

Oceanography of Glacier Bay, Alaska: Implications for Biological Patterns in a Glacial Fjord Estuary

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ABSTRACT: Alaska, U.S.A, is one of the few remaining locations in the world that has fjords that contain temperate tidewater glaciers. Studying such estuarine systems provides vital information on how deglaciation affects oceanographic conditions of fjords and surrounding coastal waters. The oceanographic system of Glacier Bay, Alaska, is of particular interest due to the rapid deglaciation of the Bay and the resulting changes in the estuarine environment, the relatively high concentrations of marine mammals, seabirds, fishes, and invertebrates, and the Bay's status as a national park, where commercial fisheries are being phased out. We describe the first comprehensive broad-scale analysis of physical and biological oceanographic conditions within Glacier Bay based on CTD measurements at 24 stations from 1993 to 2002. Seasonal patterns of near-surface salinity, temperature, stratification, turbidity, and euphotic depth suggest that freshwater input was highest in summer, emphasizing the critical role of glacier and snowmelt to this system. Strong and persistent stratification of surface waters driven by freshwater input occurred from spring through fall. After accounting for seasonal and spatial variation, several of the external physical factors (i.e., air temperature, precipitation, day length) explained a large amount of variation in the physical properties of the surface waters. Spatial patterns of phytoplankton biomass varied throughout the year and were related to stratification levels, euphotic depth, and day length. We observed hydrographic patterns indicative of strong competing forces influencing water column stability within Glacier Bay: high levels of freshwater discharge promoted stratification in the upper fjord, while strong tidal currents over the Bay's shallow entrance sill enhanced vertical mixing. Where these two processes met in the central deep basins there were optimal conditions of intermediate stratification, higher light levels, and potential nutrient renewal. These conditions were associated with high and sustained chlorophyll *a* levels observed from spring through fall in these zones of the Bay and provide a framework for understanding the abundance patterns of higher trophic levels within this estuarine system.

Introduction

Fjords are glacially-carved estuaries in high latitude environments, and worldwide constitute a volume of water similar to that of inland lakes and greater than that of drowned river estuaries (Syvitski et al. 1987). These systems are geologically very young and are evolving over relatively short time scales. Fjords range in their stage of deglaciation, from glacier-filled to completely deglaciated and infilled with sediment. Alaska, U.S.A., is one of the few areas in the world (along with Greenland, Canadian Arctic, Svalbard, Antarctica, and Chile) that has fjords that still contain tidewater glaciers (Syvitski et al. 1987). Understanding the dynamics of glacially-influenced fjords in Alaska provides some insight into what fjords worldwide experienced during their respective stages of deglaciation.

Alaska contains at least 200 major fjords, few of which have been studied in detail (Syvitski et al. 1987; Burrell 1986). The fjords of Alaska occur in two distinct regions, and differences in fjord hydrology might be expected between these regions due to differences in oceanic and terrestrial linkages. In the south-central part of the state (which includes Cook Inlet and Prince William Sound), most fjords have a direct connection to the oceanic waters of the Gulf of Alaska. In southeast Alaska, most fjords are intertwined in a network of islands and channels, with intermediate connections between the fjords and the coastal ocean. There also are differences in air temperature and precipitation rates between southeast and south-central Alaska (Royer 1982), which influence subsequent seasonal rates of freshwater discharge between these two regions (Syvitski et al. 1987).

Glacier Bay is a young silled fjord in southeast Alaska of particular interest due to its recent and rapid deglaciation of over 100 km, and the resulting changes on the marine landscape. The deglaciation that has occurred in Glacier Bay over the past 225 yr is one of the most rapid on record (Hall and Benson 1995) and has led to the highest known sedimentation rates in the world (Hallet et al. 1996;

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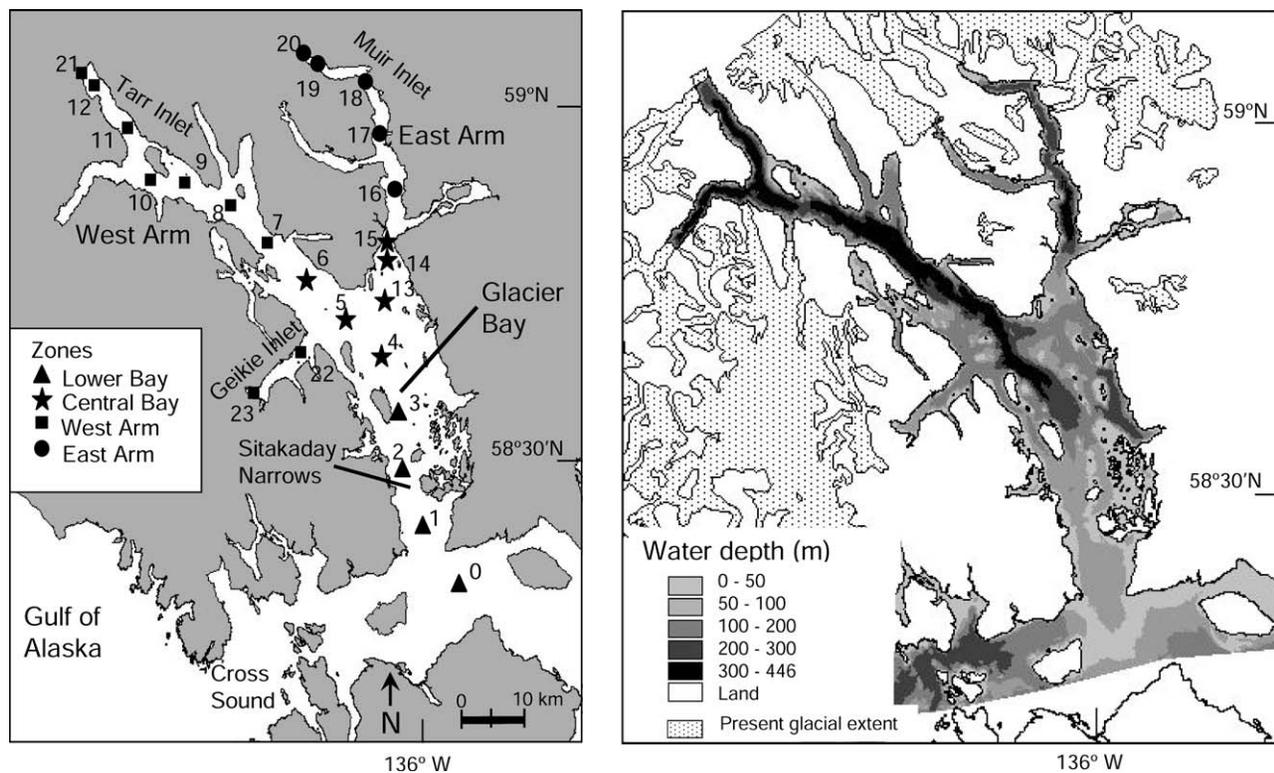


Fig. 1. Glacier Bay, Alaska, USA and the oceanographic sampling stations. Stations were grouped into four zones based on physical properties such as similarities in bathymetry, relative position to glaciers and source of oceanic waters, and general examination of oceanographic patterns. Zones were defined as lower Bay (stations 0, 1, 2, 3), central Bay (stations 4, 5, 6, 13, 14, 15), West Arm (stations 7, 8, 9, 10, 11, 12, 21, 22, 23), and East Arm (stations 16, 17, 18, 19, 20). Plan view of Glacier Bay bathymetry and location of present glacial extent. Gray and black shadings represent deeper portions of the Bay, while light gray shading represents shallower depths.

Koppes and Hallet 2002). The Bay's entrance sill is approximately 25 m deep, and multiple sills of varying depths are found within the Bay. Glacier Bay's entrance sill is fairly shallow in comparison with other Alaska fjords as well as Pacific fjords in general (Pickard 1967; Pickard and Stanton 1980). Deep basins exist between the sills, with depths to 450 m (Fig. 1). The Bay is surrounded by mountainous terrain, with many sources of freshwater, including 12 tidewater glaciers. Glacier Bay is immediately inland of the Fairweather Range (St. Elias Mountains), which reaches heights of up to 4,600 m. The regional climate is dominated by the strong Aleutian Low in the northern Gulf of Alaska from November to April, and by weak high pressure from May to October (Burrell 1986). As a result, Glacier Bay experiences a wet and moderate maritime climate.

The oceanographic properties of an estuary result from mechanisms that act to enhance or disrupt the stability of the water column, including insolation, wind stress, freshwater runoff, and tidal currents (Legendre et al. 1982; Svendsen 1986). The relative importance of these factors in influencing water

column stability and circulation can change over both time and space. The nature of fjords makes them subject to substantial seasonal change in hydrography and climate. Fjords also exhibit strong spatial differentiation from head to mouth due to diverse bathymetry (e.g., multiple shallow sills and deep basins), sources of freshwater discharge and associated sediment input, and glacier characteristics (presence, activity). The strong patterns of seasonality and heterogeneous characteristics of water column parameters along fjord axes, as well as with depth, have major influences on biological patterns (Brattegard 1980).

Alaska fjords represent important wintering, breeding, nursery, and feeding areas for various marine organisms, including many species with threatened or endangered status, as well as many fishery species of worldwide commercial importance. Glacier Bay is one such Alaska fjord that is renowned for its high concentration and diversity of top-level marine predators, including seabirds and marine mammals, as well as an abundance of commercially valuable fish and shellfish (Baker et al. 1992; Robards et al. 2003; Taggart et al. 2003;

TABLE 1. Timetable of oceanographic data collected at 24 stations within Glacier Bay, Alaska. Letters indicate which months of each year were sampled. (a) designates surveys with good coverage of the available sites (≥ 12 sites sampled), while (b) designates low to moderate coverage over all sites (< 12 sites sampled); (c) denotes periods when salinity and density data are not available, and (d) indicates times when PAR data are not available (otherwise, PAR available from November 1993 to October 2002). OBS turbidity data are available for August 1999–October 2002. Fluorescence data (chlorophyll *a*) are available from May 1994 to October 2002. Seasonal definitions for analyses include spring: February, March, April; summer: May, June, July; fall: August, September, October; and winter: November, December, January.

| | January | February | March | April | May | June | July | August | September | October | November | December |
|------|---------|----------|-------|-------|-----|------|------|--------|-----------|---------|----------|----------|
| 1993 | | | | | | | a | a | a | a | a | a |
| 1994 | b | | | b | a | | a | a | | | | |
| 1995 | | | | | | | | | | b,c | b,c | |
| 1996 | | | b | | | b | | | d | d | | |
| 1997 | | | | | d | | d | | | | d | |
| 1998 | | d | | | | a | | | | a | | a |
| 1999 | | | a | | | a | a | a | | a | | |
| 2000 | a | | a | | a | a | a | a | a | | | b |
| 2001 | | b | b | a | | | a | | | a | | |
| 2002 | a | | a | a | | | a | b | | a | | |

Mathews and Pendleton 2006). Glacier Bay was initially set aside as a national monument in 1925, and was elevated to a national park in 1980. Glacier Bay National Park is visited annually by approximately 350,000 visitors, who are attracted by tidewater glaciers and wildlife. The Bay formerly supported substantial commercial fish and crab fisheries, but these are being phased out. Understanding biological patterns and processes within Glacier Bay is important to managers charged with protecting park resources.

Determining seasonal and spatial patterns of abiotic factors in Glacier Bay is the foundation for understanding biological patterns. There is a need for baseline oceanographic data upon which to gauge ecosystem processes. Previous studies of Glacier Bay oceanography are limited in their spatial and temporal coverage (Pickard 1967; Matthews and Quinlan 1975; Matthews 1981; Cowan 1992). The temporal and spatial extent of the present oceanographic data set allowed us to examine the spatial and seasonal variation in the physical factors driving oceanographic conditions within a dynamic fjord estuarine system. The objectives of the current study were to provide a broad-scale analysis of the seasonal and spatial variability of physical oceanographic properties and phytoplankton biomass within Glacier Bay surface waters, to determine what external physical factors are driving physical oceanographic patterns as well as phytoplankton biomass within Glacier Bay, and to demonstrate how these relationships vary among seasons and zones within the Bay.

Methods

OCEANOGRAPHIC SAMPLING

Oceanographic data were collected at 24 set stations within Glacier Bay (Fig. 1). Forty-eight separate sampling trips were conducted from July

1993 through October 2002, with 2–8 trips made per year (Table 1). Not all stations were sampled during all surveys due to weather and field constraints. Several stations were added later in the program. We took a single cast at each station using a Sea-Bird SBE19 conductivity, temperature, depth (CTD) profiler (Sea-Bird Electronics, Inc., Bellevue, Washington) equipped with a Wetstar fluorometer (WET Labs, Inc., Philomath, Oregon), a D and A OBS-3 optical backscatterance sensor (D and A Instrument Co., Port Townsend, Washington), and a LI-COR LI-192SA photosynthetically available radiation (PAR) sensor (LI-COR, Inc., Lincoln, Nebraska). Data were collected for each 1-m depth bin of the water column from the surface to within 10 m of the bottom, to a maximum depth of 300 m (some stations are located at depths greater than 300 m). We measured and calculated salinity (psu), water temperature ($^{\circ}\text{C}$), density of water (σ_t , kg m^{-3}), optical backscatterance (OBS) – a measure of turbidity (mg l^{-1}), fluorescence – a measure of chlorophyll *a* (mg m^{-3}) to estimate phytoplankton biomass, and irradiance ($\text{microeinsteins s}^{-1} \text{m}^{-2}$) – a measure of PAR.

METEOROLOGICAL AND EXTERNAL PHYSICAL DATA

We obtained daily meteorological data from eight weather stations that surround Glacier Bay from the National Climatic Data Center (Asheville, North Carolina; Fig. 2), specifically: daily average air temperature ($^{\circ}\text{C}$), daily precipitation (cm), and daily average wind speed (m s^{-1}). Wind data were available only for the Juneau and Yakutat Airport stations. Monthly averages were calculated using daily weather data from the available stations for each month from January 1993 to July 2002.

We calculated the potential amount of sunlight available each month for Gustavus, Alaska (Fig. 2), from sunrise and sunset data (Astronomical Appli-

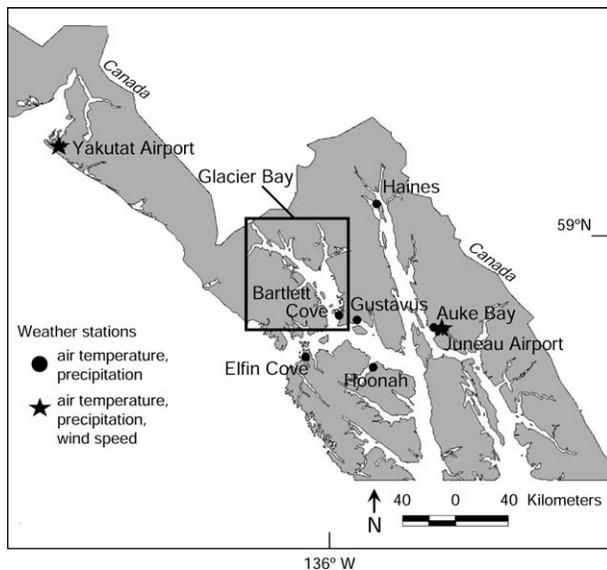


Fig. 2. Weather stations in the vicinity of Glacier Bay, Alaska. Data from the eight weather stations were averaged to obtain regional patterns of air temperature and precipitation. Data from the Juneau Airport and Yakutat Airport stations were averaged to obtain regional patterns of wind speed.

cations Department of the U.S. Naval Observatory, <http://aa.usno.navy.mil/data/>). Daily calculations of the number of minutes between sunrise and sunset were averaged over each month. These estimated values of available light do not factor in the influence of local topography (e.g., surrounding mountains) and cloud cover on irradiance, so the day length variable represents the seasonal changes in the potentially available sunlight.

TIDAL MODELING

Tidal current speed is expected to play an important role in controlling the stratification in estuarine environments. The estuarine Richardson number, which contains tidal current speed, was identified by Fischer et al. (1979) as a key parameter in determining whether an estuary would be highly stratified or well mixed. In an effort to understand the influence of tidal mixing on oceanographic patterns in Glacier Bay, detailed computational tidal simulations of Glacier Bay were conducted in place of direct measurements. The simulations were carried out using ADCIRC (Luettich and Westerink 1991) - a powerful, open source, and widely-used tidal circulation code. ADCIRC allows a user-specified domain to be forced by open boundary tides, interior tidal potential, meteorological conditions, and freshwater inflows. ADCIRC also has advanced wetting and drying algorithms, which are of great importance in regions with large tidal ranges, such as Glacier Bay. Output from ADCIRC

includes, among other things, time series and global output of water surface elevation, depth-integrated velocity, and scalar concentration distributions. ADCIRC has the ability to perform harmonic analysis on both the elevation and the velocity results. As we expected that long-term statistics on the tidal climate may have a greater bearing on observed oceanographic patterns than short-term fluctuations, a harmonic analysis of the domain was performed. To determine a single representative value of tidal current speed at each oceanographic station, the root-mean-square (RMS) speed was calculated from the results of the harmonic analysis.

The monthly assessment of meteorological and physical variables matches the broad-scale analysis of factors influencing oceanographic conditions. This choice of scale is also driven by the lack of knowledge of the time scales upon which these parameters influence hydrographic conditions, and represents an initial examination of their role in driving oceanographic conditions.

DATA AGGREGATION AND VARIABLE CALCULATION

Euphotic depth was defined as the depth at which PAR equals 1% of that measured at the surface. An index of stratification was calculated to describe the stability of the water column: differences in the density of the water column between adjacent 1-m depth bins ($\Delta\sigma_t \text{ m}^{-1}$) were calculated so that a mean of density change could be determined for a specified stratum of the water column. Similar stratification indices have been used to quantify water column stability (e.g., Bowman and Esaias 1981; Sime-Ngando et al. 1995). To convert turbidity measurements from NTU (nephelometric turbidity units) to mg l^{-1} , the OBS sensor was calibrated with representative benthic sediment from the location of sampling.

Oceanographic characteristics were determined for the upper 15 m of the water column. Means of temperature, salinity, stratification, turbidity, and chlorophyll *a* were calculated over the surface stratum of 0–15 m for each cast. This depth stratum was chosen based on examination of vertical profiles within Glacier Bay, which indicated that this stratum is the most dynamic region of the water column and is the zone of highest biological production (Etherington and Hooge unpublished data). Within Pacific fjords, including Glacier Bay, water density typically reaches 90% of the deep water value by 10–15 m (Pickard and Stanton 1980). The depth stratum of 0–15 m is a zone of high biological production in southeast Alaska estuarine systems (Ziemann et al. 1991). Depth-integrated chlorophyll *a* concentrations within Auke Bay, Alaska, were almost identical for both 0–15 m and 0–30 m intervals (Ziemann et al. 1991), suggesting that

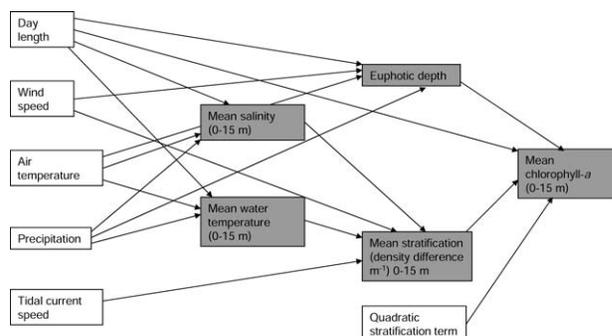


Fig. 3. Hypothesized relationships between external physical factors, oceanographic parameters, and chlorophyll *a* within Glacier Bay, Alaska. The response variables for the five separate multiple regression models are shaded in gray. The arrows connect explanatory variables to response variables, and illustrate all potential causative parameters that were included in the multiple regression selection procedure to determine the best-fit model describing the response variable.

almost all of the phytoplankton occurred in the top 15 m.

Due to the potentially large amount of spatial variation in oceanographic patterns inherent in fjord systems, we divided Glacier Bay into four zones to account for this spatial variability: lower Bay (stations 0, 1, 2, 3), central Bay (stations 4, 5, 6, 13, 14, 15), West Arm (stations 7, 8, 9, 10, 11, 12, 21, 22, 23), and East Arm (stations 16, 17, 18, 19, 20). We based the zones on their physical properties such as bathymetry and proximity to glaciers and oceanic source waters (Fig. 1). The lower Bay zone is representative of entrance sill processes, the central Bay is characteristic of the fjord basin, while the East and West Arm zones represent head of fjord conditions. Two stations located in Geikie Inlet were included in the West Arm zone due to their similar glacial influence. Months of the year were grouped into four seasons based on meteorological parameters: spring = February, March, April; summer = May, June, July; fall = August, September, October; and winter = November, December, January.

STATISTICAL ANALYSES

We created a path diagram to describe the hypothesized relationships among variables in the Glacier Bay estuarine system (Fig. 3). Arrows lead from explanatory variables to the response variables and depict hypothesized causal rather than correlative relationships. Originally, the entire system was analyzed using path analysis (e.g., Mitchell 1993), but there were too many missing data (entire observations were excluded from the analysis when any one of the possible ten variables had missing data) and the system model was not a good

representation of the data. Instead, separate multiple regression analyses were conducted for several pathways that made up the hypothesized estuarine dynamics for Glacier Bay. The response variables for the individual multiple regression models included: mean salinity 0–15 m, mean water temperature 0–15 m, mean stratification index 0–15 m, euphotic depth, and mean chlorophyll *a* 0–15 m (Fig. 3). This approach allowed us to assess the unique contribution of each explanatory variable.

Levels of turbidity (OBS) were highly variable in time, and we had a much smaller data set for turbidity than the other oceanographic parameters (Table 1), so we were unable to fit regression models describing the factors that were most influential in determining turbidity patterns. Instead, euphotic depth was modeled as a function of the four explanatory variables determining turbidity (Fig. 3). General patterns of turbidity can be described and are useful to correlate with other oceanographic characteristics within Glacier Bay.

All multiple regression models were analyzed for each combination of zone and season (Jongman et al. 1995; Legendre and Legendre 1998; JMP 2002 version 5.0. SAS Institute Inc., Raleigh, North Carolina). Explanatory variables were standardized (mean = 0, variance = 1) so that the relative strength of parameter estimates in the model could be compared. The value of a parameter describes the change in the response variable with one unit increase in the explanatory variable. The response variables were log-transformed when necessary to meet assumptions of normality. Each of the explanatory variables that is shown with an arrow connecting it to the response variable was included in the stepwise backward multiple regression procedure (probability to leave model = 0.10). Best-fit models were chosen as the simplest model with the largest amount of explained variation (R^2 ; using Cp and Adjusted R^2 criteria). Outliers were examined with Cook's D test and were removed when highly influential. Residuals of the models were examined to ensure that model assumptions were met. Quadratic terms were added to the model when preliminary examination of the data indicated that a nonlinear quadratic relationship might exist (only for chlorophyll *a* analyses). Bonferroni corrections were made to the regression results to adjust for multiple tests of significance being carried out simultaneously, due to the calculation of the five response variables from the same CTD data. As a result, we have adjusted our p values for the five response variables by multiplying by 5 and then comparing p' to the unadjusted significance level α . This method is equivalent to rejecting our hypotheses at an alpha level of 0.01, instead of 0.05 ($\alpha' = \alpha/k$; Legendre and Legendre 1998). This conserva-

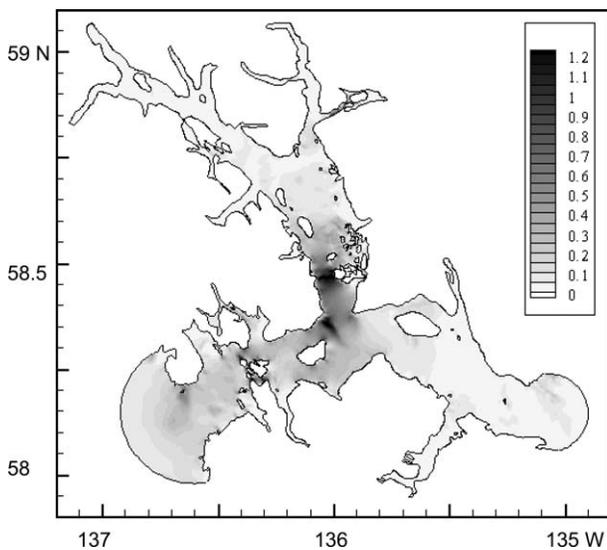


Fig. 4. Grayscale contours of root-mean-square (RMS) values of tidal current speed (m s^{-1}) for the Glacier Bay domain. Results are obtained from the harmonic analysis of ADCIRC simulations of tidal circulation in the Bay.

tive approach decreases the probability of Type I errors.

In examining the relationships between meteorological variables (air temperature, precipitation, wind speed, day length) and oceanographic parameters (salinity, water temperature, stratification index, euphotic depth, chlorophyll *a*), we used the average monthly weather values for the month in which the oceanographic sampling was conducted (e.g., if oceanographic sampling occurred on April 10–15, 1998, average weather values for April 1998 were used in the analyses).

Results

PATTERNS OF METEOROLOGICAL AND PHYSICAL PARAMETERS

Monthly air temperatures for the Glacier Bay region for the years 1993–2002 followed a fairly smooth seasonal curve, with coldest temperatures in January (mean = -2.5°C) and warmest temperatures in July and August (means = 13.5°C and 13.3°C , respectively). Air temperatures in January and February exhibited the highest variability among years, while temperatures in other months exhibited less variability among years. Average monthly precipitation varied greatly both among months and among years from 1993 to 2002. May and June exhibited the lowest precipitation rates of the year (means = 0.31 and 0.28 cm d^{-1} , respectively), and exhibited low variability in precipitation rates among years. September and October had the greatest precipitation rates (means = 0.94 and

1.01 cm d^{-1} , respectively). There was high variability in precipitation levels among years during the months of October through February. Wind speeds were highly variable among years (1993–2002), with this pattern apparent for all months. Generally, highest winds occurred during May, October, and December (means = 2.79 , 2.85 , and 2.92 m s^{-1} , respectively), with lowest winds in July and August (means = 2.34 and 2.46 m s^{-1} , respectively). Within the Glacier Bay region, the average number of minutes of daylight ranges from 389 min d^{-1} in December to a high of $1,091 \text{ min d}^{-1}$ in June. The months in between exhibit an approximately linear increase or decrease in day length.

The results of the ADCIRC simulations reveal that the lower part of Glacier Bay experiences intense tidal currents and mixing, while tidal current speeds near the heads of the arms of the Bay are extremely small (Fig. 4). Modeled RMS speeds at the lower Bay measurement stations (1–3) range from 0.329 to 0.722 m s^{-1} and the maximum RMS speed observed in the lower Bay (not at one of the stations) was approximately 1.5 m s^{-1} . Maximum instantaneous tidal current speeds in the lower Bay will be even larger than this due to two reasons: RMS values represent an average of a periodic signal, and harmonic analysis filters out spring and neap conditions to yield a long-term average. The ADCIRC simulations have shown that peak instantaneous speeds during spring conditions can exceed 2.5 m s^{-1} . These strong currents are due to the shallow entrance sill region (minimum depth of 25 m) and the narrowing of the Bay at the mouth (Fig. 1). There is a dramatic contrast between the lower Bay and the upper Bay, with much smaller RMS tidal current speeds in the upper Bay (Fig. 4). The ranges of RMS tidal current speeds at the oceanographic stations are as follows: central Bay: 0.0432 – 0.139 m s^{-1} , West Arm: 0.0011 – 0.0432 m s^{-1} , and East Arm: 0.0091 – 0.0236 m s^{-1} .

The model also demonstrates the large tidal range within Glacier Bay, with values averaging 3.86 m at the lowest portions of the Bay, steadily increasing with distance up the arms of the Bay, reaching an average of 4.59 m at the head of the inlets. This pattern of tidal range is typical of fjord systems that narrow with distance from the mouth. Glacier Bay exhibits mixed tides, with two high and two low tides per day, with successive high and low tides of significantly different heights.

SPATIAL AND SEASONAL OCEANOGRAPHIC PATTERNS

Salinity

Average salinities of surface waters within Glacier Bay were generally highest in spring and winter months, with lowest salinities in late summer and

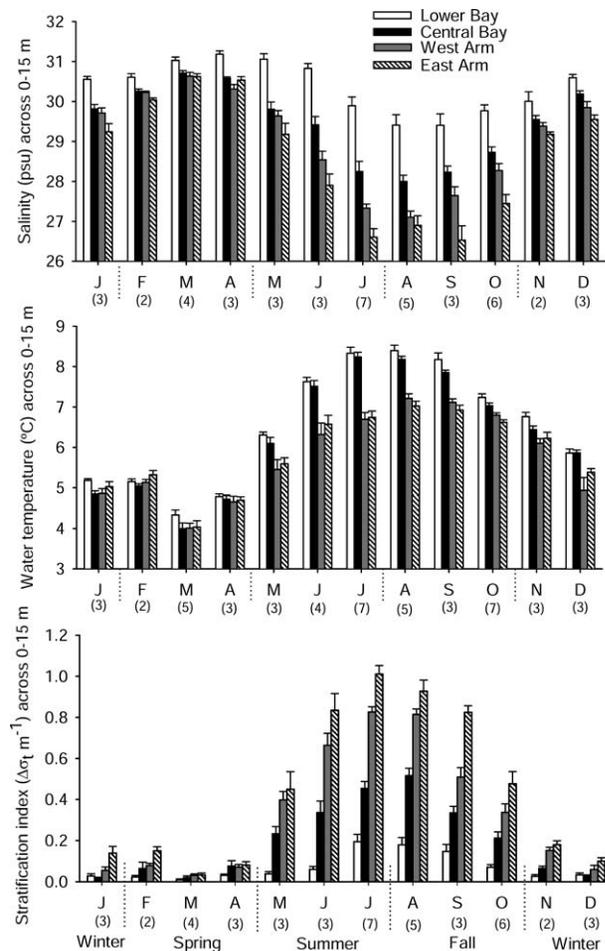


Fig. 5. Oceanographic patterns as a function of month and zone. Values represent means (+ standard error) of each of the parameters from all casts averaged over the top 15 m of the water column across each month for each zone: Salinity, water temperature, and stratification. Season definitions used in analyses are illustrated. The number of years for which data were obtained is indicated in parentheses below each month; numerous casts were taken within each zone during each sampling trip.

early fall (July–September; Fig. 5). Within Glacier Bay, there was a decrease in average surface water salinity from the mouth of the Bay to the head of the Bay, with the East Arm exhibiting lower salinity values than the West Arm. Surface salinity patterns were fairly homogeneous among zones within the Bay in spring and to a lesser degree in winter, but demonstrated large variability among zones in summer and fall.

There were substantial differences among seasons and zones in the type, strength, and explanatory power of physical variables that influenced salinity within the upper 15 m (Table 2). Air temperature had the most pervasive influence on salinity patterns of surface waters with an increase in air temperature

causing a decrease in salinity in the majority of zones in spring, summer, and fall. Precipitation had a negative influence on salinity, predominately in the fall; precipitation was also influential in determining salinity in the East Arm in summer and in the lower Bay in winter. Day length also contributed to variation in salinity during spring and winter, with opposite effects during these seasons.

Water Temperature

Average surface water temperatures in Glacier Bay were lowest in the spring, with the next coldest temperatures in winter months, with both of these seasons demonstrating little spatial differences in average temperature (Fig. 5). Average surface water temperatures were higher in summer and fall, with slight decreases in temperature moving from the lower Bay to the head of the Bay.

There were substantial differences among seasons and zones in the type, strength, and explanatory power of physical variables that influence water temperature within the upper 15 m (Table 3). Similar to the patterns exhibited for salinity, air temperature had the most pervasive influence on surface water temperature patterns, with an increase in air temperature causing an increase in water temperatures in the majority of zones throughout the year. Day length had a more sporadic influence on water temperatures, acting in a positive manner in fall and winter in various zones. Precipitation levels had less influence, explaining some variation in water temperature in the lower and central Bay in fall and in the East Arm in winter, with an increase in precipitation causing an increase in water temperature.

Stratification

Average surface water stratification within Glacier Bay was least in spring and winter, and greatest in the summer and fall months (Fig. 5). Stratification increased with distance from the mouth of the Bay, with lowest levels in the lower Bay, moderate levels in the central Bay, and highest levels at the head of the Bay; the East Arm zone exhibited higher average stratification than the West Arm. Differences in stratification levels among the zones were highest in summer and fall compared to spring and winter, when all zones displayed similar water column stability.

The measured physical factors explained a relatively large amount of the variation in surface water stratification patterns across the majority of the seasons and zones (Table 4). In general, salinity was the dominant factor determining stratification patterns, particularly in summer and fall, with decreased salinity associated with higher stratifica-

TABLE 2. Best-fit multiple regression models describing the relationship between physical variables and the mean salinity of surface waters 0–15 m for each zone × season combination. Lower Bay = stations 0, 1, 2, 3; Central Bay = stations 4, 5, 6, 13, 14, 15; West Arm = stations 7, 8, 9, 10, 11, 12, 21, 22, 23; East Arm = stations 16, 17, 18, 19, 20. Spring = February, March, April; summer = May, June, July; fall = August, September, October; winter = November, December, January. Coefficients represent standardized variables so that the magnitude of parameters can be compared. Parameter estimates are positive, except where noted as -. Empty cells indicate that a particular independent variable was not included in the best fit model. (ns) 0.05 < p < 0.10; * p < 0.05; ** p < 0.01; *** p < 0.001.

| Salinity 0–15 m | Model Fit | Day Length | Air Temperature | Precipitation |
|-----------------|---------------------------|------------|-----------------|---------------|
| Spring | | | | |
| Lower Bay | R ² = 0.28** | 0.40** | | |
| Central Bay | R ² = 0.38*** | 0.33** | -0.37* | |
| West Arm | R ² = 0.32** | | -0.62** | |
| East Arm | R ² = 0.59*** | 0.37** | -0.55** | |
| Summer | | | | |
| Lower Bay | R ² = 0.12** | | -1.02* | |
| Central Bay | R ² = 0.27*** | | -1.32*** | |
| West Arm | R ² = 0.51*** | | -2.34*** | |
| East Arm | R ² = 0.51*** | | -2.46*** | -0.97* |
| Fall | | | | |
| Lower Bay | No models fit the data | | | |
| Central Bay | R ² = 0.37*** | | -0.98*** | -0.43*** |
| West Arm | R ² = 0.34*** | | -1.39*** | -0.44** |
| East Arm | R ² = 0.20* | 2.94* | -3.15* | |
| Winter | | | | |
| Lower Bay | R ² = 0.24** | | | -0.38** |
| Central Bay | R ² = 0.40*** | -1.83*** | | |
| West Arm | R ² = 0.17(ns) | -1.33 (ns) | | |
| East Arm | R ² = 0.23(ns) | -1.09 (ns) | | |

TABLE 3. Best-fit multiple regression models describing the relationship between physical variables and the mean water temperature for surface waters 0–15 m for each zone × season combination. Lower Bay = stations 0, 1, 2, 3; Central Bay = stations 4, 5, 6, 13, 14, 15; West Arm = stations 7, 8, 9, 10, 11, 12, 21, 22, 23; East Arm = stations 16, 17, 18, 19, 20. Spring = February, March, April; summer = May, June, July; fall = August, September, October; winter = November, December, January. Coefficients represent standardized variables so that the magnitude of parameters can be compared. Parameter estimates are positive, except where noted as -. Empty cells indicate that a particular independent variable was not included in the best fit model. (ns) 0.05 < p < 0.10; * p < 0.05; ** p < 0.01; *** p < 0.001.

| Temperature 0–15 m | Model Fit | Day Length | Air Temperature | Precipitation |
|--------------------|--------------------------|------------|-----------------|---------------|
| Spring | | | | |
| Lower Bay | R ² = 0.23* | -0.46 (ns) | 0.73** | |
| Central Bay | No models fit the data | | | |
| West Arm | R ² = 0.21* | | 1.04* | |
| East Arm | R ² = 0.31** | | 1.15** | |
| Summer | | | | |
| Lower Bay | R ² = 0.50*** | | 2.02*** | |
| Central Bay | R ² = 0.60*** | | 2.04*** | |
| West Arm | R ² = 0.14** | | 1.33** | |
| East Arm | R ² = 0.17** | | 1.05** | |
| Fall | | | | |
| Lower Bay | R ² = 0.59*** | 1.63*** | | 0.45** |
| Central Bay | R ² = 0.80*** | | 1.08*** | 0.24*** |
| West Arm | R ² = 0.16*** | | 0.31*** | |
| East Arm | R ² = 0.15** | 0.31** | | |
| Winter | | | | |
| Lower Bay | R ² = 0.44*** | | 1.34*** | |
| Central Bay | R ² = 0.53*** | | 1.30*** | |
| West Arm | R ² = 0.32** | 3.34** | | |
| East Arm | R ² = 0.64*** | 1.92** | | 0.54*** |

TABLE 4. Best-fit multiple regression models describing the relationship between physical variables and the mean stratification index for surface waters 0–15 m for each zone \times season combination. Lower Bay = stations 0, 1, 2, 3; Central Bay = stations 4, 5, 6, 13, 14, 15; West Arm = stations 7, 8, 9, 10, 11, 12, 21, 22, 23; East Arm = stations 16, 17, 18, 19, 20. Spring = February, March, April; summer = May, June, July; fall = August, September, October; winter = November, December, January. Coefficients represent standardized variables so that the magnitude of parameters can be compared. Parameter estimates are positive, except where noted as -. Empty cells indicate that a particular independent variable was not included in the best fit model. (ns) $0.05 < p < 0.10$; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

| Stratification 0–15 m | Model Fit | Wind Speed | Salinity | Water Temperature | Tidal Current Speed |
|-----------------------|------------------------|------------|----------|-------------------|---------------------|
| Spring | | | | | |
| Lower Bay | No models fit the data | | | | |
| Central Bay | $R^2 = 0.27^{**}$ | | -1.05** | | |
| West Arm | $R^2 = 0.18$ (ns) | | | 0.32 (ns) | |
| East Arm | $R^2 = 0.54^{***}$ | | -1.27*** | | |
| Summer | | | | | |
| Lower Bay | $R^2 = 0.75^{***}$ | | -0.73*** | | |
| Central Bay | $R^2 = 0.57^{***}$ | | -0.53*** | | |
| West Arm | $R^2 = 0.72^{***}$ | | -0.39*** | | |
| East Arm | $R^2 = 0.70^{***}$ | | -0.41*** | | |
| Fall | | | | | |
| Lower Bay | $R^2 = 0.58^{***}$ | | -0.56*** | | |
| Central Bay | $R^2 = 0.58^{***}$ | | -0.49*** | 0.52*** | |
| West Arm | $R^2 = 0.50^{***}$ | | -0.62*** | | |
| East Arm | $R^2 = 0.34^{***}$ | | -0.43*** | | |
| Winter | | | | | |
| Lower Bay | No models fit the data | | | | |
| Central Bay | $R^2 = 0.43^{***}$ | | -0.35* | 0.25** | |
| West Arm | $R^2 = 0.51^{**}$ | 0.17* | -0.70* | 0.35* | |
| East Arm | $R^2 = 0.63^{***}$ | | -1.11*** | | |

tion. The contribution of wind speed in determining stratification had a significant effect only in winter within the West Arm. Water temperature significantly explained variation in stratification at some zones during spring, fall, and winter. Tidal current speed did not explain stratification patterns across any of the zone \times season combinations.

Turbidity

Turbidity within the surface waters demonstrated peak levels across all zones in July (particularly West and East Arms), while turbidity was also higher across all zones in August and December (Fig. 6). During September and October, higher levels of turbidity were demonstrated primarily within the East Arm. Higher monthly average turbidity in West and East Arms was associated with a large amount of variability, most likely due to high variance among both stations and years. Station-specific patterns of turbidity within the surface waters demonstrated that the higher levels within the West and East Arms were dominated by stations at the head of the Arms (stations 12 and 21, and stations 19 and 20, respectively), with higher levels also noted for stations 22 and 23 in Geikie Inlet.

Euphotic Depth

Average euphotic depths within Glacier Bay were shallowest in summer months, followed by fall, with spring and winter exhibiting deeper euphotic

depths (Fig. 6). Spatial differences in average euphotic depth varied among seasons. In the summer and fall, the lower Bay exhibited the deepest euphotic depth, followed by the central Bay, West Arm, and then East Arm. During spring and winter months, euphotic depth levels were fairly similar among zones, with the lower Bay generally having the shallowest euphotic depth and the central Bay having the greatest euphotic depth. Euphotic depth varied much less among seasons within the lower and central Bay zones compared with larger seasonal differences in euphotic depth in West and East Arms.

In general, the measured physical variables did not consistently explain variation in euphotic depth across all seasons and zones (Table 5). The ability of the models to fit the data was poor in summer months for all zones, as well as in winter for the lower and central Bay zones, and in the lower Bay for spring and fall. In spring months, the models that best described euphotic depth were relatively consistent among zones, with most physical variables significantly influencing patterns of euphotic depth across all zones. In the fall months, the physical variables that explained euphotic depth differed among zones, with many of the variables demonstrating influences on euphotic depth that were opposite those shown during spring. During winter, values of euphotic depth within West and East Arms could be described only by one or two physical variables that differed between the zones.

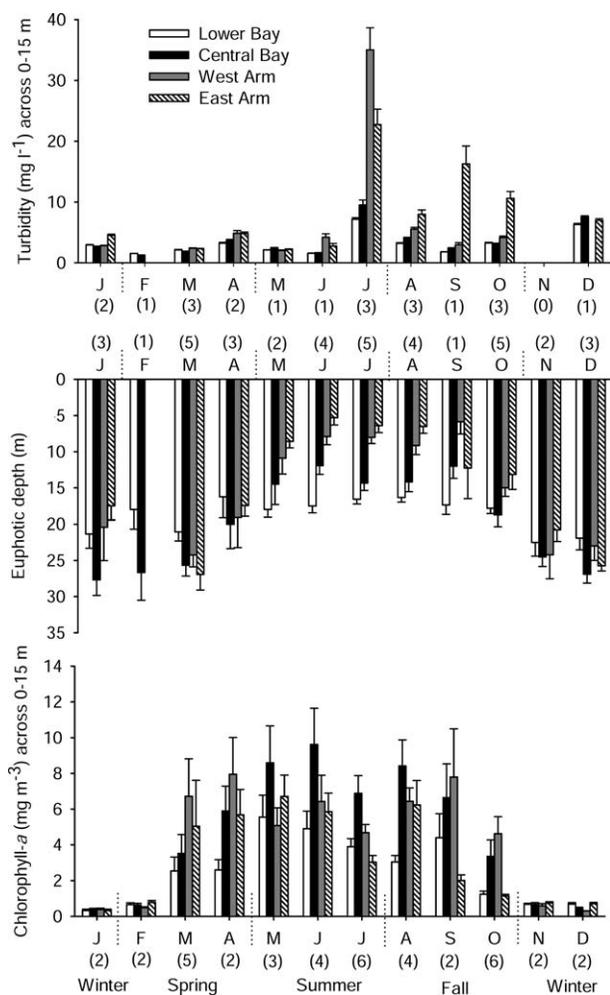


Fig. 6. Oceanographic patterns by month and zone. Values represent means (+ standard error) of each of the parameters from all casts averaged over the top 15 m of the water column across each month for each zone: turbidity (optical backscatterance), euphotic depth, and chlorophyll *a*. The euphotic depth is defined here as the depth at which the amount of light (photosynthetically available radiation – PAR) measured is 1% of that at the surface. The number of years for which data were obtained is indicated in parentheses below each month; numerous casts were taken within each zone during each sampling trip.

Chlorophyll *a*

Average chlorophyll *a* levels within surface waters were lowest and least variable in the winter months and highest in the summer months, with high levels also found in spring and fall (Fig. 6). During the months of highest chlorophyll *a* abundance (March–October), the lower Bay had the lowest average chlorophyll *a* levels of the four zones in four of the months, while East Arm had the lowest levels in three of the months. The zone with the highest chlorophyll *a* levels changed among seasons. In the spring months, West Arm had the highest chloro-

phyll *a* followed by East Arm and central Bay, but variability in chlorophyll *a* levels was high. In the summer, the central Bay had a substantially greater average concentration of chlorophyll *a*, with similar levels of chlorophyll *a* between the lower Bay, West Arm, and East Arm. During fall months, the central Bay and West Arm zones had similar levels of chlorophyll *a* that were substantially higher than East Arm and the lower Bay.

The amount of variation in chlorophyll *a* concentration explained by the measured physical factors was highly variable among zones within each season, as well as among seasons (Table 6). For winter months, the physical variables did not significantly describe patterns of chlorophyll *a*, while the amount of explained variation was generally lower in summer compared to spring and fall. In general, euphotic depth had the most consistent significant association with chlorophyll *a* levels across seasons and zones compared with the other measured physical variables, primarily demonstrating a negative relationship between euphotic depth and chlorophyll *a*. Day length also contributed significantly to the amount of chlorophyll *a*, exhibiting the most influence in the fall season. The degree of surface water stratification demonstrated some influence on chlorophyll *a* levels in spring and summer, but was most influential in the fall, with an increase in stratification generally associated with an increase in chlorophyll *a*. The quadratic term of stratification (used to model a nonlinear relationship between stratification and chlorophyll *a*) had an influence on chlorophyll *a* levels only at West and East Arms in the spring and fall, indicating that the highest chlorophyll *a* was found at intermediate stratification levels.

Discussion

PATTERNS OF SEASONAL AND SPATIAL VARIATION IN OCEANOGRAPHIC CONDITIONS

This paper describes the first comprehensive record of the seasonal periodicity and spatial distribution in phytoplankton biomass and oceanographic conditions within the high latitude temperate glacial fjord of Glacier Bay. It also represents one of the few long-term, detailed studies of a fjord system within southeast Alaska. This broad-scale analysis of the oceanographic properties within Glacier Bay provides the framework for further analyses examining interannual variability in these parameters and the mechanisms driving these changes.

Over the 10 yr that were sampled (1993–2002), the largest seasonal changes in the physical oceanographic system occurred from May to October. May represents a period of initial late spring-early

TABLE 5. Best-fit multiple regression models describing the relationship between physical variables and the absolute value of the euphotic depth (the depth at which the amount of available light equals 1% of that measured at the surface) for each zone × season combination. Lower Bay = stations 0, 1, 2, 3; Central Bay = stations 4, 5, 6, 13, 14, 15; West Arm = stations 7, 8, 9, 10, 11, 12, 21, 22, 23; East Arm = stations 16, 17, 18, 19, 20. Spring = February, March, April; summer = May, June, July; fall = August, September, October; winter = November, December, January. Coefficients represent standardized variables so that the magnitude of parameters can be compared. Parameter estimates are positive, except where noted as -. It should be noted that since euphotic depth is measured as a negative number, the absolute value of euphotic depth was used in the analyses to aid in interpretation of parameter estimates (i.e., as the absolute value of euphotic depth gets larger, the euphotic depth increases to a deeper depth). Empty cells indicate that a particular independent variable was not included in the best fit model. (ns) 0.05 < p < 0.10; * p < 0.05; ** p < 0.01; *** p < 0.001.

| Euphotic Depth | Model Fit | Day Length | Wind Speed | Air Temperature | Precipitation |
|----------------|---------------------------|------------|------------|-----------------|---------------|
| Spring | | | | | |
| Lower Bay | No models fit the data | | | | |
| Central Bay | R ² = 0.55*** | -62.98*** | 11.13** | 40.26** | -30.08*** |
| West Arm | R ² = 0.45** | -19.51* | 33.78** | | -40.68** |
| East Arm | R ² = 0.54** | -64.45** | | 38.08(ns) | -20.78* |
| Summer | | | | | |
| Lower Bay | No models fit the data | | | | |
| Central Bay | No models fit the data | | | | |
| West Arm | No models fit the data | | | | |
| East Arm | No models fit the data | | | | |
| Fall | | | | | |
| Lower Bay | No models fit the data | | | | |
| Central Bay | R ² = 0.41** | 47.85** | 3.99** | -45.57** | |
| West Arm | R ² = 0.21** | | | -4.94** | |
| East Arm | R ² = 0.51*** | | | | 3.94*** |
| Winter | | | | | |
| Lower Bay | No models fit the data | | | | |
| Central Bay | No models fit the data | | | | |
| West Arm | R ² = 0.59(ns) | | | 39.10* | -15.93 (ns) |
| East Arm | R ² = 0.30* | -0.07* | | | |

TABLE 6. Best-fit multiple regression models describing the relationship between physical variables and the mean concentration of chlorophyll *a* for surface waters 0–15 m for each zone × season combination. Lower Bay = stations 0, 1, 2, 3; Central Bay = stations 4,5,6,13,14,15; West Arm = stations 7, 8, 9, 10, 11, 12, 21, 22, 23; East Arm = stations 16, 17, 18, 19, 20. Spring = February, March, April; summer = May, June, July; fall = August, September, October; winter = November, December, January. Coefficients represent standardized variables so that the magnitude of parameters can be compared. Parameter estimates are positive, except where noted as -. Empty cells indicate that a particular independent variable was not included in the best fit model. (ns) 0.05 < p < 0.10; * p < 0.05; ** p < 0.01; *** p < 0.001.

| Chlorophyll <i>a</i> 0–15 m | Model Fit | Day Length | Euphotic Depth | Stratification | Quadratic Stratification |
|-----------------------------|----------------------------|------------|----------------|----------------|--------------------------|
| Spring | | | | | |
| Lower Bay | R ² = 0.16* | 0.82* | | | |
| Central Bay | R ² = 0.62*** | | -1.04*** | | |
| West Arm | R ² = 0.71*** | | -0.98*** | 12.29* | -82.31 (ns) |
| East Arm | R ² = 0.43** | | -1.08** | | |
| Summer | | | | | |
| Lower Bay | No models fit the data | | | | |
| Central Bay | R ² = 0.18* | | -0.52* | | |
| West Arm | R ² = 0.09 (ns) | | 0.34 (ns) | | |
| East Arm | R ² = 0.49*** | 2.26* | | -0.61*** | |
| Fall | | | | | |
| Lower Bay | R ² = 0.52*** | 0.66*** | 0.58* | 0.51* | |
| Central Bay | R ² = 0.28*** | 0.97*** | | | |
| West Arm | R ² = 0.28*** | | | 1.62** | -1.11 (ns) |
| East Arm | R ² = 0.59*** | 1.39*** | | | -0.25* |
| Winter | | | | | |
| Lower Bay | No models fit the data | | | | |
| Central Bay | No models fit the data | | | | |
| West Arm | No models fit the data | | | | |
| East Arm | No models fit the data | | | | |

summer change in southeast Alaska, with a large increase in freshwater runoff due to snowmelt (Royer 1982). Oceanographic changes in May were a decrease in salinity, increase in temperature, increase in stratification, and decrease in euphotic depth. July and August marked the mid point of change, leading to a reversal of these parameters until October, after which conditions became more similar (both among zones and among months) from November through April. The changes in salinity, temperature, and stratification did not coincide with changes in phytoplankton abundance (see below). Within Glacier Bay surface waters, the upper Bay zones were the areas of greatest change over the course of the year for all measured physical oceanographic factors except for water temperature, which exhibited a greater range of values within the lower and central Bay zones. These spatial patterns were most likely due to the stronger influence of freshwater discharge on the upper portions of the Bay.

INFLUENCE OF FRESHWATER INPUT

Freshwater discharge integrates the seasonal and annual changes in atmospheric forcing and represents a strong link between the terrestrial and marine systems. Presently there are no discharge data available for Glacier Bay. In the absence of actual measurements or estimates, other parameters have been used to infer variability in freshwater input to this system. To examine the temporal variability in freshwater discharge, we used measurements of air temperature, day length, and precipitation to approximate the role of this factor on the oceanographic system. Although all three variables were influential in determining salinity patterns, air temperature had the most pervasive influence on surface salinity (as well as water temperature), suggesting that this variable could be a good indicator of how climate variability can potentially influence this oceanographic system.

The greatest degree of change (both seasonally and spatially) in oceanographic properties within Glacier Bay appeared to be driven by freshwater input. Freshwater input is one of the most important factors affecting water properties of a fjord (Pickard and Stanton 1980). It influences water column stability and flow dynamics, and introduces suspended and dissolved materials (including sediment and nutrients), drastically altering water column properties and biological activity (Smetacek 1986). Freshwater discharge rates result from direct and stored precipitation and ensuing runoff. In glacially fed fjords, sources of freshwater can also include melting of tidewater glaciers below the surface and melting of icebergs and sea ice at the surface (Cowan 1992). The dynamics of freshwater

discharge from Alaska's coastal region is of particular importance, as this input is one of the dominant factors influencing the circulation of the northern Gulf of Alaska (Royer 1981).

The substantial changes in salinity across the Glacier Bay fjord zones and seasons suggest that this system is characteristic of a high-runoff fjord (Pickard 1961, 1967), mainly influenced by freshwater discharge from glacier and snowfield melt entering the upper fjord zones, with maximum rates in July and August. The generalized regional model of freshwater discharge for southeast and south-central Alaska predicts an initial discharge peak in May associated with spring snowmelt, followed by continual increases in freshwater input during summer due to snow and glacial melting, and then an annual maximum in October due to direct precipitation (Royer 1982). Our findings for Glacier Bay highlight local variation in the generalized model of freshwater discharge for southeast and south-central Alaska (Royer 1982) and suggest that some fjords within southeast Alaska, particularly those along the mainland (Pickard 1967), contribute more to summer than fall discharge rates.

Despite their superficial similarities as upper fjord zones, the East and West Arms of Glacier Bay exhibited differences in oceanographic patterns (e.g., consistently lower salinity and higher stratification levels within the East Arm compared to the West Arm) that suggest differences in the influence of freshwater discharge. These patterns may suggest differences in the rates of direct or stored precipitation in these upper fjord zones. Alternatively, these salinity and stratification differences could have resulted from differences in watershed to surface area ratios (e.g., Gay and Vaughan 2001) or circulation patterns between the two inlets (e.g., the shallower sill of 60 m at the entrance of the East Arm may decrease the flow of higher salinity water into the East Arm). Differences in the oceanographic parameters at these zones at the head of Glacier Bay likely resulted from a combination of local differences in freshwater input as well as inlet topography.

Our understanding of freshwater input to the system would be greatly enhanced by direct measurements at various locations within the Bay. Annual changes in the amount of coastal freshwater discharge are linked to the Pacific Decadal Oscillation and could have a major influence on biological production in the northeast Pacific Ocean (Royer et al. 2001). It is estimated that since 1950, the volume of glaciers in Glacier Bay has decreased by 3,000 km³, which has contributed to a sea level rise of 8 mm during this time period (Echelmeyer unpublished data). Direct information on the dynamics of freshwater discharge in Glacier Bay

would aid in our understanding of the connection of Glacier Bay to the Gulf of Alaska ecosystem and global ocean dynamics.

ROLE OF TIDAL CURRENTS IN GLACIER BAY

The ADCIRC model results illustrate the dramatic contrast in tidal current speeds throughout Glacier Bay (Fig. 4). In much of the Bay, tidal current speeds are fairly low, particularly within the upper reaches of the Arms. Intense tidal currents and mixing are observed in the lower Bay (in particular, near Sitakaday Narrows and Point Carolus) with high tidal current speeds also found in a localized area in Adams Inlet (an inlet off of the East Arm).

The relative importance of tidal currents in driving oceanographic patterns within Glacier Bay was found to vary both in time and space. The interaction of tidal currents with bottom topography influences patterns of mixing; we might expect that the influence of tidal currents in determining stratification would vary depending on the zone within Glacier Bay, which is related to water column depth. Seasonal differences in the relative role of tidal currents might also be expected, given the seasonality in those processes that enhance the stability of the water column, most importantly freshwater runoff.

By grouping our stations into zones, we are essentially removing the greatest source of spatial variation in tidal current speed (particularly the high speed conditions within the lower Bay zone; Fig. 4). Closer examination of the lower Bay stratification levels illustrates the lower values, as well as lower variability, in stratification within this zone (Fig. 5), highlighting the stronger influence of tidal mixing within this area, which is the shallowest region of the Bay. Once this large-scale variation in tidal currents was factored out (by grouping stations into zones), our results suggest that variation in the average tidal current speed did not play a significant role in determining smaller-scale (within-zone) patterns of stratification, since current speeds within a zone are relatively uniform.

To examine these patterns further and to illustrate the case of the differences among zones, we conducted additional analyses aggregating the zones so that a single analysis for all of Glacier Bay was conducted for each season. These analyses indicate that in spring and winter (when stratification levels were lower and fairly homogenous among the zones of the Bay), only salinity and water temperature were important in explaining variation in stratification. In summer and fall (when stratification levels were very high in some zones and varied dramatically among the zones), salinity and tidal current speed (but not water temperature) explained most variation in stratification levels. The

relationship between tidal current speed and stratification in summer and fall was negative – increased tidal current speed reduced stratification. On a bay-wide scale, different factors are important in affecting stratification in different seasons, and tidal current speed only appears to be important in summer and fall when contrast between strata is most marked. Separation of stations by zones is effective in removing this coarser spatial variation in the influence of tidal current speed. Our results suggest that in this system, broad-scale spatial variation in stratification levels are driven both by forces that act to disrupt stability (tidal current speed) and enhance stability (salinity, water temperature), while finer-scale spatial and temporal variation in stratification levels are driven by properties that enhance stability (salinity, water temperature).

ROLE OF WINDS IN GLACIER BAY

Winds did not appear to be highly influential in determining the stability of surface waters within Glacier Bay. One reason for the minor influence of winds could be the limited fetch of the winds in Glacier Bay, due to its lack of direct connection to the Gulf of Alaska, making its maximum fetch the length of the Bay. This low wind fetch is in contrast with other Alaskan fjord estuaries (e.g., Prince William Sound, Cook Inlet, Disenchantment Bay), which have a more direct connection with the Gulf of Alaska and are more exposed to wind, with fetch from some angles reaching thousands of kilometers. Strong stratification from high freshwater discharge in most of the Bay throughout much of the year may create water layers that resist wind-induced mixing. If wind speeds were high enough and fetch was large enough, we would expect wind speed to influence stability of surface waters. Alternatively, because the scales of the wind and oceanographic measurements differed, we may not have been able to detect the smaller-scale effects of wind on oceanographic parameters. Winds may influence surface water characteristics on shorter time scales, with stronger winds causing destabilization of the water column one day and weaker winds allowing stratification to form the next (Wroblewski and Richman 1987).

In temperate systems, the spring phytoplankton bloom is thought to be initiated by the cessation of stronger winter winds, causing the mixed layer to shoal. This shoaling coupled with increased insolation strengthens the stratification that retains phytoplankton within surface waters and initiates the spring bloom (Mann and Lazier 1996). Oceanographic data from Glacier Bay suggest that a mixed layer does not develop in early spring surface waters, and average monthly weather data do not demon-

strate decreased winds during the spring season. In other parts of southeast Alaska, a mixed layer does not generally form in spring (e.g., Auke Bay, Ziemann et al. 1991), and factors other than winds are influential in the initiation of the spring bloom (Ziemann et al. 1991; see below).

SPATIAL PATTERNS OF STRATIFICATION WITHIN GLACIER BAY

Glacier Bay is a complex fjord that can be defined by three different patterns of oceanographic conditions and circulation (Syvitski et al. 1987; Mann and Lazier 1996). The lower part of Glacier Bay is an area of low stratification and intense mixing due to tidal currents within the shallow entrance sill region (Fig. 4). The upper parts of the fjord are characterized by high stratification and a two-layer system due to the dominance of freshwater discharge. An intermediate section of the fjord within the central Bay can be classified as a body of water with moderate stratification, with stronger mixing relative to stabilizing inputs, compared to the upper regions of the Bay. These spatial differences in stratification are most apparent from May to October, but are evident throughout most of the year.

Finer-scale spatial patterns of stratification within an estuarine system could indicate locations of oceanographic fronts (e.g., Perry et al. 1983), which represent the boundary between two water masses. Fronts are often associated with enhanced surface nutrients and higher biological activity, including aggregations of phytoplankton, zooplankton, forage fishes, and marine birds and mammals. These patterns are attributed to accumulation of materials at the frontal boundary (Pingree et al. 1975; Perry et al. 1983; Parsons 1986; Largier 1993; Mann and Lazier 1996) as well as the injection of energy into stratified layers causing the upward movement of nutrient-rich water to the surface (Mann and Lazier 1996). Downwelling of water masses at fronts is often apparent, which could directly transfer pelagic nutrients and biological biomass to the benthic system (Largier 1993). Fronts can influence the spatial structure of both the pelagic and benthic communities.

In Glacier Bay, spatial patterns of stratification suggest several locations where oceanographic fronts may exist. The most noticeable location is within the lower Bay entrance region, where the well-mixed higher salinity lower Bay waters meet the more stratified lower salinity central Bay waters. Stations 1 and 2 in the lower Bay zone exhibited the lowest stratification levels of all stations, while a substantial increase in stratification (associated with a dramatic change in depth) was demonstrated among stations 2, 3, and 4 (Fig. 7). Continuous horizontal salinity measurements within this section

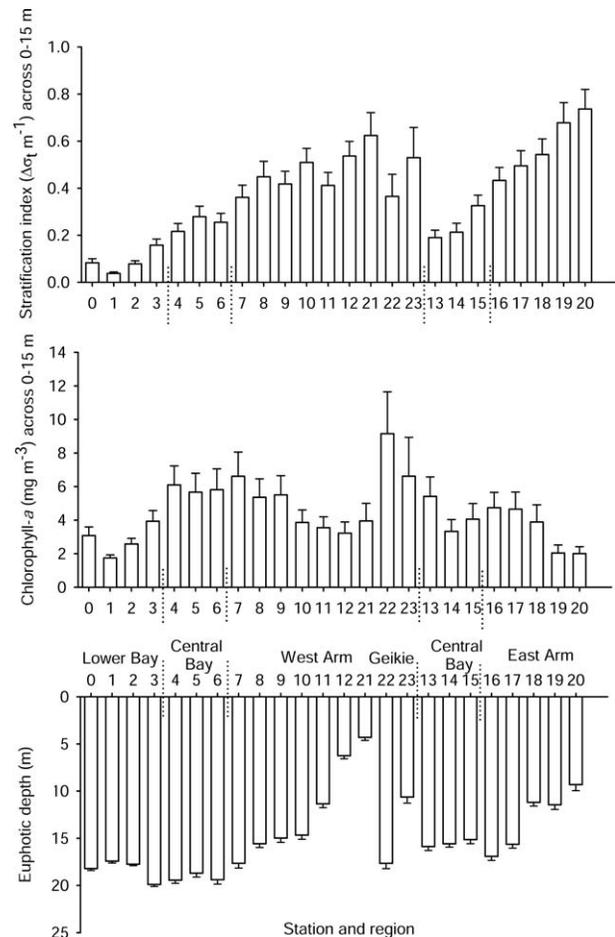


Fig. 7. Oceanographic patterns by station within Glacier Bay. Values represent means (+ standard error) of each of the parameters from all casts and averaged across each station: stratification, chlorophyll *a*, and euphotic depth. Zones (as defined for analyses) are indicated below the station numbers. Stations are oriented from the mouth to the head of the Bay, with stations 0–12 and 21 representing the axis of the Bay from Icy Strait to the head of Tarr Inlet (West Arm), stations 22 and 23 characterizing Geikie Inlet, and stations 13–20 representing the Muir Inlet (East Arm) axis. The euphotic depth is defined here as the depth at which the amount of light (photosynthetically available radiation – PAR) measured is 1% of that at the surface.

of the Bay confirm the presence of such a density front that shifts its position with the tides (Cokelet et al. 2007; Etherington unpublished data). This location was associated with some of the highest levels of chlorophyll *a* in the mid-channel areas of central Glacier Bay. Further work focused on determining the existence and characteristics of potential frontal zones could provide vital information on many of the biological processes within Glacier Bay, including the spatial aggregation of biological biomass, the behavioral responses of predators and prey, the dispersal and settlement of planktonic larvae, the transfer of pelagic material

to the benthic system, and potential mechanisms influencing high phytoplankton abundance.

PHYTOPLANKTON ABUNDANCE PATTERNS

*Temporal Patterns of Chlorophyll *a**

Determining the timing, duration, and magnitude of the spring phytoplankton bloom is a central objective of biological oceanography. The onset of the spring bloom is thought to be the result of favorable light conditions (threshold of radiation) and stabilization of the water column that confines phytoplankton to nutrient-rich surface waters (replenished by winter mixing) where available light allows photosynthesis (Sverdrup 1953; Mann and Lazier 1996). In Glacier Bay we might expect an increase in chlorophyll *a* concentration during May, when the degree of stratification within the Bay increased dramatically. Instead, chlorophyll *a* concentrations substantially increased in March. A similar discontinuity of physical oceanographic characteristics and phytoplankton biomass has been demonstrated within Auke Bay (Ziemann et al. 1990). One explanation is that the spring bloom was initiated by transient stratification events that did not persist, and were not detected by the time scale of our sampling. Alternatively, the stratification levels observed in March may be sufficiently high for bloom conditions, and solar irradiation in March reaches a threshold whereby photosynthesis rates dramatically increased. Other studies in high latitude systems have also demonstrated that incident light controls the initiation of spring blooms (Ziemann et al. 1991). The results of our analyses suggest that the amount of available sunlight (day length) was influential on spring bloom dynamics only within the lower Bay zone, while stratification played a role in spring chlorophyll *a* levels only within the West Arm. Within the West Arm, highest chlorophyll *a* levels were associated with intermediate stratification levels. The factor most consistently associated with spring chlorophyll *a* levels was euphotic depth, with a negative relationship suggesting that phytoplankton self-shading may limit photosynthesis and influence bloom dynamics. The relative importance of various factors in promoting the spring phytoplankton bloom appears to vary spatially within Glacier Bay.

A key finding of our study was that high chlorophyll *a* concentrations within Glacier Bay are sustained throughout the spring and summer and into the fall. This seasonal pattern of phytoplankton biomass contrasts with classical models of nutrient limited systems (maximum spring peak followed by depressed levels in summer and a secondary moderate peak in fall) and with observed patterns within many mid-latitude systems (Mann and Lazier 1996), fjords

worldwide (Matthews and Heimdal 1980), as well as Alaska estuaries (Burrell 1986; Auke Bay: Ziemann et al. 1991; Prince William Sound: Eslinger et al. 2001). Our observations suggest that the hydrography of Glacier Bay may replenish nutrients to moderately stratified surface waters, which could lead to a highly productive system that fuels an abundance of higher trophic levels.

Relatively sustained chlorophyll *a* throughout the summer is characteristic of shelf-break regions and fjord systems where turbulent mixing at sills replenishes nutrients within stratified surface waters (Parsons 1986). Sustained high levels of primary productivity have been observed within Kachemak Bay, Alaska, from May to August (Larrance and Chester 1979). Higher levels of chlorophyll *a* abundance throughout the spring, summer, and fall in Glacier Bay may have been caused by persistent stratification (due to high levels of freshwater discharge) coupled with the renewal of nutrients from deeper areas into the euphotic zone from localized tidal turbulence, entrainment-driven estuarine circulation, wind mixing, and the presence of density fronts (Syvitski et al. 1987). In summer and fall in those zones exhibiting the highest chlorophyll *a* levels, physical factors explained only a small amount of the variation in chlorophyll *a*. This lack of relationship suggests that there are variables that were not measured that were influential in determining phytoplankton abundance. One hypothesis is that phytoplankton abundance was being driven by top-down biological processes (i.e., zooplankton grazing). This potential explanation for summer and fall patterns is in contrast to the spring pattern, when high phytoplankton levels may have been driven by bottom-up physical processes (i.e., available light, water column stability) before zooplankton had responded to the initial bloom. Further work is needed to separate the influence of bottom-up versus top-down forces influencing phytoplankton abundance, as well as how these patterns may change throughout the year and throughout Glacier Bay.

*Spatial Patterns of Chlorophyll *a**

The highest levels of chlorophyll *a* were generally found within the central Bay (except stations 14 and 15, which exhibited slightly lower levels) and the lower reaches of both the East and West Arms (Fig. 7). This spatial pattern becomes more evident when average chlorophyll *a* levels by station are plotted against the distance from the head of the fjord, highlighting that phytoplankton biomass is highest within the middle region of Glacier Bay (Fig. 8).

Several factors may be responsible for the spatial patterns of chlorophyll *a*. Conditions within the

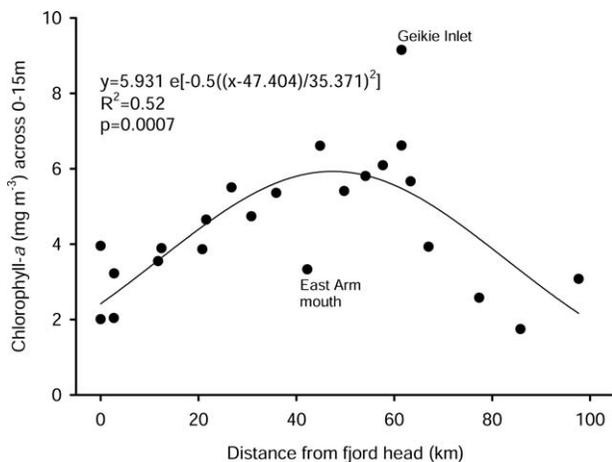


Fig. 8. Relationship between the distance from the head of the fjord and chlorophyll *a* abundance. Chlorophyll *a* values represent averages over the top 15 m of the water column pooled over all sampling periods for each station. Each data point represents the value for one station. Results from nonlinear regression analyses are presented. The data point that lies far above the model fit at approximately 65 km represents station 22 (high chlorophyll *a* values in Geikie Inlet), and the data point below the model fit at approximately 40 km is the value for station 14 (situated at the East Arm sill in shallower, less-stratified water).

lower Bay zone may be too turbulent for phytoplankton to remain within surface waters where sufficient light is available for photosynthesis. This hypothesis is supported by the lower levels of stratification in this zone throughout the year (present study) and moderate chlorophyll *a* levels throughout the water column, even though nutrients are likely plentiful (Eisner unpublished data). Within West and East Arms, highest chlorophyll *a* levels were found at intermediate stratification levels (indicated by the negative quadratic term for stratification), and highest stratification levels were associated with low chlorophyll *a* abundance. Low chlorophyll *a* levels within the most stratified waters of the upper fjord zones could be caused by the water column becoming too stable for regenerated nutrients in the lower water column to be mixed into surface waters. Spatial patterns of phytoplankton abundance similar to Glacier Bay have been observed in an Arctic sound system where lowest chlorophyll was found at the extremes of highest and lowest salinities that were related to lowest and highest water column stability, respectively, and highest chlorophyll abundance was detected at intermediate salinities (Legendre et al. 1982). The decreased levels of chlorophyll *a* in the upper parts of the West and East Arms could also be due to the net outflow of surface waters caused by freshwater discharge. Horizontal advection due to freshwater discharge has been demonstrated as a highly influential factor driving phytoplankton distribution

in surface waters of other estuarine systems (Stocker et al. 1979). Alternatively, high turbidity levels associated with high stratification levels (both due to high freshwater discharge) could directly decrease phytoplankton abundance by causing increased settling rates due to flocculation with sediment particles (Cowan 1995) or indirectly decrease abundance through decreased light levels. Spatially-specific high turbidity levels within the East Arm zone were correlated with depressed levels of chlorophyll *a* during September and October. Higher abundance of phytoplankton within the central Bay and the lower portions of the West and East Arms (Fig. 8) were likely due to the optimal conditions of moderate stratification (Fig. 7), higher light levels (due to decreased sediment concentrations in the surface waters), and regenerated surface nutrients.

Conclusions

Glacier Bay is a complex estuarine system, representing a combination of fjord types, with three zones of varying oceanographic conditions. Our results suggest that this fjord exhibited strong competing forces influencing water column stability: at the head of the fjord, strong stratification was promoted through much of the year, likely due to high levels of freshwater discharge, while strong tidal currents over the shallow entrance sill enhanced vertical mixing. Where these two processes met in the central deep basins there were optimal surface conditions of intermediate stratification, decreased sedimentation and higher light levels, and potential nutrient renewal. These conditions can explain the high and sustained chlorophyll *a* levels observed in the central parts of the Bay. The complex dynamics of this oceanographic system, integrated with the spatial location of the fjord relative to oceanic sources of upwelled high nutrient waters, could be one of the main factors leading to Glacier Bay's high concentration of marine mammals, seabirds, fish, and invertebrates.

This broad-scale analysis of the seasonal and spatial oceanographic patterns in Glacier Bay will be useful in assessing multiple issues related to fjord ecosystems, including the connectivity of fjords and outside waters through exchange and dispersal of materials and organisms, the locations and time periods with higher phytoplankton biomass that could elucidate the high abundance of upper trophic levels, the locations of oceanographic fronts that can influence distribution patterns and form aggregations of organisms, and the spatial patterns of benthic-pelagic coupling and the identification of critical benthic habitats. The findings of this study further our understanding of physical-biological linkages within fjord estuaries and provide informa-

tion necessary for making management decisions and understanding the ecosystem properties of critical marine protected areas, such as Glacier Bay National Park.

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LITERATURE CITED

- BAKER, C. S., J. M. STRALEY, AND A. PERRY. 1992. Population characteristics of individually identified humpback whales in southeastern Alaska: Summer and fall 1986. *Fishery Bulletin* 90: 429–437.
- BOWMAN, M. J. AND W. E. ESAIAS. 1981. Fronts, stratification, and mixing in Long Island and Block Island Sounds. *Journal of Geophysical Research* 86:4260–4264.
- BRATTEGARD, T. 1980. Why biologists are interested in fjords, p. 53–66. *In* H. J. Freeland, D. M. Farmer, and C. D. Levings (eds.), *Fjord Oceanography*. Plenum Press, New York.
- BURRELL, D. C. 1986. Interaction between silled fjords and coastal regions, p. 187–216. *In* D. W. Hood and S. T. Zimmerman (eds.), *The Gulf of Alaska: Physical environment and biological resources*. National Oceanic and Atmospheric Administration, U.S. Government Printing Office, Washington, D.C.
- COKELET, E. D., A. J. JENKINS, AND L. L. ETHERINGTON. 2007. A transect of Glacier Bay ocean currents measured by Acoustic Doppler Current Profiler (ADCP), p. 80–83. *In* J. F. Piatt and S. M. Gende (eds.), *Proceedings of the Fourth Glacier Bay Science Symposium*. U.S. Geological Survey Scientific Investigations Report 2007-5047, Washington, D.C.
- COWAN, E. A. 1992. Meltwater and tidal currents: Controls on circulation in a small glacial fjord. *Estuarine, Coastal and Shelf Science* 34:381–392.
- COWAN, E. A. 1995. Characteristics of suspended particulate matter and sedimentation of organic carbon in Glacier Bay fjords, p. 24–28. *In* D. R. Engstrom (ed.), *Proceedings of the Third Glacier Bay Science Symposium, 1993*. U.S. Department of the Interior, National Park Service, Anchorage, Alaska.
- ESLINGER, D. L., R. T. COONEY, C. P. MCROY, A. WARD, T. C. KLINE, JR., E. P. SIMPSON, J. WANG, AND J. R. ALLEN. 2001. Plankton dynamics: Observed and modeled responses to physical conditions in Prince William Sound, Alaska. *Fisheries Oceanography* 10:81–96.
- FISCHER, H. B., E. J. LIST, R. C. Y. KOH, J. IMBERGER, AND N. H. BROOKS. 1979. *Mixing in Inland and Coastal Waters*. Academic Press, New York.
- GAY, S. M. AND S. L. VAUGHAN. 2001. Seasonal hydrography and tidal currents of bays and fjords in Prince William Sound, Alaska. *Fisheries Oceanography* 10:159–193.
- HALL, D. K. AND C. S. BENSON. 1995. Changes of glaciers in Glacier Bay, Alaska, using ground and satellite measurements. *Physical Geography* 16:27–41.
- HALLET, B., L. HUNTER, AND J. BOGEN. 1996. Rates of erosion and sediment evacuation by glaciers: A review of field data and their implications. *Global and Planetary Change* 12:213–235.
- JONGMAN, R. H., C. J. F. TER BRAAK, AND O. F. R. VAN TONGEREN. 1995. *Data Analysis in Community and Landscape Ecology*, new edition. Cambridge University Press, Cambridge, New York.
- KOPPES, M. N. AND B. HALLET. 2002. Influence of rapid glacial retreat on the rate of erosion by tidewater glaciers. *Geology* 30: 47–50.
- LARGIER, J. L. 1993. Estuarine fronts: How important are they? *Estuaries* 16:1–11.
- LARRANCE, J. D. AND A. J. CHESTER. 1979. Source, composition, and flux of organic detritus in lower Cook Inlet. U.S. Department of Commerce, NOAA. Outer Continental Shelf Environmental Assessment Program Final Report 46:1–71.
- LEGENDE, L., R. G. INGRAM, AND Y. SIMARD. 1982. Aperiodic changes of water column stability and phytoplankton in an arctic coastal embayment, Manitousuk Sound, Hudson Bay. *Naturaliste Canadien* 109:775–786.
- LEGENDE, P. AND L. LEGENDE. 1998. *Numerical Ecology*, Second English edition. Elsevier Science, Amsterdam, The Netherlands.
- LUETTICH, R. A. AND J. J. WESTERINK. 1991. A solution for the vertical variation of stress, rather than velocity, in a three-dimensional circulation model. *International Journal for Numerical Methods in Fluids* 12:911–928.
- MANN, K. H. AND J. R. N. LAZIER. 1996. *Dynamics of Marine Ecosystems: Biological-physical Interactions in the Oceans – 2nd edition*. Blackwell Science, Inc., Malden, Massachusetts.
- MATTHEWS, J. B. 1981. The seasonal circulation of the Glacier Bay, Alaska fjord system. *Estuarine, Coastal and Shelf Science* 12:679–700.
- MATTHEWS, J. B. L. AND B. R. HEIMDAL. 1980. Pelagic productivity and food chains in fjord systems, p. 377–398. *In* H. J. Freeland, D. M. Farmer, and C. D. Levings (eds.), *Fjord Oceanography*. Plenum Press, New York.
- MATHEWS, E. A. AND G. W. PENDLETON. 2006. Declines in harbor seal (*Phoca vitulina*) numbers in Glacier Bay National Park, Alaska, 1992–2002. *Marine Mammal Science* 22:167–189.
- MATTHEWS, J. B. AND A. V. QUINLAN. 1975. Seasonal characteristics of water masses in Muir Inlet, a fjord with tidewater glaciers. *Journal of the Fisheries Research Board of Canada* 32:1693–1703.
- MITCHELL, R. J. 1993. Path analysis: Pollination, p. 211–232. *In* S. M. Scheiner and J. Gurevitch (eds.), *Design and Analysis of Ecological Experiments*, 1st edition. Chapman and Hall, New York.
- PARSONS, T. R. 1986. Ecological relations, p. 561–570. *In* D. W. Hood and S. T. Zimmerman (eds.), *The Gulf of Alaska: Physical environment and biological resources*. National Oceanic and Atmospheric Administration, U.S. Government Printing Office, Washington, D.C.
- PERRY, R. I., B. R. DIKLE, AND T. R. PARSONS. 1983. Tidal mixing and summer plankton distributions in Hecate Strait, British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences* 40: 871–887.
- PICKARD, G. L. 1961. Oceanographic features of inlets in the British Columbia mainland coast. *Journal of the Fisheries Research Board of Canada* 18:907–999.
- PICKARD, G. L. 1967. Some oceanographic characteristics of the larger inlets of southeast Alaska. *Journal of the Fisheries Research Board of Canada* 24:1475–1506.
- PICKARD, G. L. AND B. R. STANTON. 1980. Pacific Fjords – A Review of Their Water Characteristics, p. 1–51. *In* H. J. Freeland, D. M. Farmer, and C. D. Levings (eds.), *Fjord Oceanography*. Plenum Press, New York.
- PINGREE, R. D., P. R. PUGH, P. M. HOLLIGAN, AND G. R. FORSTER. 1975. Summer phytoplankton blooms and red tides along tidal

- fronts in the approaches to the English Channel. *Nature* 258: 672–677.
- ROBARDS, M., G. DREW, J. PIATT, J. M. ANSON, A. ABOOKIRE, J. BODKIN, P. HOOGE, AND S. SPECKMAN. 2003. Ecology of selected marine communities in Glacier Bay: Zooplankton, forage fish, seabirds and marine mammals. U.S. Geological Survey, Alaska Science Center, Anchorage, Alaska.
- ROYER, T. C. 1981. Baroclinic transport in the Gulf of Alaska, II. Fresh water driven coastal current. *Journal of Marine Research* 39: 251–266.
- ROYER, T. C. 1982. Coastal freshwater discharge in the Northeast Pacific. *Journal of Geophysical Research* 87:2017–2021.
- ROYER, T. C., C. E. GROSCH, AND L. A. MYSAK. 2001. Interdecadal variability of Northeast Pacific coastal freshwater and its implications on biological productivity. *Progress in Oceanography* 49:95–111.
- SIME-NGANDO, T., M. GOSSELIN, S. ROY, AND J.-P. CHANUT. 1995. Significance of planktonic ciliated protozoa in the Lower St. Lawrence Estuary: Comparison with bacterial, phytoplankton, and particulate organic carbon. *Aquatic Microbial Ecology* 9:243–258.
- SMETACEK, V. S. 1986. Impact of freshwater discharge on production and transfer of materials in the marine environment, p. 85–106. In S. Skreslet (ed.), *The Role of Freshwater Outflow in Coastal Marine Ecosystems*, Proceedings of a workshop held in Bodø, Norway, May 21–25, 1985. NATO Advanced Science Institute Series, Series G: Ecological Sciences, Volume 7, Springer-Verlag, Berlin.
- STOCKNER, J. G., D. D. CLIFF, AND K. R. SHORTREED. 1979. Phytoplankton ecology of the Strait of Georgia, British Columbia. *Journal of Fisheries Research Board Canada* 35:657–666.
- SVENDSEN, H. 1986. Mixing and exchange processes in estuaries, fjords and shelf waters, p. 13–45. In S. Skreslet (ed.), *The Role of Freshwater Outflow in Coastal Marine Ecosystems*, Proceedings of a workshop held in Bodø, Norway, May 21–25, 1985. NATO Advanced Science Institute Series, Series G: Ecological Sciences, Volume 7, Springer-Verlag, Berlin.
- SVERDRUP, H. U. 1953. On conditions for the vernal blooming of phytoplankton. *Journal du Conseil Permanent International pour l'Exploration de la Mer* 18:287–295.
- SWITSKI, J. P. M., D. C. BURRELL, AND J. M. SKEI. 1987. *Fjords: Processes and Products*. Springer-Verlag Inc, New York.
- TAGGART, S. J., P. N. HOOGE, J. MONDRAGON, E. R. HOOGE, AND A. G. ANDREWS. 2003. Living on the edge: Distribution of Dungeness crab *Cancer magister* in a recently deglaciated fjord. *Marine Ecology Progress Series* 246:241–252.
- WROBLEWSKI, J. S. AND J. G. RICHMAN. 1987. The non-linear response of plankton to wind mixing events – implications for survival of larval northern anchovy. *Journal of Plankton Research* 9:103–123.
- ZIEMANN, D. A., L. D. CONQUEST, K. W. FULTON-BENNETT, AND P. K. BIENFANG. 1990. Interannual variability in the physical environment of Auke Bay, Alaska, p. 99–128. In D. A. Ziemann and K. W. Fulton-Bennett (eds.), *APPRISE: Interannual variability and fisheries recruitment*. The Oceanic Institute, Honolulu, Hawaii.
- ZIEMANN, D. A., L. D. CONQUEST, M. OLAIZOLA, AND P. K. BIENFANG. 1991. Interannual variability in the spring phytoplankton bloom in Auke Bay, Alaska. *Marine Biology* 109:321–334.

SOURCES OF UNPUBLISHED MATERIALS

- EHELMEYER, K. unpublished data. University of Alaska, Department of Geology and Geophysics, P.O. Box 755780, Fairbanks, Alaska 99775.
- EISNER, L. unpublished data. National Oceanic and Atmospheric Administration, Auke Bay Laboratory, 11305 Glacier Highway, Juneau, Alaska 99801.

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