Structure of marine predator and prey communities along environmental gradients in a glaciated fjord

Martin Renner, Mayumi L. Arimitsu, and John F. Piatt

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Abstract: Spatial patterns of marine predator communities are influenced to varying degrees by prey distribution and environmental gradients. We examined physical and biological attributes of an estuarine fjord with strong glacier influence to determine the factors that most influence the structure of predator and prey communities. Our results suggest that some species, such as walleye pollock (*Theragra chalcogramma*), black-legged kittiwake (*Rissa tridactyla*), and glaucous-winged gull (*Larus glaucescens*), were widely distributed across environmental gradients, indicating less specialization, whereas species such as capelin (*Mallotus villosus*), harbor seal (*Phoca vitulina*), and Kittlitz's murrelet (*Brachyramphus brevirostris*) appeared to have more specialized habitat requirements related to glacial influence. We found that upper trophic level communities were well correlated with their mid trophic level prey community, but strong physical gradients in photic depth, temperature, and nutrients played an important role in community structure as well. Mid-trophic level forage fish communities were correlated with the physical gradients more closely than upper trophic levels were, and they showed strong affinity to tidewater glaciers. Silica was closely correlated with the distribution of fish communities, the mechanisms of which deserve further study.

Résumé : La répartition spatiale de communautés de prédateurs marins est influencée à divers degrés par la répartition des proies et des gradients environnementaux. Nous examinons les attributs physiques et biologiques d'un fjord estuarien fortement influencé par les glaciers afin de cerner les facteurs qui ont la plus grande incidence sur la structure des communautés de prédateurs et de proies. Nos résultats suggèrent que certaines espèces, comme le goberge de l'Alaska (*Theragra chalcogramma*), la mouette tridactyle (*Rissa tridactyla*) et le goéland à ailes grises (*Larus glaucescens*), sont largement distribuées le long de gradients environnementaux, témoignant d'une spécialisation limitée, alors que des espèces comme le capelan (*Mallotus villosus*), le phoque commun (*Phoca vitulina*) et le guillemot de Kittlitz (*Brachyramphus brevirostris*) semblent nécessiter des habitats plus spécialisés en ce qui concerne l'influence de glaciers. Nous avons constaté que les communautés de niveaux trophiques supérieurs sont bien corrélées avec leur communauté de proies de milieux trophiques intermédiaires, mais que de forts gradients physiques de la profondeur photique, de la température et des nutriments jouent également un important rôle dans la détermination de la structure des communautés. Les communautés de poissons fourrage de niveaux trophiques intermédiaires sont corrélées plus fortement aux gradients physiques que les communautés de niveaux trophiques supérieurs, et elles présentent une plus grande affinité pour les glaciers de marée. Le mécanisme associé à une forte corrélation entre la silice et la répartition des communautés de poissons mérite notamment plus d'attention.

[Traduit par la Rédaction]

Introduction

Community structure may be defined as the distribution of species assemblages within a particular environmental setting. Identifying the biotic and abiotic factors that structure communities has long been a subject of ecological research, particularly in terrestrial and nearshore intertidal habitats (Paine 1980; Strong et al. 1984). Community structure in pelagic marine environments has been more challenging to assess, in part because many marine organisms are highly mobile, the structural complexity of pelagic marine habitats is relatively low, and environmental gradients are manifested over much larger spatial scales than those found in terrestrial systems (Ballance et al. 1997; Schick et al. 2011). Seabirds and marine mammals offer some advantages for at-sea studies because they are visible above the water surface all or some of the time, and so it is relatively easy to assess distribution of entire communities over a range of spatial scales (Ballance et al. 1997; Tynan et al. 2005). Technological advances in remote sensing and oceanographic modelling have also made it easier

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to measure or predict gradients in corresponding biotic (e.g., primary production, prey density) and abiotic (temperature, salinity, bottom depth) variables while conducting surveys for birds and mammals.

In recent decades, studies have demonstrated that prey availability is an important factor influencing the distribution of seabirds and marine mammals (e.g., Ainley et al. 2005; Friedlaender et al. 2006; Fauchald 2009). Predator distributions have also been correlated with habitat features that influence prey distribution, such as oceanic fronts, sea surface temperature, or primary production (Schneider 1990; Ballance et al. 1997; Ainley et al. 2009). Some of this historical work has focused on a select number of common species and analyzed those individually (e.g., Hyrenbach and Veit 2003; Sinclair et al. 2005; Ainley et al. 2005) or examined community structure after aggregating species into foraging guilds (e.g., Burger et al. 2004; Renner et al. 2008).

Only a few multidisciplinary studies of marine communities have collected adequate data to examine the relative importance of prey abundance versus lower trophic level productivity, as well as oceanography (e.g., temperature, fronts, stratification, etc.), in structuring upper trophic level communities (e.g., Tynan et al. 2005; Ainley et al. 2009). In some cases the prey distribution has an overwhelming influence on predator community structure, while at other times, features such as fronts may structure both predator and prey together. Because some ocean features may be more predictable or visible than small prey, it is conceivable that physical features may be even better predictors than the distribution of actual prey. For example, Ainley et al. (1992) found that the distribution of sea ice was more important than prey distribution to the distribution of Antarctic seabirds.

In this study, we tested two competing hypotheses while examining the distribution of communities. Hypothesis 1 predicts that predators depend on and (or) shape the community composition of their prey, and thus we would expect a relatively strong correlation between upper trophic level (UTL) and mid trophc level (MTL) community compositions. We would further predict that correlations between UTL communities and communities at lower trophic levels (LTL) decrease with trophic level, as each trophic level adds an additional source of variation and mechanistic coupling is mediated by an increasing number of steps. The distribution of UTL communities is then primarily a function of the availability of their prey, with succeeding levels of underlying trophic and abiotic factors diminishing in strength (Fig. 1, hypothesis 1). This proposed system of hierarchical correlations should be present irrespective of top-down or bottom-up control. Because we are using only a snapshot in time, we have no means of testing for the direction of the effect, as would be required if testing for bottom-up versus top-down control. Alternatively, hypothesis 2 is that the predator communities are structured more directly by physical factors rather than by the community structure of their prey alone. For this scenario, we predict the distribution of UTL community composition to be correlated with communities of underlying trophic levels in a similar way to that under hypothesis 1, but would expect increased correlations with measures of the abiotic physical environment (Fig. 1, hypothesis 2). A planktonic predator community that grows in place with its prey may be unlikely to show such a pattern. However, mobile predators like large fish, seabirds, or marine mammals can cover a large area searching for patches of prey, and physical factors contributing to the habitat may become more important than the actual distribution of prey.

We studied the community structure of seabirds and marine mammals, UTL marine predators in Glacier Bay, Alaska. From the old-growth rainforests at its entrance to the barren glacial landscape of its upper arms, Glacier Bay is a living laboratory for the study of community structure in a highly variable environmental setting. While much is known about terrestrial communities bordering Glacier Bay (e.g., Chapin et al. 1994; Williamson et al. 2001, Milner et al. 2007), little is known about the structure of marine communities within the bay itself. We do know, however, that the marine ecosystem of Glacier Bay is complex and characterized by several strong environmental gradients (Etherington et al. 2007).

Because of management concerns about recent fluctuations in marine bird and mammal populations (Mathews and Pendleton 2006; Piatt et al. 2011) in Glacier Bay, Alaska, we conducted bay-wide surveys for marine birds and mammals to evaluate species abundance and distribution patterns. Applying sampling methods used elsewhere (e.g., Speckman et al. 2005; Arimitsu et al. 2012), we simultaneously measured environmental variables likely to influence their distribution, including a variety of physical factors and biological factors such as food supply. Although this study lacks replication among years, the considerable replication in spatial sampling during a critical foraging period for breeding birds (Drew and Piatt 2008) and marine mammals (Mathews and Pendleton 2006) permitted us to align community assemblages with biophysical factors across trophic levels.

We concurrently sampled the waters of Glacier Bay at seven levels: bathymetry, physical oceanography, nutrients, chlorophyll *a* (as a proxy for phytoplankton density), lower trophic level (zooplankton, LTL), mid trophic level (forage fish and macrozooplankton, MTL), and upper trophic level (marine birds and mammals, UTL) communities. In our analyses, we used multivariate ordinations to investigate how species associate into distinct communities along environmental gradients (Speckman et al. 2005; Schick et al. 2011). Given that the distribution and abundance of species in a community are correlated (Brown 1984), we can summarize the distribution data of an entire community using ordination to explore the dominant patterns of variation in community composition. For this, we used correspondence analysis (CA), which has been particularly popular in the study of plant and invertebrate communities (Legendre and Legendre 1998), and has been used in at least one study on seabirds (Abrams and Underhill 1986), in part because it captures the structure of the community in the first major axis of a CA. We used principal component analysis (PCA) to reduce environmental variables down to a few axes of environmental gradation with which to correlate CA scores (Ballance et al. 1997; Speckman et al. 2005). Comparing correlations between ordinations of UTL and MTL communities with the distribution of LTL biomass and major trends (PCAs) in the chemical, oceanographic, and topographic environment should allow us to distinguish between these two hypotheses.

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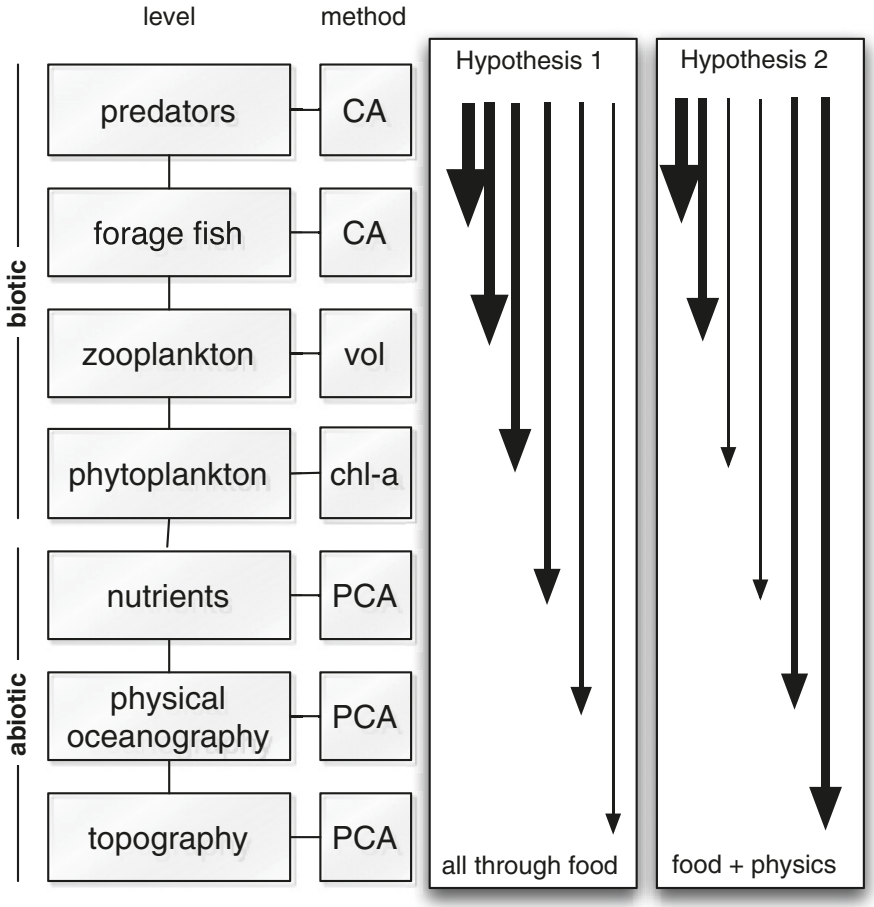
Fig. 1. Conceptual diagram of the analytical approach taken to relate abiotic to biotic factors and predator communities within Glacier Bay. Three individual principal component analyses (PCA) were used to summarize topographic, physical, and chemical variables, respectively. Mid and upper trophic level communities were each reduced to an ordination axis each using correspondence analysis (CA). Zooplankton density (lower trophic level) was measured as volume per standardized trawl. We tested two competing hypotheses. Hypothesis 1: The UTL community is driven by the distribution of prey communities. Under this hypothesis we expected the correlations of CA of UTL to gradually decrease with increasing distance in the trophic chain, each layer introducing some additional error and reducing the coupling to higher layers. Hypothesis 2: Physical processes are important to making food available to surface-feeding predators. Under hypothesis 2, we expected correlations between predator communities and forage fish as well as topography and physical oceanography.



Materials and methods

Study area

Glacier Bay is a Y-shaped glacial fjord located in southeast Alaska, USA, that stretches over 100 km northwestward from its mouth on Icy Strait (Fig. 2). Adjacent to some of the highest mountain peaks and largest glacial ice fields in North America, Glacier Bay is fed by numerous glacier-melt rivers and contains eight tidewater glaciers in its upper reaches. Filled by ice little more than 200 years ago, glaciers have rapidly retreated since the end of the Little Ice Age and are now restricted to the upper arms, leaving most of the Glacier Bay marine ecosystem ice-free (Molnia 2008). Glacial melting continues today at an accelerated pace (Larsen et al. 2005).

The marine ecosystem of Glacier Bay is complex and characterized by several strong environmental gradients (Etherington et al. 2007). The two inner arms that form the head of the bay are influenced by input of cold freshwater from tidewater glaciers, silt-laden glacial river runoff, and rainfall. The main bay features deep channels carved by glaciers, shallow sills, and narrow passes around islands. Near the mouth of the bay, strong tidal currents mix estuarine waters with deep water from the Gulf of Alaska (Hill et al. 2009). The close combination of strong currents, freshwater inflow, sediments, mixing, stratification, and complex topography create a dynamic environment in Glacier Bay, supporting locally abundant populations of forage fish and their predator populations within the bay.

These communities include some distinct fauna, some of which have exhibited dramatic changes in abundance or distribution in recent decades. Capelin (*Mallotus villosus*), an important forage species that largely disappeared from the Gulf of Alaska following the 1977 regime shift (Anderson and Piatt 1999), continues to spawn in the cold-water refugium of Glacier Bay and remains locally abundant there (Arimitsu et al. 2008). Other common forage taxa include Pacific sand lance (*Ammodytes hexapterus*), Pacific herring (*Clupea pallasii*), northern lampfish (*Stenobrachius leucopsarus*), and

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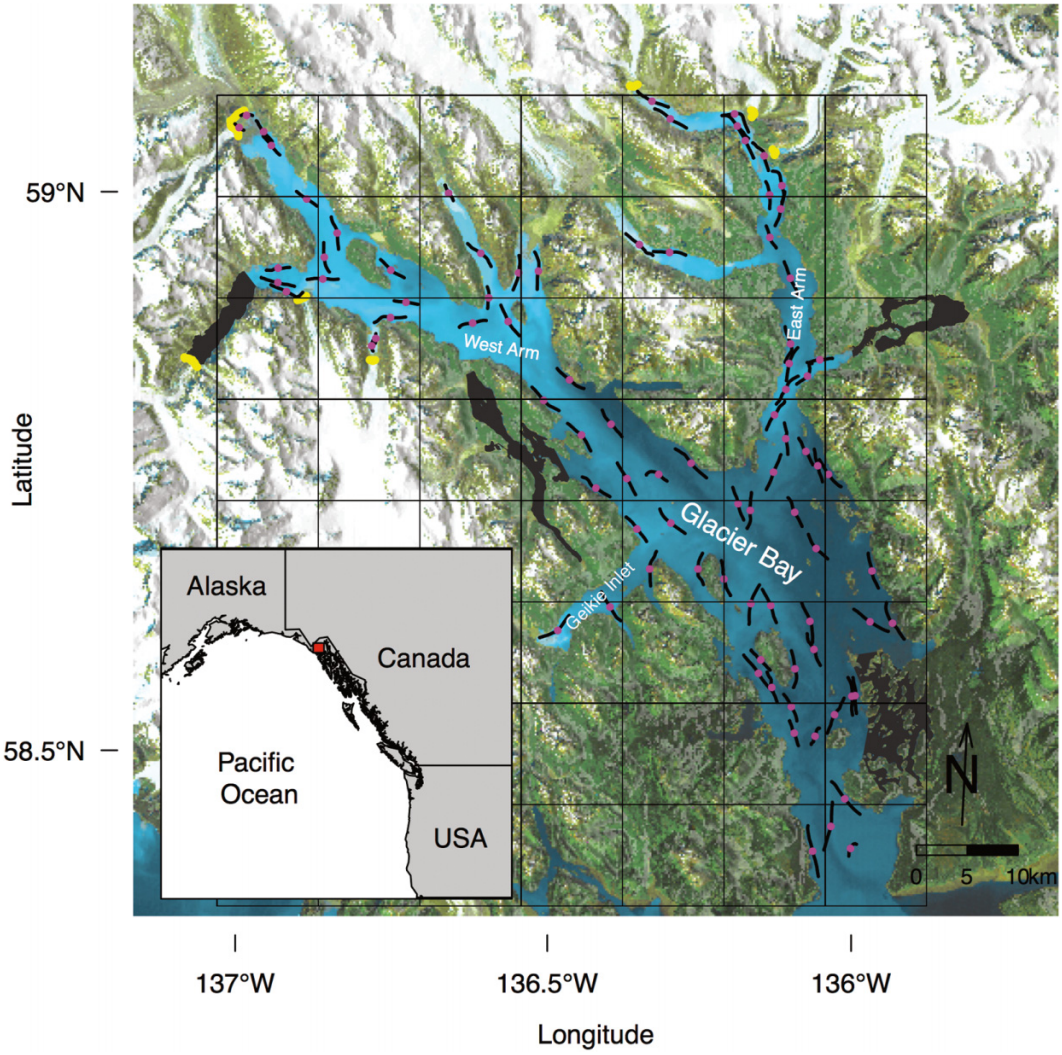
Fig. 2. Study area and sampling locations in Glacier Bay, Alaska, overlaid on a visible-light Landsat image and shaded relief. Stations (pink dots represent the midpoint of black transect lines) were randomly selected from the nodes of a 2 km grid. The fronts of eight tidewater glaciers are shown in yellow and sensitive National Park exclusion zones in dark gray. We dropped stations and transects within exclusion zones from the planned samples. For the analysis, we aggregated stations over the 10 km grid shown.



walleye pollock (*Theragra chalcogramma*) (Abookire et al. 2002; Arimitsu et al. 2008). Glacier Bay hosts about one-fifth of the world's population of the rare Kittlitz's murrelet (*Brachyramphus brevirostris*), a fish-eating seabird in the Auk family that is intimately associated with glacial-marine habitats and whose numbers in Glacier Bay declined by more than 85% during the 1990s (Piatt et al. 2011). The closely related marbled murrelet (*Brachyramphus marmoratus*) is more abundant in Glacier Bay, and not strongly associated with ice, but has also declined by a similar amount during the same period (Piatt et al. 2007). The marine avifauna is dominated (>75%) by a few piscivorous species, including murrelets, black-legged kittiwakes (*Rissa tridactyla*), pigeon guillemots (*Cepphus columba*), and glaucous-winged gulls (*Larus glaucescens*). Harbor seals (*Phoca vitulina*) depend on glacial ice for pupping, and numbers declined by more than 60% during the 1990s (Mathews and Pendleton 2006). In contrast, populations of humpback whales (*Megaptera novaeangliae*) and Steller sea lions (*Eumetopias jubatus*) increased dramatically (by 55% and 485%, respectively) during this same period (Gelatt et al. 2007; Mathews and Pendleton 2006), as did those of some other common seabirds and sea otters (Drew and Piatt 2008; Bodkin et al. 2007).

Study design and sample collection

Sample stations were randomly selected from a 2 km grid overlaid upon navigable waters within the bay, permitted by the park service (Fig. 2). Not all preselected sites could be sampled owing to logistical problems related to local bathymetry and current conditions, leaving a sample of 83 stations. To improve our measure of gradients related to tidewater glaciers, we added four stations close to the face of tidewater glaciers, resulting in a total of 87 stations. Our sampling appears to cover all major geographical features of the bay (Figs. 2 and 3).

We sampled each station once in 2004 between 23 June and 14 July (coinciding with the middle of the breeding season for most seabird species) with the 22 m stern trawler M/V *Stellar*.

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Sampling at each station included a 45 min pelagic trawl and survey transect for UTL marine predators that was conducted at a speed of about 2 kn (1 kn = 1.853 km·h^{-1}). We used a modified herring trawl with a net mouth opening that was approximately 50 m^2 and with diminishing mesh size from 5 cm at the mouth to 1 cm at the cod end. The net was equipped with a 3 mm mesh cod-end liner and a 1 mm mesh collecting cup. We towed the net within the upper 30 m of the water column (mean depth ± standard deviation (SD) = 12 ± 6.7 m) to sample within the usual foraging depth range of the most common seabird species. During each trawl two observers counted all marine bird and mammals encountered within 150 m of either side or ahead of the vessel (300 m strip), using the methods of Tasker et al. (1984), except that we counted all flying birds continuously. All marine predator observations were entered in real time using DLog (Ford Consulting, Portland, Ore., USA), which recorded time and geographic coordinates for each observation along with the survey track.

At the end of each trawl or predator transect, we sampled zooplankton as well as physical and chemical oceanographic parameters. Zooplankton were sampled with a 0.25 m^2 opening MultiNet plankton sampler equipped with five nets made of 335 μm mesh. The net was deployed to a maximum depth of 50 or 5 m above the seafloor on a vertical haul. Oceanography was sampled with a SeaBird Electronics conductivity–temperature–depth profiler equipped with a fluorometer, oxygen sensor, photosynthetically active radiation sensor, and beam transmissometer. Water samples for nutrient analysis and chlorophyll *a* extraction were collected using a rosette-style carousel, and bottles were closed at 2, 8, and 40 m.

Data preparation

Simultaneously trawling for fish while recording seabirds and mammals meant that we had to travel substantially slower than usual practice (2 kn compared with 7–16 kn). The effects of ship attraction and ship avoidance (Hyrenbach 2001) were likely modified (more attraction and less avoidance). Slow survey speed also must have increased counts of flying birds, but we did not apply flux corrections (Spear et al. 1992), since absolute density estimates were not required for our methods.

Transect distance was measured from global positioning system (GPS) tracks and ranged from 0.9 to 5.2 km (mean 3.3 ± 0.77 km). A bird density index was calculated as the number of birds per area surveyed (densities reported here should not be used to estimate population size or trends for reasons mentioned above). Trawl catch per unit effort (CPUE) was calculated for fish as the number of fish per distance towed and for gelatinous zooplankton and euphausiids as the volume per distance towed. Zooplankton displacement volume was determined by adding the plankton to a graduated cylinder, filling the cylinder to a known volume, filtering out the plankton, and subtracting the volume of water remaining from the original volume (Speckman et al. 2005). In situ chlorophyll *a* was calibrated according to the linear relationship between the measured values and the acetone-extracted laboratory values at discrete depths (see Arimitsu et al. 2008 for details). Surface salinity was calculated from an average of the upper 2 m of the water column, where the freshwater signal was strongest. A stratification index was calculated by averaging the difference between subsequent 1 m binned density data within the top 10 m, following Etherington et al. (2007). Photic depth was calculated as the depth at which photosynthetically active radiation values reached 1% of the surface value. A turbidity index was calculated using the ratio of beam transmission to chlorophyll *a*. Temperature, salinity, and turbidity were averaged over the top 40 m of the water column. Dissolved oxygen was sampled but excluded from the analysis, since oxygen provided virtually the same information as temperature (r^2 = 0.98).

In addition to the variables measured in situ, we calculated the shortest distance over water to the high tide line, nearest tidewater glacier, and distance to the entrance of the bay in GIS (GRASS Development Team 2009). Bottom depth was averaged over the survey track, and we calculated bathymetric slope as the maximum slope of $\log_e$ bathymetry within 3 km of the track. The root-mean-square speed of the currents was derived from a circulation model by David Hill (Etherington et al. 2007; Hill et al. 2009). We divided the current speed by depth to obtain a current shear factor that, as a proxy for turbulent mixing, might be more relevant to the UTL — which rely on prey close to the surface — than current speed by itself. Because mean current speed and shear factor were derived from a spatial model rather than measured in situ (or calculated for the particular time and space of the sampling), and because RMS current speed in Glacier Bay is largely a function of bathymetry, we included these two variables under the category geography rather than physics. We imputed two missing zooplankton samples using multiple imputation with 10 iterations (Allison 2001; Little and An 2004), as implemented in Hmisc (Harrell 2009).

We expected some of the variables to be spatially autocorrelated at the scale of data collection. As a measure of spatial autocorrelation, we calculated Moran's I for each variable using all sampling stations within a 40 km search radius, using inverse distances, and measured distance over water rather than in a straight line. Moran's I measures the correlation between adjacent stations and can range from –1 for the perfectly dispersed case to +1 for the perfectly clustered case. While Moran's I values were near zero for most predators (Table 1), indicating lack of spatial autocorrelation, values were moderately elevated for most abiotic variables and some predators. This pattern indicated that some degree of sample binning would benefit the analysis and increase the likelihood of finding meaningful correlations. We aggregated the original sampling stations over a 10 km × 10 km grid, putting on average three samples into every grid cell (Fig. 2). This reduced the number of samples from 87 to 29 but also moved us into a more appropriate spatial scale (Schneider 2002; Burger et al. 2004; Ainley et al. 2005). Since the choice of scale can affect correlations between the distribution of seabirds and their prey considerably (Schneider and Piatt 1986), we repeated our analysis at several different spatial scales to ensure that our results were independent of the chosen scale.

Statistical analysis

To normalize the data and bring the variables into an appropriate scale for a linear analysis, we applied log+1 transformation to the raw data of all species density estimates (predators, fish, zooplankton) and log transformation to all measured environmental variables except for temperature and turbidity, prior to analysis (Abookire and Piatt 2005; Speckman et al. 2005). We used the squared inverse distance

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Table 1. Summary statistics and groupings of all raw variables after spatial aggregation (10 km grid, 87 stations binned into 29 aggregated stations).

Variable	Abbreviation	Unit	Mean	CV	Min.	Max.	Moran's I
Geography							
Depth	depth	m	152.28	0.52	51.19	350.64	0.217
Bathymetric slope ($\log_e$)	slope	dec deg.	0.10	0.39	0.03	0.20	0.209
Distance to land	dst-land	km	0.91	0.60	0.27	2.33	0.114
Distance to entrance	dst-entr	km	60.22	0.41	8.77	100.65	0.785
(Distance to glacier)$^{-2}$	dst-glcr	km^{-2}	26.94	0.75	1.08	69.91	0.757
RMS current speed	current	m·s^{-1}	0.12	1.54	0.00	0.91	0.474
RMS current shear	shear	s^{-1}	1676.38	2.17	6.40	18 465.60	0.348
Physics							
Temperature	temp	°C	6.91	0.12	5.08	8.31	0.718
Salinity	sal	psu	29.50	0.02	28.46	30.95	0.366
Stratification	strat	$\Delta\sigma_t$·m^{-1}	1.00	0.50	0.09	1.91	0.449
Turbidity	turb		1.56	1.14	0.44	7.45	0.439
Photic depth	phtc-dpth	m	9.74	0.49	2.00	20.00	0.369
Chemistry							
Phosphate	PO_4^{3-}	μmol·L^{-1}	1.13	0.34	0.60	2.01	0.249
Silica	$Si(OH)_4$	μmol·L^{-1}	19.87	0.20	13.58	30.71	0.158
Nitrate	NO_3^-	μmol·L^{-1}	9.39	0.33	3.39	17.01	0.309
Nitrite	NO_2^-	μmol·L^{-1}	0.32	0.47	0.04	0.60	–0.026
Ammonium	NH_4^+	μmol·L^{-1}	1.89	0.38	0.81	4.34	0.048
Phytoplankton							
Chlorophyll *a*	chl-a	mg·m^{-3}	113.62	0.51	42.59	286.31	0.348
Lower trophic level							
Zooplankton volume	zoopkt	CPUE	2.29	0.68	0.76	6.41	0.117
Mid trophic level							
Euphausiids	euphau	CPUE	18.96	3.41	0.00	288.48	0.317
Gelatinous zooplankton	jellies	CPUE	33.24	1.70	2.91	243.62	0.058
Pacific herring	herring	CPUE	10.32	3.83	0.00	213.58	–0.009
Capelin	capelin	CPUE	33.52	1.66	0.00	198.59	0.063
Pink salmon	pink	CPUE	14.76	1.69	0.00	109.65	0.112
Northern lampfish	lampfsh	CPUE	11.97	4.07	0.00	259.30	0.011
Walleye pollock	pollock	CPUE	373.51	2.25	0.00	3760.73	–0.016
Pacific sand lance	sandlnc	CPUE	26.33	4.87	0.00	692.39	0.005
Upper trophic level							
Common merganser	COME	km^{-2}	0.09	3.75	0.00	1.36	–0.024
Red-breasted merganser	RBME	km^{-2}	0.34	4.84	0.00	8.73	–0.001
Common loon	COLO	km^{-2}	0.01	5.39	0.00	0.21	–0.014
Pacific loon	PALO	km^{-2}	0.26	2.36	0.00	2.77	0.230
Red-throated loon	RTLO	km^{-2}	0.38	4.67	0.00	9.61	–0.002
Pelagic cormorant	PECO	km^{-2}	0.20	2.10	0.00	1.90	–0.022
Parasitic jaeger	PAJA	km^{-2}	0.01	3.77	0.00	0.23	–0.015
Herring gull	HEGU	km^{-2}	0.08	2.36	0.00	0.87	–0.001
Glaucous-winged gull	GWGU	km^{-2}	5.72	1.98	0.00	57.28	0.034
Mew gull	MEGU	km^{-2}	0.73	1.50	0.00	4.62	0.087
Bonaparte's gull	BOGU	km^{-2}	0.19	3.26	0.00	3.16	0.001
Black-legged kittiwake	BLKI	km^{-2}	23.72	1.57	0.00	147.85	0.023
Arctic tern	ARTE	km^{-2}	3.63	4.88	0.00	95.61	–0.009
Common murre	COMU	km^{-2}	0.05	4.06	0.00	1.14	–0.008
Pigeon guillemot	PIGU	km^{-2}	2.01	1.59	0.00	14.73	0.028
Marbled murrelet	MAMU	km^{-2}	32.21	2.01	0.00	291.28	0.373
Kittlitz's murrelet	KIMU	km^{-2}	10.86	1.42	0.00	57.49	0.123
Tufted puffin	TUPU	km^{-2}	0.20	1.68	0.00	1.08	–0.020
Horned puffin	HOPU	km^{-2}	0.03	4.24	0.00	0.65	–0.019
Sea otter	SEOT	km^{-2}	0.09	3.29	0.00	1.49	0.261
Harbor seal	HASE	km^{-2}	0.31	2.54	0.00	3.22	–0.002
Steller sealion	STSL	km^{-2}	0.00	5.39	0.00	0.13	–0.015
Harbor porpoise	HAPO	km^{-2}	0.07	3.04	0.00	1.05	0.099
Humpback whale	HUWH	km^{-2}	0.03	2.81	0.00	0.38	–0.014

Note: Variables under the geography heading were derived from a GIS; all other variables were measured in situ. Moran's I was calculated prior to data aggregation. CV, coefficient of variation; RMS, root mean square.

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to tidewater glaciers assuming that effects from these features, such as ice, sediment, or upwelling near the face of tidewater glaciers, would dissipate quickly with distance rather than glacier effects, which might respond in a linear fashion with distance from the entrance of the bay (Table 1).

We preferred orthogonal CA over nonmetric multidimensional scaling (NMDS) for two reasons. First, CA is more suitable because it is a linear, parametric method that fits into our linear analysis framework. Second, preliminary results showed that CA and NMDS were highly correlated with each other ($r^2 > 0.8$). However, the first axis of the CA showed consistently higher correlations than NMDS did with environmental variables. We only used the first major axis of the CA, avoiding the controversies associated with correcting the various problems in the second and higher dimensions (Wartenberg et al. 1987; Jackson and Somers 1991; van Groenewoud 1992).

We applied a two-pronged approach to address our study objectives (Fig. 1). First, we compared dimension-reducing axes to test our main hypotheses, then a detailed analysis to reveal the most important variables driving the spatial arrangement of predator communities. We correlated the CA axis of predators and forage fish to the first major PCA axis of the underlying levels, to test whether correlations gradually decrease with every step further away from the top level or whether there is an increased correlation again at the lowest, physical levels. We standardized variables before calculating PCAs by subtracting the mean and dividing by the standard deviation. Rare species were down-weighted in the UTL CA. We included gelatinous zooplankton and euphausiids in the CA of the fish community because they were sampled with the same method and are more likely to be meso-predators of the prevalent zooplankton species sampled in the vertical tow rather than prey to most MTL predators. Because these euphausiids and gelatinous zooplankton were measured as a volume rather than counts, we used Wisconsin standardization (Legendre and Gallagher 2001) prior to calculating the MTL CA.

To find the best set of variables matching the community data we calculated BIO-ENV analyses (Clarke and Ainsworth 1993; Balkenhol et al. 2009). For this procedure we calculated distance matrices between sites, one for the environmental variables and one for the community. Each of the two matrices was then unfurled by stacking the columns on top of each other. The two resulting vectors were then correlated (as in a Mantel test). A site can be characterized by a set of one or more environmental variables. To find the set with the greatest correlation between environmental variables and the community, all combinations of environmental variables were tried. We conducted one BIO-ENV analysis for the MTL and one for the UTL community.

Our matrix of environmental variables included all abiotic variables listed in Table 1, chlorophyll *a*, and zooplankton. For the UTL analysis we also included all MTL species with the environmental data. The number of possible subsets increases with the number of environmental variables (v) according to $s = 2^v$. This meant searching through 524 000 and 134 million combinations for the MTL and UTL and predator analysis, respectively. For each set size we retained the three best sets of environmental variables. We used Jaccard distances to calculate the community distance matrix, Euclidian distance for the environmental distances, and Pearson's correlation coefficients, rather than rank statistics, making this a parametric analysis. We chose a parametric approach because rank statistics would not have been able to distinguish between the effects of distance from the entrance of the bay and the inverse of distance from tidewater glaciers (Figs. 3*d* and 3*e*). The effect of glaciers can be expected to drop off comparatively rapidly, which would be undetectable by a nonparametric approach.

All statistical analysis were performed using R version 2.10.1 (R Development Core Team 2009) with package vegan (Oksanen et al. 2009) for CA and a custom version of the bioenv function, optimized for speed and memory efficiency for BIO-ENV calculations.

Results

Summary statistics and categories for all variables after binning into aggregated stations are shown in Table 1. The coefficients of variation for biotic variables, especially those of MTL and UTL, were higher than those for abiotic variables. Conversely, Moran's I was higher for abiotic than for biotic variables (Table 1). Among the abiotic variables, nitrite and ammonia had relatively low Moran's I values. Marbled murrelet, phytoplankton, euphausiids, and sea otters stand out among the biotic variables with relatively high Moran's I values.

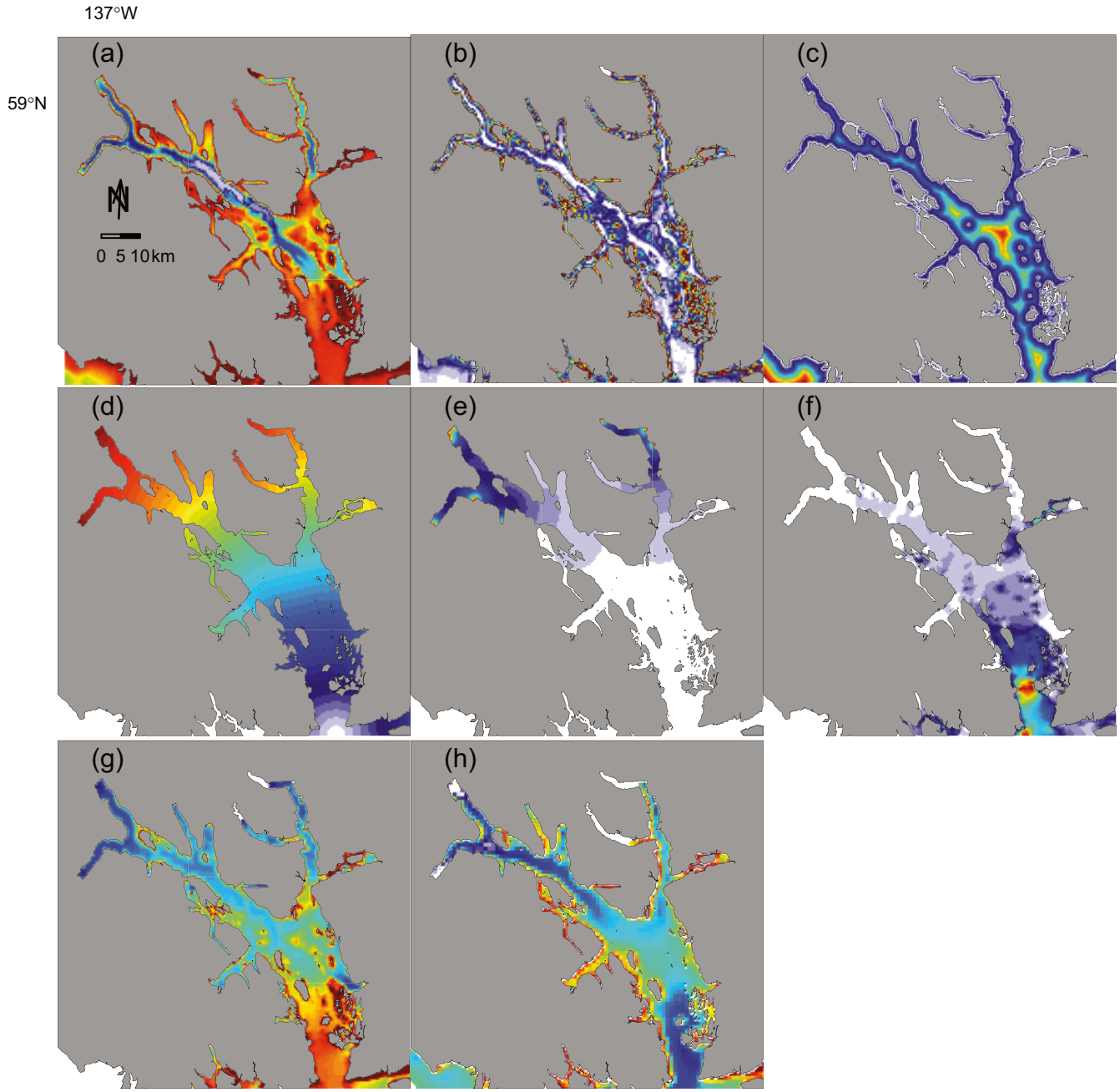
Abiotic variables

The first major PCA axes of geographic, physical, and chemical variables captured between 43% and 60% of the total variation (Table 2). The geographic PCA1 primarily captured information in the variables tidal current speed, current shear, and distance to entrance. Geographic PCA2 was chiefly influenced by depth, bathymetric slope, and distance to glacier or shore. Hence, PC1 essentially reflects an axis along the bay, whereas PCA2 captures variability across the bay (Fig. 4). PCA1 of the physical variables contained temperature, turbidity, and photic depth, all of which are signals related to glacial river run-off, supported by the spatial pattern of this axis (Fig. 4). Physics PCA2 is driven largely by salinity and stratification (Table 2), and values differed most between the east and the west arms but showed average values in the central bay (Fig. 4). PCA1 of the chemistry parameters captured substantially less of the overall variance than the respective first major axes of the geographic and physics PCAs. Phosphate and nitrate had the strongest influence on the chemistry PCA1 (Table 2). The spatial distribution of the chemistry PCA1 revealed a pattern with proximity to tidewater glaciers and major stream influence at opposing ends of the gradient (Fig. 4).

Biotic variables

Phytoplankton (chlorophyll *a*) and zooplankton (LTL) showed generally opposing or neutral distributions. Phytoplankton concentrations were lowest in the head of the west arm, where the highest zooplankton concentrations were found (Fig. 4). The highest concentrations of phytoplankton, however, were measured in the lower east side of the bay and they were not matched with correspondingly low densities of zooplankton. Overall, both phytoplankton and zooplankton density gradients were aligned mostly along the bay rather than across. Note that phytoplankton and zooplankton values do represent density indices, in contrast to the CA axes of fish and preda-

Fig. 3. Topography and physical parameters used as environmental variables from remote sensing or GIS to compare with mid and upper trophic level communities of Glacier Bay. Shown are (*a*) bathymetry, (*b*) slope of the $\log_e$ bathymetry, (*c*) distance from land, (*d*) distance from mouth of the bay, (*e*) distance^{-2} from tidewater glaciers, (*f*) root-mean-square current speed from a circulation model by David Hill (Etherington et al. 2007; Hill et al. 2009), (*g*) current shear factor (current/depth), and (*h*) mean sea surface temperature from AVHRR satellite data. Colors are scaled from white (low values) to red (high values), but this is reversed for panels (*a*) and (*e*).



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tors, which represent an ordination along a community axis rather than density. The first CA axes of the MTL ordination captured 38% of the overall variance (total of seven axes), and the UTL ordination captured 21% of the variance with the first CA axis (total of 23 axes).

Community analysis

The ordination of the MTL community (mostly fish, but including gelatinous zooplankton and euphausiids) range from juvenile pink salmon, Pacific herring, and Pacific sand lance on one extreme to capelin, euphausiids, and northern lampfish on the other end (Fig. 5). Pollock and gelatinous zooplankton tended to occupy the middle ground, although they were common in all areas. Geographically, sites on the right end of the CA axis are found at the heads of the upper arms near tidewater glaciers (Figs. 4 and 6), while the left end of the axis reflected sites in the central and lower bay (Figs. 4 and 6).

Table 2. PCA of abiotic parameters.

	Proportion of variance	Var1	rot	Var2	rot	Var3	rot	Var4	rot
Geography									
PCA 1	0.512	current	–0.48	shear	–0.46	dst-entr	0.46	slope	0.35
PCA 2	0.174	depth	0.55	slope	–0.48	dst-glcr	0.48	dst-land	0.45
Physics									
PCA 1	0.596	temp	–0.51	phtc-dpth	–0.50	turb	0.49	strat	0.36
PCA 2	0.317	sal	–0.62	strat	0.60	turb	–0.36	phtc-dpth	0.27
Chemistry									
PCA 1	0.366	NO_2^-	0.56	$Si(OH)_4$	–0.55	NH_4^+	0.51	NO_3^-	–0.33

Note: Shown are the proportions of variance captured by each PCA axis and the rotations (rot) of the four standardized variables with the greatest influence on the respective PCA axis. See Table 1 for abbreviations.

Fig. 4. Spatial distribution of the first two major PCA axes of geographic, physical, and chemical ocean parameters, chlorophyll *a* and zooplankton concentrations, and correspondence analysis (CA) of middle (fish) and upper (seabirds and marine mammals) trophic level predators. Prior to plotting, all data were standardized to a mean of zero and standard deviation of one. Dots are proportional to the size of these standardized values. Negative values are shown in blue, positive values in red. See Table 2 for composition of PCA axes and Figs. 6 and 7 for CAs of fish and predators.

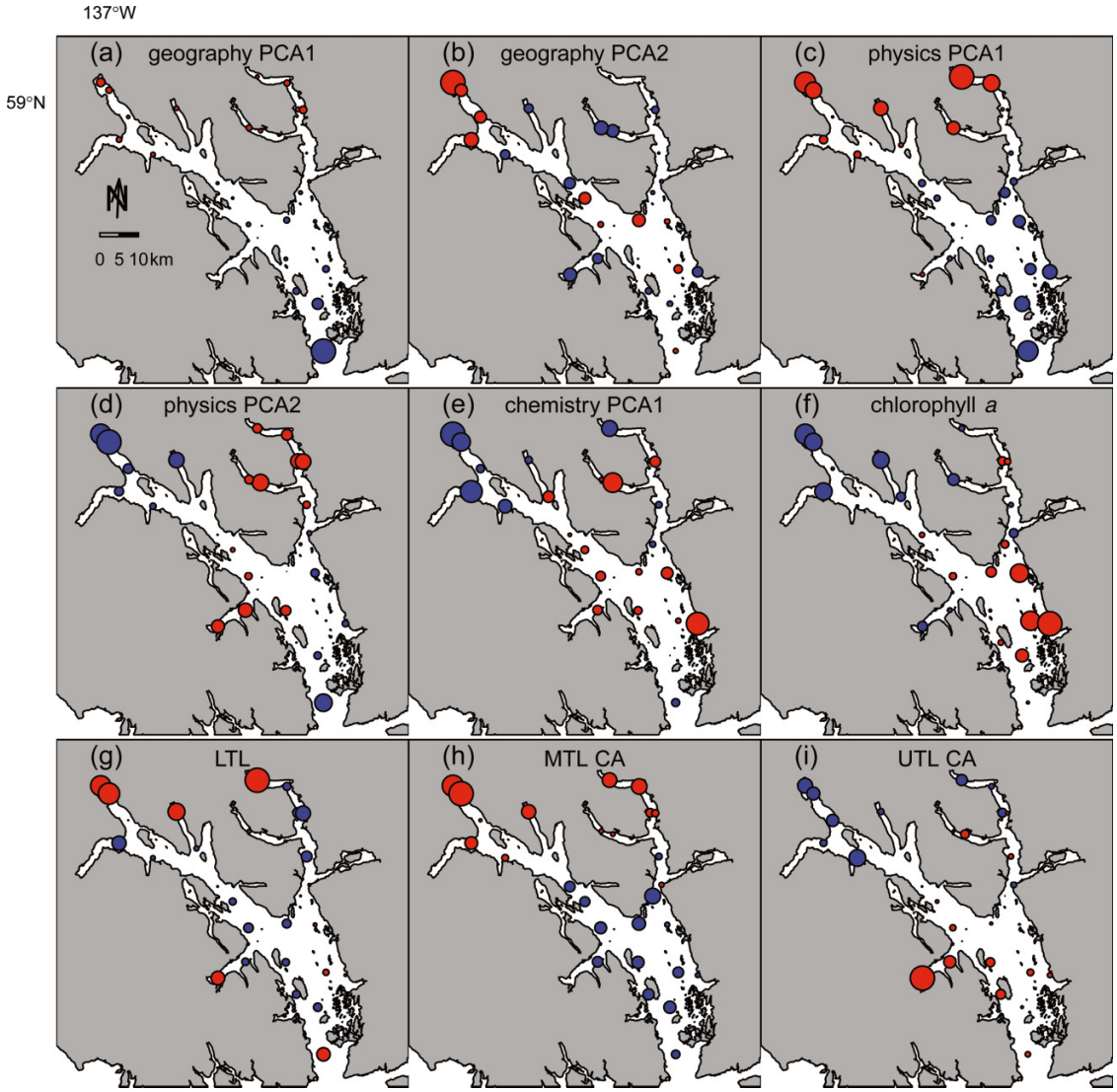

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Fig. 5. Correspondence analysis (CA) of middle trophic level (fish) communities. The *x* axis is the first major axis of a CA of fish abundance. For each station, the relative abundance of each species is plotted on the *y* axis. The CA score for each station is shown as colored circles in the top row, corresponding to the symbols in Fig. 4. The vertical gray bars mark the species means that would be shown in a traditional CA biplot.

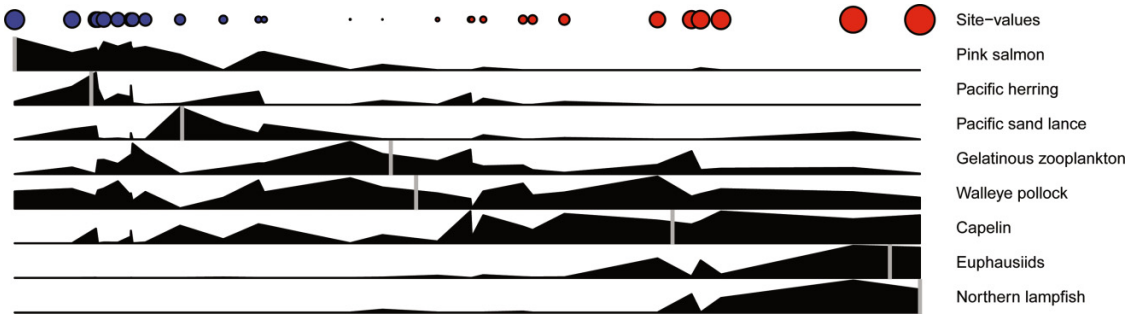
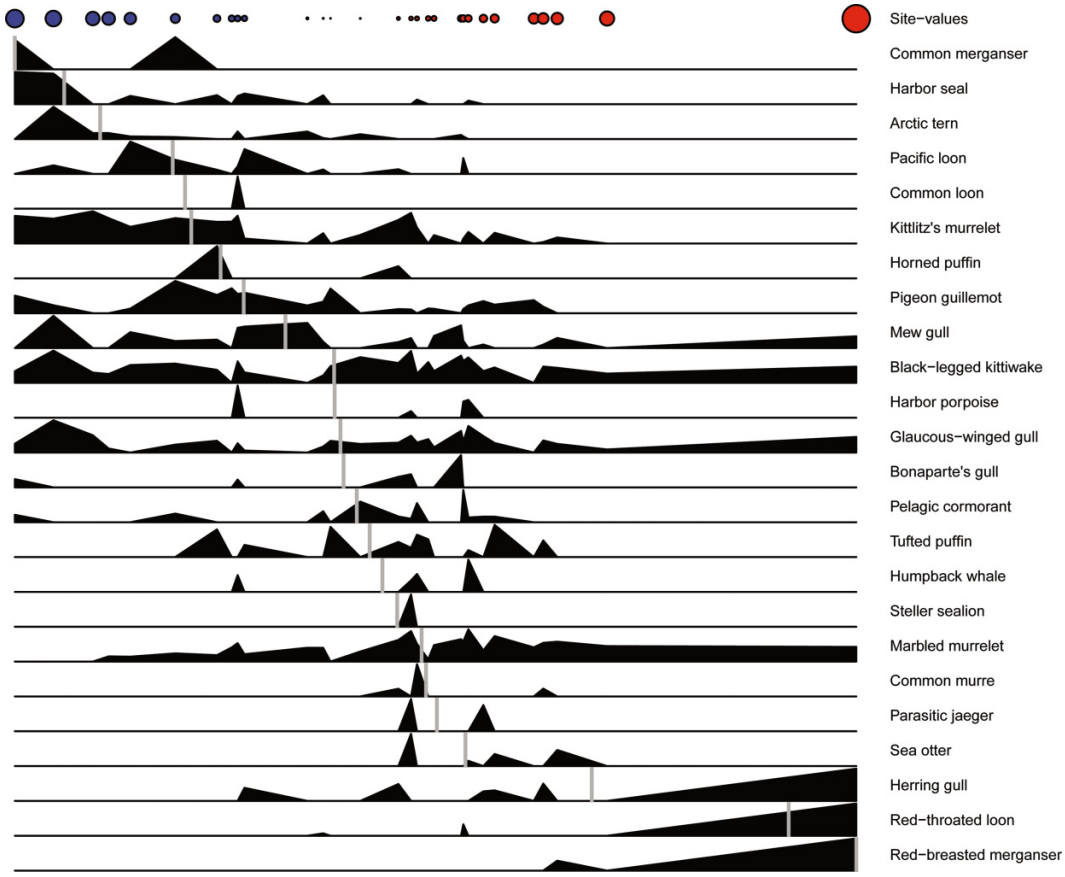


Fig. 6. Correspondence analysis (CA) of upper trophic level (seabirds and marine mammals) communities. The *x* axis is the first major axis of a CA of fish abundance. For each station, the relative abundance of each species is plotted on the *y* axis. The CA score for each station is shown as colored circles in the top row, corresponding to the symbols in Fig. 4. The vertical gray bars mark the species means that would be shown in a traditional CA biplot.



The UTL community (marine birds and mammals) presented a similar ordination, although with more species and many of them relatively uncommon (Fig. 6). In contrast to the MTL ordination, the two extremes of the UTL community axis ranged from sites in the upper arms near tidewater glaciers on the left to sites in the lower bay without tidewater glaciers on the right (Fig. 6). Species that appeared to concentrate mostly in the upper arms at the time of sampling include common merganser, harbor seal, Arctic tern, Pacific loon, and Kittlitz's murrelet. Common species concentrated in the central and lower bay included herring gull, sea otter, marbled murrelet, humpback whale, and tufted puffin. Mew gull, black-legged kittiwake, and glaucous-winged gull were widespread species populating mostly the center of the axis, but also found throughout most of the range. Several uncommon UTL species were found almost exclusively on a transect in Geikie Inlet

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(Figs. 2, 4, 7), resulting in an extreme value on the PCA (Fig. 6). The general make-up of the community axis was robust, however, as little changed in this or subsequent results when this point was removed or through exploratory rank statistics.

The graphical display of the community structure (Figs. 6 and 7) gives a convenient visual representation of which species are relative generalists (walleye pollock, black-legged kittiwake, glaucous-winged gull) or have a more restricted distribution, suggesting a specialized ecological niche within Glacier Bay (northern lampfish, euphausiids, harbor seal, Kittlitz's murrelet).

When we compared the correlation coefficients of UTL CA with the variables at lower levels (Fig. 7), we found a pattern of correlations that was best predicted by hypothesis 2 (Fig. 1). The UTL community was strongly correlated with MTL forage fish, but much less so with the next two lower trophic levels. Furthermore, correlations with physical and geographical PCs were higher than those with the lowest trophic levels. The MTL community had the weakest correlation with zooplankton, although the correlation increased with phytoplankton. Still, the strongest correlations were observed between MTL community and the physical and geographical PCs.

The general patterns of these relations were independent of the spatial scale of data aggregation (Fig. 8): At every scale we find a better match with hypothesis 2 than with hypothesis 1. The correlation of UTL CA consistently is high with the CA of MTL community and low with zooplankton (LTL). Also in accordance with hypothesis 2, correlations were higher again with the physical and geographical PCAs. As already seen (Fig. 7), not all the predictions of hypothesis 2 are reflected in the data, however. The MTL community had the weakest correlation with zooplankton volume (Fig. 8*b*) compared with other trophic levels — we expected a comparatively strong correlation, as between UTL and MTL (Fig. 8*a*). The confidence intervals of these correlations (Fig. 7) also confirm that the patterns described at a large spatial scale are robust.

BIO-ENV analysis

Distance to the entrance of the bay was the best single predictor of the MTL community, followed by photic depth and temperature (Table 3). The best set of variables comprised three environmental variables that include distance to entrance, photic depth, and silica concentrations. The best single environmental predictor for the UTL community was photic depth, followed by ammonium and capelin. The best explanatory set for the UTL community comprised seven environmental variables, including photic depth, nitrite, ammonium, capelin, pollock, pink salmon, and gelatinous zooplankton. Ammonia and nitrite nutrients were found in many of the sets and featured in the two highest ranking sets listed here. Capelin and gelatinous zooplankton were part of almost every top-ranking set size three and above. For both MTL and UTL communities, the one physical variable of greatest importance was photic depth. For MTL, distance to entrance was a consistently important variable in almost every set.

Discussion

Our analysis indicates that the UTL community in Glacier Bay was strongly correlated with both prey composition and environment. Owing to high metabolic demands, and the need for high density prey patches (Piatt 1990), it is not surprising to find that the piscivorous UTL community was aligned with the forage fish community. The community of piscivorous UTL in Glacier Bay is diverse in terms of feeding strategies, from lunge-feeding humpback whales (*Megaptera novaeangliae*), pursuit-diving murrelets, benthic-searching cormorants and harbor seals (*Phoca vitulina*) to plunge-diving terns (*Sterna* spp.). At the same time, many of these niches are occupied by several species (e.g., five gull, two tern, two murrelet, two puffin species). Therefore we expected an alignment of community axes between these predators and their prey community. Similar to the results of the CA, the BIO-ENV analysis indicated that the UTL community was closely correlated with the distribution of prey; the top four sets all contained the important forage fish species capelin, pollock, and pink salmon. However, strong correlations with environmental gradients suggest that the UTL community is also structured by the physical environment.

In some cases, direct effects of physical variables may underpin the structuring of higher trophic levels. For example, areas of high turbidity, such as those near glacial river outflows, may hinder foraging success for some visual predators while creating exclusive foraging habitat for species such as Kittlitz's murrelet adapted for foraging under low light conditions (Ainley 1977; Day et al. 2003). Likewise, proximity to the entrance of the bay may limit the foraging distance for transient marbled murrelets that fly into Glacier Bay from nesting habitat outside the bay (Whitworth and Nelson 2000). However, evidence of direct effect of physical factors on predator communities is quite limited.

Alternatively, and perhaps more likely, the strength of the correlation between the UTL community axis and physical variables may be explained by indirect effects, such as the strong and well-documented effects of marine habitat characteristics (e.g., temperature, salinity, turbidity) on prey distribution (Abookire and Piatt 2005; Speckman et al. 2005) or the predictability of prey distribution. Indeed, the most robust correlation was found between the forage fish community and physical PCA1 axis, which illustrates the important role of glaciers in providing cold, fresh, stratified, and sediment-laden marine habitat (see also Etherington et al. 2007; Arimitsu et al. 2012). BIO-ENV analysis also indicated that physical factors closely associated with the locations of glacial river outflows, including distance to the entrance, photic depth, stratification, turbidity, and temperature, were paramount in the alignment of the forage fish community. The gradient attributed to physical PCA1 explained nearly 74% (r = 0.86) of the variation in community structure of small schooling fish, explaining more variation than any other relationship. Abookire and Piatt (2005) found that dominant physical features in Cook Inlet, Alaska, temperature, salinity, and depth explained 41% of the variation in fish community structure.

Counterintuitively, euphausiid density was highest in areas of low phytoplankton density within the most turbid glacier outflows at the head of the bay. As in other studies (Abookire et al. 2002; Arimitsu et al. 2012), we found enigmatic daytime near-surface occurrence of euphausiids and northern lampfish, both species that typically are found in deep waters during the daytime (Beamish et al. 1999; Coyle and Pinchuk 2005). Heavy grazing could cause a negative relationship between zooplankton biomass and standing stock of phytoplankton

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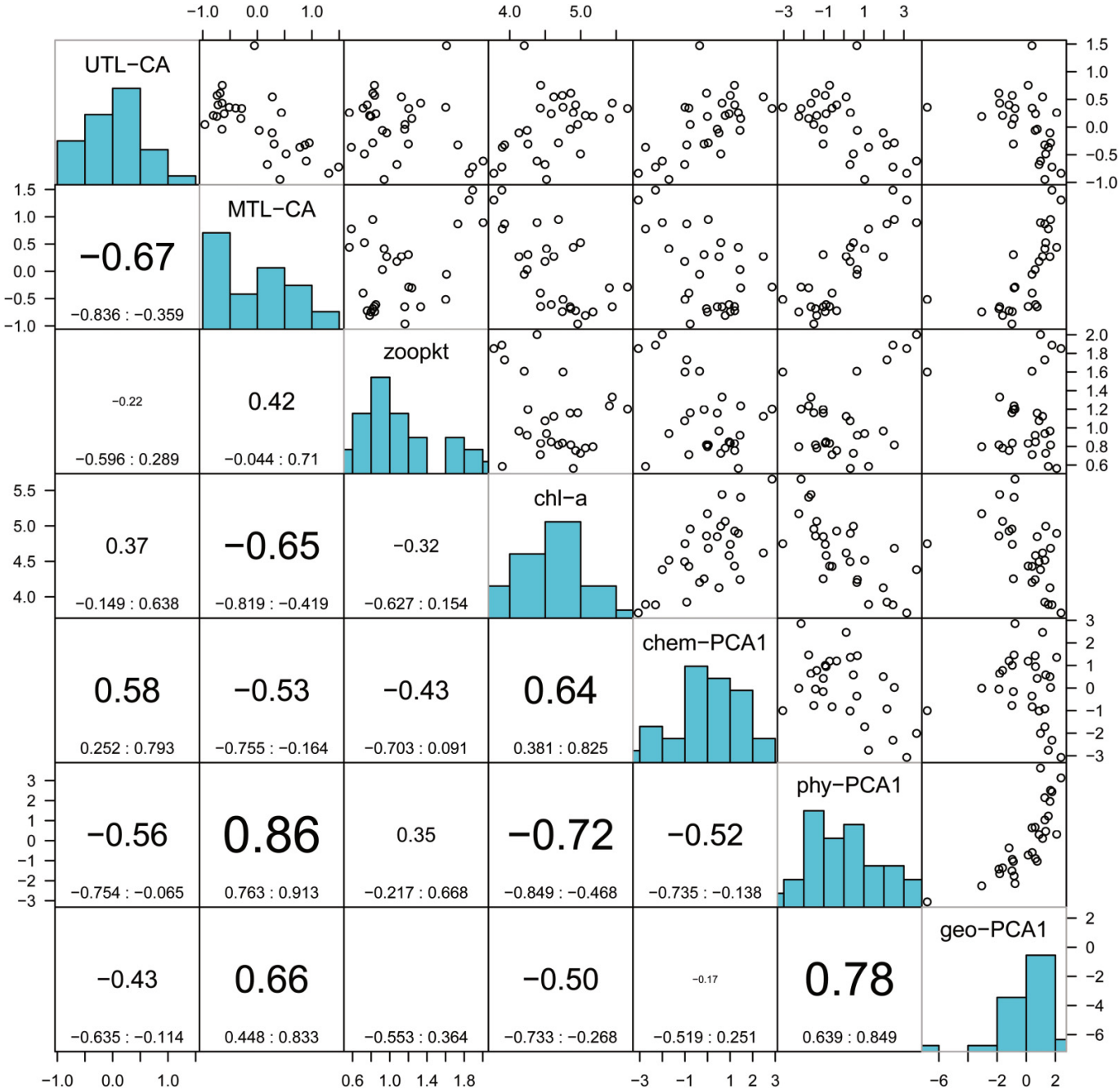
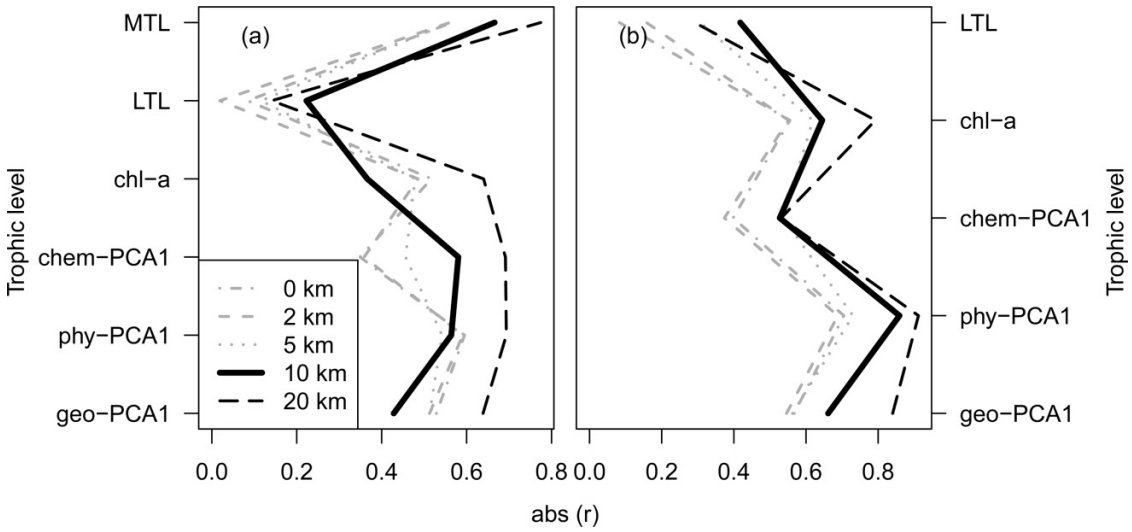
Fig. 7. Relationships among ocean environment, physical oceanography, phytoplankton (chlorophyll *a*), zooplankton, mid (MTL) and upper (UTL) trophic level communities. The upper panels show scatterplots with lowess smoothers of the variables from the diagonal intersecting at the respective square. The lower panels show the Pearson's correlation coefficients of the intersecting variables, with the size of the font scaled by the absolute of the coefficient and their corresponding confidence intervals (from 999 bootstrap replicates). The plots in the diagonal are univariate histograms of the labeled variables. Compare the pattern of correlations between the CA scores of MTL and UTL with Fig. 1. Note that the sign of the correlations with CA scores is arbitrary because the direction of ordination is arbitrary. The strength of the correlation is of interest, however.



(Frost 1991). However, the high silt load in glacial waters results in virtually no light penetrating the water column, suppressing photosynthesis and phytoplankton production. Arimitsu et al. (2012) suggested that the lack of a photic cue may interfere with the physiological trigger that induces vertical migration. High concentrations of zooplankton in the surface waters near tidewater glaciers were found near tidewater glaciers elsewhere (Węsławski et al. 2000; Piwosz et al. 2009).

Zooplankton density was not strongly correlated with any of the biotic or abiotic factors we examined. It is possible that the response of zooplankton to these factors involved complex

Fig. 8. Scale dependence of the correlations (see Fig. 7 and Fig. 1) of upper (*a*) and middle (*b*) trophic level communities with the lower levels listed. The *x* axis shows the absolute of the correlation coefficient at different grid cell sizes (see Fig. 2). Legend: 0 km indicates no aggregation; 10 km is the scale chosen for analysis in this paper.



interactions with other trophic levels that were not detected with the methods we employed. Complex interactions between lower trophic levels and their environment are often difficult to predict, for example, if the combined influences of predators and limiting nutrient availability are equally strong (McQueen et al. 1989) or when weaker linkages are dampened by stronger and more apparent ecological relationships (Paine 1980). It is quite possible that the resolution of our zooplankton measure was not adequate to reveal ecological relationships at the scale of this study. For example, if the high concentrations of zooplankton at both the head of the fjord and the mouth of the bay were due to differences in their species composition (i.e., different species produced high concentrations at either end of the environmental gradient), our analysis of density alone would not have uncovered the relationship. Zooplankton community structure in Glacier Bay is an ecosystem component that clearly deserves further research.

Gargett (1997) hypothesized that primary productivity is regulated through the "optimum stability window," whereby intermediate stability in the water column provides sufficient light and nutrients to stimulate production, and this phenomenon appears to hold true in glacially influenced fjord ecosystems. Etherington et al. (2007) demonstrated that the chlorophyll maxima in Glacier Bay occurred in the central bay, where there was intermediate stratification, lower sedimentation, and potential nutrient renewal through tidal action. In this study, chlorophyll concentrations were well correlated with the dominant physical gradient, and this corroborates findings of Etherington et al. (2007) by extending the observed phytoplankton pattern into nearshore areas, as well as by demonstrating that chlorophyll concentrations were indeed related to nutrient gradients.

Hood et al. (2009) suggest that glacially derived dissolved organic matter is an important source of highly bioavailable nutrients for marine heterotrophs. In this study, mean nutrient concentrations were comparable to those reported from south-central Alaska (Childers et al. 2005). The highest levels of phosphate and ammonium were often found near glacier outflows, and silica values were below average through the central bay and lower west arm. Silica values were lowest at the head of Geikie Inlet and another glacial river outflow in the upper west arm. We found that variation in silica values was consistently included in the best set of predictors for the MTL community, and other nutrients such as ammonium and phosphate were also important in predicting the structure of the MTL and UTL communities. Yen et al. (2005) found a positive correlation between some top predator species and nitrate concentrations, although for most species nitrate was not well correlated with species abundance. These correlations are somewhat perplexing, given that it is unlikely that seabirds or other UTL predators react directly to changes in nutrient levels. In both cases, the mechanism behind these correlations may be due in part to the fact that large aggregations of marine predators may locally enrich nutrient levels in nearshore surface waters (Bédard et al. 1980). At larger scales, nutrient transport in the euphotic zone was the leading factor controlling marine fish production (Iverson 1990).

Rapid glacial recession and reduction in the number of tidewater glaciers during recent decades (Molnia 2008) could have had a direct effect on predators such as seals and Kittlitz's murrelets that depend on glacial breeding habitats (Mathews and Pendleton 2006) or an indirect effect on all marine predators by altering marine habitats and therefore the abundance or availability of forage species to predators (Arimitsu et al. 2012). For example, capelin are an important diet item for Kittlitz's murrelet throughout much of their range. Both capelin and murrelets favor cold, turbid, stratified waters found downstream of glacial river outflows. Any response of capelin to changing marine climate would almost certainly be reflected in the ecology of Kittlitz's murrelet, and both species could be expected to diminish locally if glacial and glacial-marine environments in Glacier Bay continue to diminish. Recent dynamic changes in predator populations may also reflect stochastic changes, competition among predators for food or foraging space, or predation from apex predators (Herreman et al. 2009).

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Table 3. BIO-ENV analyses, one for of best sets of variables that correlate (Pearson r^2) with middle trophic level communities (forage fish) communities and one for upper trophic level communities (seabirds and marine mammals).

Variables in set	Size	r^2
Middle trophic level		
dst-entr phtc-dpth $Si(OH)_4$	3	0.6018
dst-entr strat phtc-dpth turb $Si(OH)_4$	5	0.6009
dst-entr strat phtc-dpth temp $Si(OH)_4$	5	0.5995
dst-entr phtc-dpth temp $Si(OH)_4$	4	0.5967
dst-entr strat phtc-dpth turb temp $Si(OH)_4$	6	0.5966
dst-entr phtc-dpth	2	0.5931
dst-entr phtc-dpth turb $Si(OH)_4$	4	0.5927
dst-entr current strat phtc-dpth turb temp $Si(OH)_4$	7	0.5923
dst-entr strat phtc-dpth $Si(OH)_4$	4	0.5913
dst-entr shear strat phtc-dpth turb temp $Si(OH)_4$	7	0.5895
dst-entr slope strat phtc-dpth turb temp $Si(OH)_4$	7	0.5894
dst-entr phtc-dpth temp sal $Si(OH)_4$	5	0.5891
dst-entr phtc-dpth turb temp sal $Si(OH)_4$	6	0.5887
dst-entr current strat phtc-dpth turb temp $Si(OH)_4$ NH_4^+	8	0.5879
dst-entr current strat phtc-dpth turb temp PO_4^{3-} $Si(OH)_4$	8	0.5875
dst-entr current phtc-dpth turb temp $Si(OH)_4$	6	0.5871
dst-entr slope current strat phtc-dpth turb temp $Si(OH)_4$	8	0.5858
dst-entr strat phtc-dpth	3	0.5856
dst-entr slope current strat phtc-dpth turb temp PO_4^{3-} $Si(OH)_4$	9	0.5856
dst-entr slope current strat phtc-dpth turb temp $Si(OH)_4$ NH_4^+	9	0.5838
dst-entr slope shear strat phtc-dpth turb temp PO_4^{3-} $Si(OH)_4$	9	0.5834
dst-entr slope current strat phtc-dpth turb temp PO_4^{3-} $Si(OH)_4$ NH_4^+	10	0.5814
dst-entr slope shear strat phtc-dpth turb temp PO_4^{3-} $Si(OH)_4$ NH_4^+	10	0.5793
dst-entr slope current strat phtc-dpth turb temp $Si(OH)_4$ NH_4^+ chl-a	10	0.5780
dst-entr phtc-dpth sal	3	0.5777
dst-entr turb	2	0.5553
dst-entr	1	0.5546
dst-entr $Si(OH)_4$	2	0.5332
phtc-dpth	1	0.4576
temp	1	0.4053
Upper trophic level		
phtc-dpth NO_2^- NH_4^+ capelin pollock pink jellies	7	0.4629
temp NO_2^- NH_4^+ capelin pollock pink jellies	7	0.4543
phtc-dpth NH_4^+ capelin pollock pink jellies	6	0.4507
dst-land phtc-dpth NH_4^+ capelin pollock pink jellies	7	0.4488
current shear turb temp zoopkt capelin pink lampfsh euphau	9	0.4483
turb sal $Si(OH)_4$ NH_4^+ capelin sandlnc pollock herring euphau	9	0.4482
temp NH_4^+ capelin pollock pink jellies	6	0.4464
current shear strat turb $Si(OH)_4$ chl-a capelin pink euphau	9	0.4446
depth phtc-dpth NO_2^- NH_4^+capelin pollock pink jellies	8	0.4442
dst-entr strat temp NO_3^- chl-a zoopkt capelin lampfsh	8	0.4442
phtc-dpth NO_2^- capelin pollock pink jellies	6	0.4436
depth dst-land phtc-dpth NH_4^+ capelin pollock pink jellies	8	0.4429
NH_4^+ capelin pollock pink jellies	5	0.4316
phtc-dpth capelin pollock pink jellies	5	0.4292
phtc-dpth NH_4^+ pollock pink jellies	5	0.4280
strat sal $Si(OH)_4$ NH_4^+ chl-a zoopkt sandlnc pollock pink herring	10	0.4231
strat sal $Si(OH)_4$ NO_2^- NH_4^+ chl-a capelin pink herring jellies	10	0.4170
phtc-dpth pollock pink jellies	4	0.4139
strat sal $Si(OH)_4$ NO_2^- chl-a pollock pink herring euphau	10	0.4088
NH_4^+ capelin pink jellies	4	0.4080
phtc-dpth NH_4^+ pink jellies	4	0.4039
NH_4^+ capelin jellies	3	0.3714
NH_4^+ pink jellies	3	0.3710
NH_4^+ capelin pink	3	0.3703
NH_4^+ capelin	2	0.3434
phtc-dpth NH_4^+	2	0.3235
NH_4^+ pink	2	0.3223
phtc-dpth1	1	0.2539
NH_4^+	1	0.2533
capelin	1	0.2001

Note: Shown are the three best sets per size, up to 10 variables per set, ordered by the strength of their correlations with the communities. See Table 1 for abbreviations. Note that this is an analysis of community composition, not of biomass, and therefore it does not address ecological regulation. See text for more details on BIO-ENV.

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Our overall findings about the structure of UTL communities generally parallel those of Ainley et al. (2005), whereby a few physical features and food were the dominant factors influencing the distribution of seabirds. This is the only other published study that relates top predator distribution to a suite of simultaneously measured physical and biological factors. The two analyses differed, however, because we used multivariate methods to examine community response to habitat, whereas Ainley et al. (2005) used univariate methods to examine individual species' response to prey and environment. Through the use of multivariate ordination and Mantel statistics used in the BIO-ENV procedure, we did not partition variance of species response to individual factors, as one would with linear models (Legendre and Legendre 1998). However, we could examine changes in predator and prey communities relative to one another and their environment and also determine the most important habitat features that shape the ecosystem. Our methods therefore precluded us from quantitatively addressing questions regarding changes in density as described in the theory of bottom-up versus top-down regulation (see Cury et al. 2003 and references within).

Long-term studies at a large spatial scale are critical to understanding trophic interactions because fluctuations in community structure typically span many years or decades (Carpenter et al. 1987). Although strong trophic interactions, such as those between apex predators and their prey, may produce predictable and persistent patterns in resource guilds, weaker trophic links are much harder to demonstrate (Paine 1980). Our study represents a single snapshot in time. While this approach afforded an in-depth spatial analysis of the factors most important to the marine community at the height of the summer breeding and foraging season for most UTL species, a single sampling event is not capable of uncovering the complex interactions that occur at the lowest trophic levels. We therefore recommend an integrated sampling approach with fewer replicates through space and more replicates in time to better understand temporally variable food web interactions within Glacier Bay marine communities.

In summary, our analysis demonstrates that the contribution of glacial freshwater to the marine ecosystem is the primary structuring feature of marine communities in Glacier Bay. The UTL and MTL communities comprised species well adapted to cold, dark, turbid, icy, stratified waters and also those adapted to opposing conditions. We predict that within the Glacier Bay marine ecosystem, species that will be most negatively affected by disappearance of glacial influence will include euphausiids, capelin, harbor seal, arctic tern, Pacific loon, and Kittlitz's murrelet, while other species are more likely to be tolerant (e.g., gelatinous zooplankton, walleye pollock, mew gull, glaucous-winged gull) or benefit (pink salmon, Pacific sand lance, marbled murrelet, herring gull) from reduced glacial input.

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