale	1	65.60				von Ziegesar et al. 1994
Minke whale	1	336.86				Nishimoto 1988
Sea otter	24	51.178	9.7146	1.3023	202.76	Johnson 1984, Nishimoto 1988, Zwiefelhofer & Forsell 1989, Burn 1994, Bodkin et al. 2000, Garshelis & Johnson 2001
Steller sea lion	39	95.51	6.89	26.36	190.81	Zwiefelhofer & Forsell 1989, Calkins et al. 1994

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