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Impacts of moderate hypoxia on fish and zooplankton prey distributions in a coastal fjord

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ABSTRACT: Hypoxia can cause significant disturbances in aquatic ecosystems, but the impacts of moderately low dissolved oxygen (DO) where physiological tolerance levels vary among organisms and likely have consequences for key food web linkages are not well understood. We hypothesized that the greater sensitivity of fish to DO, compared with their zooplankton prey, would reduce spatial overlap between fish and zooplankton at moderately low DO (2–4 mg l^{-1}). We used a combination of multifrequency acoustics and net samples to characterize distributions and abundances of zooplankton and pelagic fish in Hood Canal, Washington, a seasonally hypoxic fjord. We employed a sampling design that included both high and moderately low DO sites sampled prior to, during, and after the onset of seasonally low DO over 2 yr. Contrary to our hypothesis, we found that fish and their zooplankton prey did not change their horizontal or vertical distributions during periods and in locations with moderately low DO levels. Consequently, the vertical overlap between fish and zooplankton did not change with DO concentration. The apparent lack of response of fish to moderately low DO in our system may result from decreased metabolic oxygen demand due to cool temperatures, availability of prey in moderately low DO waters, increased predation risk at shallower depths, and/or phenotypic adaptations to chronic exposure. Stability in distributions of pelagic communities suggests resilience of trophic coupling to moderately low DO in Hood Canal.

KEY WORDS: Hypoxia · Temperature · Hood Canal · Pacific herring · Pacific hake · Zooplankton

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INTRODUCTION

Hypoxia, defined as dissolved oxygen (DO) concentrations <2 mg l^{-1}, is an increasing threat for coastal and estuarine ecosystems, affecting the quantity and quality of habitat available to aquatic organisms (Ludsin et al. 2001, Breitburg et al. 2009). The occurrence and spatial extent of hypoxic events are increasing (Diaz & Rosenberg 2008, Stramma et al. 2010) and coastal ecosystems are particularly vulnerable due to anthropogenic eutrophication and climate change (Keeling et al. 2010). Hypoxia also extends vertically into pelagic regions (Stramma et al. 2010), limiting the maximum inhabitable depth of pelagic communities (Bertrand et al. 2010, Netburn & Koslow 2015). These recent studies have focused on extreme hypoxic conditions, but there have been few efforts to study the potential impacts of moderately low DO levels (2–4 mg l^{-1}) on pelagic ecosystems. With the increasing occurrence and expansion of

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hypoxia, many coastal ecosystems are experiencing moderately low DO levels, yet their impacts on pelagic ecosystems are not well understood.

While tolerance to hypoxia varies among species and life stages, fish are generally more sensitive to low DO than zooplankton. The lethal limit for most fish species is DO <2 mg l^{-1}, and many species show behavioral and physiological responses to DO <4 mg l^{-1} (Vaquer-Sunyer & Duarte 2008, Ekau et al. 2010). Exceptions include mesopelagic taxa observed within hypoxic layers of ~0.7 mg l^{-1} in the California Current System (Koslow et al. 2011, Netburn & Koslow 2015), and dense aggregations of Atlantic herring *Clupea harengus* found in waters of ~2.9 mg l^{-1} in a Norwegian fjord (Dommasnes et al. 1994). In contrast, many zooplankton are tolerant of DO <1 mg l^{-1}. For example, the euphausiid *Nematoscelis gracilis* lives in depths with DO <0.15 mg l^{-1} (Sameoto et al. 1987), and the amphipod *Orchomene obtusus* can survive 10–33 h of anoxia through anaerobic respiration (De Robertis et al. 2001).

Hypoxia can cause indirect effects on pelagic communities through distributional and behavioral changes, potentially affecting food web dynamics. Distributional shifts of mobile species towards more oxygenated waters are common (Pihl et al. 1991, Breitburg 1992). Owing to species-specific DO tolerance levels (Miller et al. 2002), the consequences of changes in vertical distributions on predator–prey interactions are not consistent among studies (e.g. Prince & Goodyear 2006, Koslow et al. 2011). For example, shoaling of fish to avoid hypoxia could increase vulnerability to their visual predators, while accessibility to their prey may be reduced or enhanced depending on the DO tolerance level of their prey. Alteration of predator–prey interactions may lead to changes in energy fluxes through food webs (Taylor & Rand 2003, Baird et al. 2004). Ecosystems heavily impacted by human disturbances, such as eutrophication and hypoxia, transmit a reduced fraction of energy from primary producers to planktivorous fish, and then to their predators (Baird et al. 1991). Although these previous studies have focused on hypoxic conditions, moderately low DO conditions would likely have similar consequences for key food web linkages due to differences in physiological DO tolerances between fish and zooplankton.

Hood Canal is a hypoxia-prone fjord located in southwest Puget Sound, Washington (see Fig. 1). Relatively high DO concentrations are maintained by periodic intrusions of coastal water at the northern canal, while DO concentrations in the southern regions decline through summers and the development of hypoxia near the bottom becomes a regular phenomenon (Newton 2002). Historically, hypoxic conditions led to extensive fish kills during September 2006 and 2010 (Newton et al. 2007, Palsson et al. 2008), when DO levels as low as 0.25 mg l^{-1} were observed at the Oceanic Remote Chemical Analyzer (ORCA) buoy. Strong spatial contrasts in the timing and intensity of low DO across the canal provide an ideal *in situ* field site to test the effects of moderately low DO on pelagic communities. Namely, the predictability of moderately low DO events in time and space, accompanied by sharp gradients in DO across space, allows for cross-site comparisons that can decouple spatial distributional shifts associated with natural phenology from those associated with moderately low DO values.

We predict that distributional shifts of fish and zooplankton occur horizontally and vertically in response to reductions in DO levels. Horizontal shifts involve movements of organisms across the canal, and would be reflected in localized density reductions of DO-sensitive species in areas and times with moderately low DO levels. Vertical shifts involve movements of organisms through the water column within a region. Either shift — if sustained over ecologically significant time periods — could influence energy transfer through the food web by either enhancing or diminishing overlap of zooplankton and planktivorous fishes. Laboratory-based DO thresholds (Miller et al. 2002, Vaquer-Sunyer & Duarte 2008) suggest that moderately low DO will induce distributional shifts in planktivorous fish but not zooplankton, thereby reducing spatial overlap. We employed a multi-site sampling design that included 2 high DO (DO >4 mg l^{-1}) sites in northern Hood Canal and 2 seasonally, moderately low DO sites in the southern canal. We sampled these sites from summer through fall across 2 yr to encompass environmental conditions prior to, during, and after the onset of low DO, using a combination of multi-frequency acoustics and net sampling.

MATERIALS AND METHODS

Study site

Hood Canal is a 110 km long fjord with a maximum depth of 188 m (Finlayson et al. 2000). A shallow sill (55 m depth) located at the northern entrance of the fjord limits exchanges of dense water, which further limits the exchange at the southern end of the canal. Renewals of deep, oxygenated water gener-

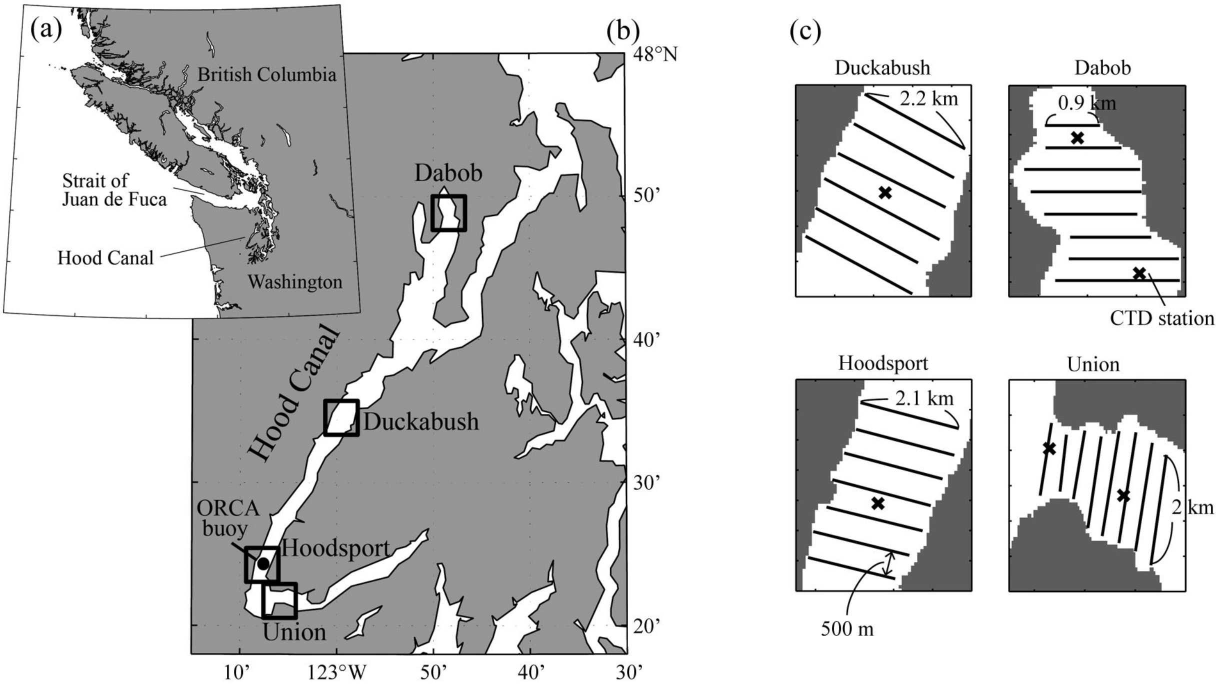


Fig. 1. (a) Study site located in the southwestern Puget Sound, Washington, USA. (b) Four sampling sites located along Hood Canal: Dabob, Duckabush, Hoodsport, and Union. Historical environmental data were collected at the ORCA buoy located at Hoodsport. (c) Representative transect lines spaced 500 m apart and CTD stations (✖) are shown at each site

ally occur during fall, when dense, high-salinity ocean waters associated with upwelling intrude over the sill (Barnes & Collias 1958), displacing bottom waters of the canal upward and increasing the oxygen content of the canal. After these renewals, DO concentrations in the canal steadily decrease and reach moderately low or hypoxic conditions in the southern canal due to the long residence times of deep waters (64–121 d; Babson et al. 2006) and high primary productivity.

Potential acoustic scatterers in Hood Canal are pelagic fish and mesozooplankton. Dominant pelagic fish species are Pacific herring *Clupea pallassii* and Pacific hake *Merluccius productus* (London et al. 2002). Herring feed on euphausiids and copepods (Hay et al. 2001), while hake primarily consume euphausiids (Tanasichuk et al. 1991). We knew from the earlier acoustic and trawl surveys in the canal that herring, hake, euphausiids, and copepods are strong diel vertical migrants, staying at depth during the day and moving into shallower waters at night (Bollens & Frost 1991, Parker-Stetter & Horne 2009).

Survey design

We used a sampling design that included sites with seasonally, moderately low DO (Union and Hoodsport) and high DO (Dabob and Duckabush) that otherwise have similar environmental features (Fig. 1) to distinguish the effects of low DO from those caused by other factors. Maximum bottom depths within the site are relatively consistent at Hoodsport (~120 m) and Duckabush (~173 m), while they vary at Union (43–81 m: shallower on the east end) and Dabob (56–118 m: shallower on the north end). Ship-based sampling was conducted during June, July, August, September, and October, targeting prior to, during, and after the onset of low DO in 2012 and 2013. Simultaneous measurements using multifrequency acoustics, net sampling, and CTD (conductivity, temperature, depth) profiles were conducted by 2 vessels (RV 'Centennial' and RV 'Clifford A. Barnes') during paired day and night sampling at each site in each month.

Data collection

Oceanographic data

To characterize the temporal and spatial variability of water properties, we collected vertical profiles of CTD (SBE 911plus, Sea-Bird Electronics) and DO (SBE 43) during day and night. The DO sensor was calibrated using the modified Winkler titration method during the field surveys (Carpenter 1965, Herrmann 2014). At each site, 2–4 profiles were collected each month (Fig. 1c) and data were averaged into 1 m depth bins. Based on similar vertical profiles between shallow and deep stations within Union and Dabob, we assumed horizontally uniform environmental conditions within the site. To characterize DO levels relevant to our hypotheses, we calculated the proportion of the water column with DO <4 mg l^{-1} for each site. For comparison with our study, 10 yr of oceanographic data in Hood Canal were obtained from the ORCA buoy located at Hoodsport (Fig. 1b; 47.42° N, 123.11° W). An autonomous, moored profiling system on the ORCA buoy recorded vertical profiles of temperature and DO from the surface to ~120 m depth at a vertical resolution of 0.2 m (Dunne et al. 2002) and a sampling interval of every 2 h from October 2005 to May 2015. Data were averaged over 24 h by 1 m vertical bins. Data gaps less than 72 h were linearly interpolated, while significant data gaps (>72 h of no data) comprised 29% of the time frame.

Acoustic data

To characterize distributions and biomass of the dominant pelagic species, acoustic backscatter data were collected using Simrad EK60 split-beam echosounders operating at 38, 70, 120, and 200 kHz during day and night. Transducers were deployed 2 m below the surface on a pole mounted to the vessel's starboard side. The centers of each transducer were no more than 47 cm apart to maximize spatial overlap of the beams. The 38 kHz transducer had a beam width of 12°, while the 70, 120, and 200 kHz transducers all had beam widths of 7°. Echosounders operated at 0.5–2.0 pings s^{-1}, with a pulse duration of 512 µs and vertical resolution of 10 cm. All echosounders were calibrated using a 38.1 mm diameter tungsten carbide sphere (Demer et al. 2015). At each of the 4 sites, a grid consisting of 6–8 parallel transects spaced 500 m apart were sampled (Fig. 1c). The combined lengths of transects at each site ranged from 12 to 14 km. The vessel speed during the acoustic surveys was 5–6 knots.

Biological samples

To determine species composition and length distributions of organisms within regions of high acoustic backscatter, biological samples were collected. Fish and large invertebrates were sampled using a Marinovich midwater trawl, fitted with a 3.2 mm knotless liner in the codend and towed at a vessel speed of 2–3 knots. Vertical opening of the trawl varied between 4.8 and 7.0 m. A total of 149 trawls (day: 79; night: 70) were conducted, usually with 2 replicate trawls at each site and time of day. The fishing depth of each trawl was selected to sample high acoustic backscatter, with trawl depth being monitored and directed using a real-time pressure sensor (PI50, Kongsberg Maritime) attached to the headrope of the net. Trawl duration was typically 8 min, but varied from 3 to 33 min depending on the observed density of backscatter. Catches were identified, enumerated, weighed, and a subsample of each species (up to 100 individuals) was measured for fork length (FL) or total length depending on fish species, and bell diameter was measured for jellyfish. Up to 50 stomachs each of herring and hake per trawl were preserved in 95% ethanol. Stomach contents were analyzed in the laboratory for percent composition by mass for each taxonomic group under a dissecting microscope.

Zooplankton were sampled using a HydroBios MultiNet system configured with 5 opening–closing 335 µm mesh nets with a 0.25 m^2 mouth opening and double flowmeters. A total of 79 depth-stratified oblique tows (day: 41; night: 38) were conducted at a vessel speed of 2–4 knots. All MultiNet tows were conducted within 2 h of the acoustic measurements to minimize spatial and temporal mismatches between net sampling and acoustic measurements. MultiNet sample depths were set to target acoustic backscatter layers observed on the echosounders. Tow duration within a targeted layer varied between 1–7 min depending on the vertical thickness of the observed layer. Samples were fixed in 5% formalin in seawater buffered with sodium borate. In the laboratory, a subsample from each zooplankton tow was identified to taxa, counted, and measured for length. Euphausiid length was measured from the posterior base of the eye stalk to the end of the sixth abdominal segment (Mauchline 1980). Total body length along the longest axis was measured for all other zooplankton taxa.

Day vs. night surveys

Although the field surveys were conducted both during day and night, we only describe daytime surveys here because that was the period when fish and zooplankton were most likely to be affected by low

DO concentrations developed at depth. To confirm that fish were feeding during daytime and therefore daytime distributions were relevant for examining predator–prey overlap, we evaluated whether mean stomach fullness of herring varied by time of day, after accounting for sampling site or month. We fitted linear mixed-effects models with sampling site, month, and time of day as fixed effects and each trawl as a random effect. To account for possible differences in fish size and feeding capacity, we restricted the analysis to herring 15–18 cm in length collected over 91 trawls, resulting in total of 790 observations. We found no difference in mean stomach fullness between day and night samples with a 95% confidence interval (CI) on the effect of diel period equal to −0.15–0.013. Because hake tended to be captured at deeper depths than herring during the day, resulting in everted stomachs due to barotrauma when brought to the surface in the midwater trawl, we did not perform a similar analysis for hake.

Acoustic data analysis

Acoustic data were processed using Echoview (version 5.4. Vessel noise estimated during the acoustic surveys was removed by linear subtraction. Data shallower than 5 m depth were removed from analyses to eliminate near-field transducer effects and surface bubbles. Data within 0.5 m of the echosounder-detected bottom were also removed from the analysis. Averages of CTD downcasts collected through the water column at each site during each sampling period were used to estimate sound speed and absorption coefficients, which were then used in calculations of volume backscattering strength (S_v; dB re 1 m^{-1}).

Acoustic backscatter was classified as zooplankton (dominated by euphausiids and copepods), herring, or hake based on morphologies and backscatter frequency response, following the procedure of Sato et al. (2015) briefly described here. First, raw S_v data were categorized into (1) aggregations (backscatter with discrete, closed edges), (2) single targets (targets at densities lower than one per sampling volume), and (3) layers (backscatter without discrete, closed edges) based on morphologies. Fish aggregations and single targets often appeared within zooplankton layers during daytime. To avoid misdetections of such mixed compositions, we first classified aggregations and single targets as fish, and removed them from the data at each frequency leaving layers. Fish aggregations were further classified into 'herring aggregation' or 'other aggregation'. S_v data within each category were averaged into 20-ping horizontal by 2-m vertical cells.

Cells categorized as layers were classified to dominant taxa using differences in mean volume backscattering strength ($\Delta MVBS_{i-j} = MVBS_i - MVBS_j$, where i and j denote frequency in kHz). Based on the full exploration of the frequency differences, we used 38 and 200 kHz to separate fish and zooplankton, and 38 and 120 kHz to separate herring and hake (Sato et al. 2015). To minimize background noise, only cells with MVBS values greater than −90 dB and signal-to-noise ratios greater than 10 dB were used for further analysis. Backscatter with $-16 \text{ dB} < \Delta MVBS_{200-38} \leq 2 \text{ dB}$ was classified as fish, and $2 \text{ dB} < \Delta MVBS_{200-38} < 30 \text{ dB}$ as zooplankton. Backscatter identified as fish was further classified as hake when $\Delta MVBS_{120-38} < -4.8 \text{ dB}$, and herring when $\Delta MVBS_{120-38} \geq -4.8 \text{ dB}$. Jellyfish present near the surface were often a significant part of trawl catches, and their acoustic backscatter can be similar to those of fish (Brierley et al. 2001, De Robertis & Taylor 2014). To minimize the misclassification of jellyfish as fish, acoustic data analysis was limited to data deeper than 20 m depth (see 'Fish and jellyfish' in 'Results' for justification). Using this classification method, acoustic backscatter were classified to 5 categories: fish (aggregations, single targets, and layers combined), herring (herring aggregations and herring layers combined), hake (hake layers), unclassified fish (other aggregations and single targets combined), and zooplankton.

We characterized distributions of fish and zooplankton across the canal (horizontal distributions) and within the site (vertical distributions) relative to a representative DO profile at each site. The nautical area scattering coefficient (NASC; m^2 nmi^{-2}), which is an integrated backscatter over the water column, was calculated along all transects at each site using the classified MVBS data with 20-ping horizontal averages. To compare with a single DO profile collected per site, NASC values were averaged over all transects at each site. Here, NASC values of unclassified fish at each site were further categorized into herring or hake based on the proportions of NASC values that were classified as herring and hake, assuming that their proportions remained consistent in unclassified fish backscatter and that they were the only backscattering taxa, which was supported by their dominance in midwater trawl catches. These NASC values were then used as indices of the total abundance for herring, hake, and zooplankton at each site to characterize horizontal distributions.

Vertical distributions, including predator–prey overlap, were characterized by calculating horizontal averages of the volume backscattering coefficient (s_v; m^{-1}) across all transects at each site, keeping the vertical resolution of 2 m and resulting in 1 vertical profile per site. Horizontal averages of the acoustic data were taken to compare with a single DO profile per site. Unclassified fish s_v were categorized into herring or hake based on the proportions of their s_v values classified as herring and hake at each depth bin. Degrees of overlap between fish (herring and hake) and zooplankton were estimated based on the percentages of overlap area between fish and zooplankton s_v, where both s_v values were normalized between 0 and 1.

We evaluated the effects of year, sampling site, month, and DO levels on the daytime NASC values of herring (n = 40), hake (n = 40), and zooplankton (n = 40), and percentage of overlap area between herring/hake and zooplankton (n = 40). We used linear mixed-effects models with random effects on sampling site and fixed effects on year, month, and DO levels to account for the repeated measures of the sample sites (Gelman & Hill 2006).

RESULTS

We present the results of daytime field observations only, because pelagic fish and zooplankton were most abundant during daytime at depth where moderately low DO developed. Comparison of stomach fullness of herring confirmed that fish were feeding during daytime (see 'Day vs. night surveys' in 'Materials and methods'), suggesting predator–prey interactions. During night, fish and zooplankton migrated near the surface where the effects of near-bottom hypoxia were unlikely.

Environmental conditions

Vertical DO profiles indicated spatial and temporal development of stratification and low DO in Hood Canal (Fig. 2). There were differences in the timing of moderately low DO and/or hypoxia, and deep-water renewal between sites over the 2 yr. Seasonal development of hypoxia occurred near the bottom in the southern canal (Union and Hoodsport), but not at the northern sites (Dabob and Duckabush). In 2012, hypoxia was observed only at Union in October where DO exhibited a sharp oxycline, reaching hypoxic levels below 35 m depth with a minimum value of 1.8 mg l^{-1}. In 2013, bottom-layer hypoxia occurred below 93 m during August at Hoodsport (minimum DO = 1.8 mg l^{-1}), and below 54 m during August and 64 m during September at Union (minimum DO = 1.7 mg l^{-1}). Based on the DO time series collected by the ORCA buoy, Hood Canal experienced chronic exposure to low DO conditions and no diel cycle of such condition was observed. In early fall, the hypoxic layer at the southern sites (minimum DO = 1.4 mg l^{-1}) shoaled to ~10–20 m depth due to an intrusion of oxygenated, warm, saline deep-water. At the northern sites, bottom DO gradually decreased towards fall to moderately low DO levels, but did not transition to hypoxic levels in either year. The timing of the deep-water renewal with warm, oxygenated water also differed between the northern and southern sites. In 2012, the renewal occurred in October at the northern sites but did not influence the southern canal. In 2013, the deep-water renewal began 1 mo earlier than in 2012 and was observed throughout the canal by October.

Species composition

Fish and jellyfish

Herring and hake were the dominant fish species collected in the daytime midwater trawls at all sites, constituting 82–100% at Dabob, 53–100% at Duckabush, 84–100% at Hoodsport, and 82–100% at Union by wet weight. The trawl captured herring of FL 12–22 cm, and hake of FL 13–40 cm. Age-0 herring (FL = 7–12 cm) and hake (FL = 2–13 cm) were captured in late summer–early fall, constituting 0.3–1.0% of herring and hake catches by wet weight in August, 0.2–8.0% in September, and 19–30% in October. Other fish species commonly caught included tadpole sculpin *Psychrolutes paradoxus*, blackfin sculpin *Malacocottus kincaidi*, and plainfin midshipman *Porichthys notatus*.

Jellyfish, including *Cyanea capillata*, *Phacellophora camtschatica*, *Aequorea victoria*, and *Aurelia aurita*, were also abundant, constituting 36% of the total trawl catches by number in 2012 and 37% in 2013, with peak abundances in June followed by a persistent decline through summer and into fall. The vast majority of the jellyfish by number were small *A. victoria*. Because the decline in jellyfish abundance corresponded to the disappearance of near-surface backscatter layers at 38 kHz that were present earlier in the season, we attributed jellyfish catches to incidental bycatch from surface layers during net re-

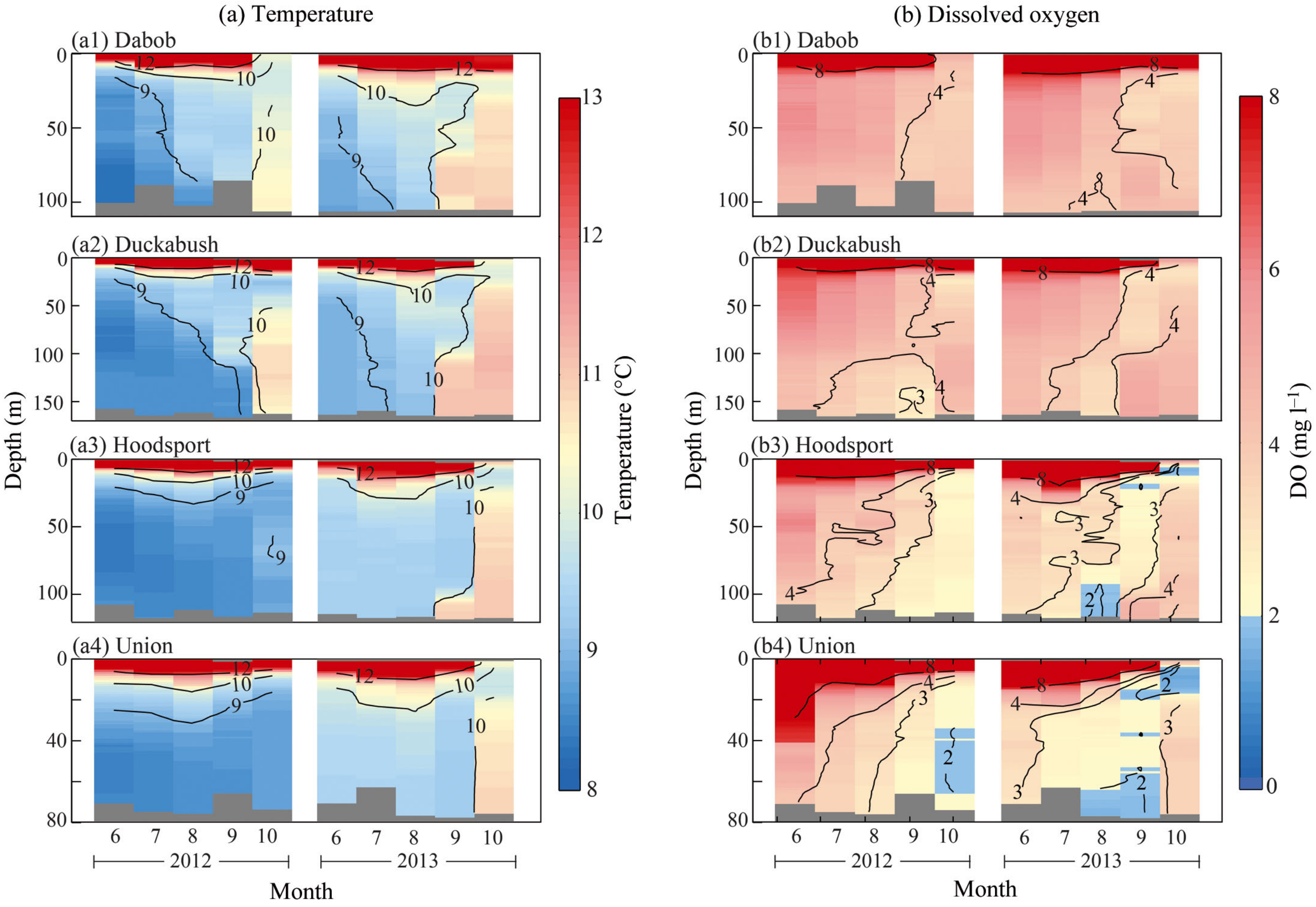


Fig. 2. (a) Temperature and (b) DO concentrations collected during daytime from June through October in 2012 and 2013 at 4 sites in Hood Canal. The only exception was the data collected at Duckabush in July 2013, where only the nighttime cast was available due to equipment malfunction. Gray bars represent the bottom

trieval, and removed the upper 20 m from acoustic data analyses. Acoustic backscatter classified as fish at upper 20 m varied between 6–31% of the total backscatter in the water column.

Fish stomach contents

We standardized the stomach content analysis to account for possible effects of fish length on feeding capability by selecting the most common lengths of fish captured by the daytime trawls: 13–20 cm herring constituted 96–97% (range across years) of the herring sampled for stomach contents (n = 1393), and 15–30 cm hake constituted 92–96% of hake stomachs sampled (n = 1269). Euphausiids were the dominant prey of both species across the sampling sites, constituting 68–89% of stomach contents by wet weight for herring, and 59–71% for hake. Other prey included crab larvae and amphipods. We found differences in mean stomach fullness between the 4 sites, with Union having marginally but significantly lower than average stomach fullness (95% CI on zero-centered data = −0.16 to −0.005), and Hoodsport having significantly higher than average stomach fullness (95% CI = 0.07–0.32).

Zooplankton

Euphausiids (*Euphausia pacifica*, *Thysanoessa raschii*, and *T. spinifera*) and copepods were the dominant taxa collected from daytime backscatter layers throughout the canal, constituting 53–91% of wet weight at Dabob, 61–98% at Duckabush, 49–96% at Hoodsport, and 54–91% at Union. Euphausiids were

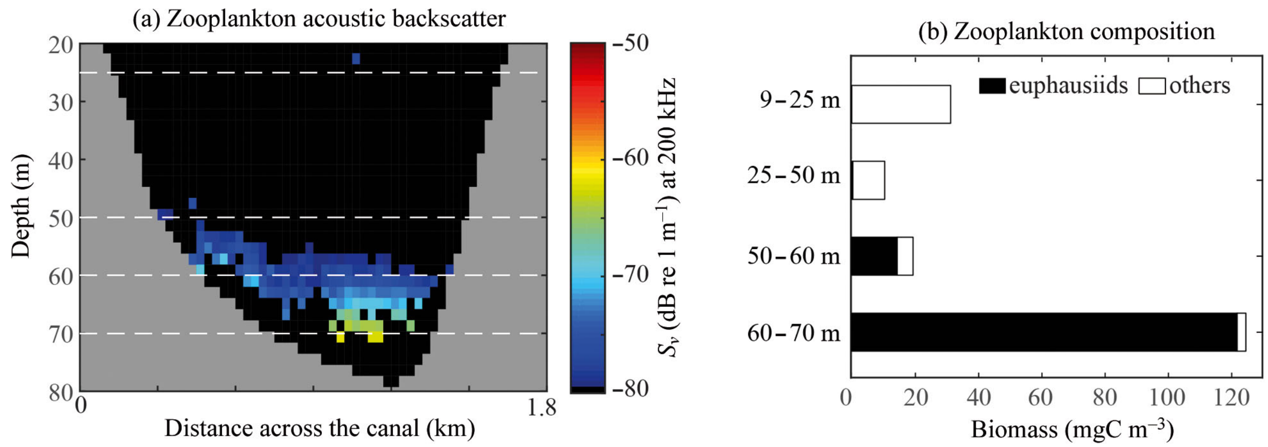


Fig. 3. (a) An example transect of zooplankton daytime backscatter at 200 kHz at Dabob collected in September 2012. (b) Zooplankton community composition collected within and outside of the acoustic backscatter layer. Targeted net sampling depths are shown by the white dotted lines in (a)

more effectively detected by the acoustics due to their larger body sizes and stronger backscatter compared with copepods (Fig. 3). Organisms such as thecosome pteropods *Limacina helicin*, gastropods, and siphonophores with gas-filled pneumatophores (e.g. *Nanomia bijuga*) are strong acoustic targets and contribute high S_v values (Stanton et al. 1994), but were relatively rare in our samples. Thecosome pteropods were observed in 8 samples at densities >10 ind. m^{-3} out of 41 daytime samples. Gastropods were present in 6 samples with densities of 2–16 ind. m^{-3}. No pneumatophore-bearing siphonophores were sampled. Because of the relatively low densities of the organisms with strong acoustic backscatter characteristics, we conclude that the multifrequency differencing method provided robust measures of the density and distributions of euphausiids, the dominant prey of zooplanktivorous fish.

Daytime distributions of pelagic communities

Comparison of the echograms during high and moderately low DO conditions suggested that there was no apparent avoidance of moderately low DO waters by herring, hake, or zooplankton (Fig. 4). During both high and moderately low DO conditions, there was a persistent deep backscatter layer associated with fish that was dominated by herring or hake, while zooplankton backscatter layers were usually present just above the fish layers. Fish aggregations were commonly located within the zooplankton layers.

Daytime abundance of pelagic communities varied among years, sampling sites, and months. A higher abundance of herring was observed at Union during most months in 2012 and 2013 (Fig. 5a). When hypoxia was observed at Union and Hoodsport in late summer or fall, NASC values of herring varied from the same order of magnitude to nearly 6 times larger than the northern sites. Comparison of their abundance with DO levels showed similar NASC values across the range of moderately low DO waters (Fig. 5b). A higher abundance of hake was observed in 2012 than in 2013, with increased abundance at Duckabush (Fig. 5c). Zooplankton abundance was high at Hoodsport and Duckabush, while low at the shallower Union and Dabob sites (Fig. 5e). Similarly, a wide range of NASC values were observed regardless of DO levels in the water column (Fig. 5f). Using the linear mixed-effects models, we found no difference in the daytime NASC values of herring and zooplankton across years, months, or during periods with DO <4 mg l^{-1} (Table 1). There was a statistically significant effect of moderately low DO on the daytime NASC of hake (95% CI = −11.81 to −0.41), but the magnitude of the effect was small (i.e. a reduction of 11.81 m^2 nmi^{-2} corresponding to 3.5% of the mean). Within each site, the degree of vertical overlap between fish and zooplankton was examined. In general, there was higher percentage of overlap between herring and zooplankton than between hake and zooplankton. There was no clear trend in herring–zooplankton and hake–zooplankton overlap among years, sites, months, or DO levels (Fig. 6). Consequently, there was no significant effect of year, month, or low DO on herring– and hake–zooplankton overlap (Table 1). There were only 5 occasions when DO levels became hypoxic (October 2012 in Union, August and September 2013 in Union and

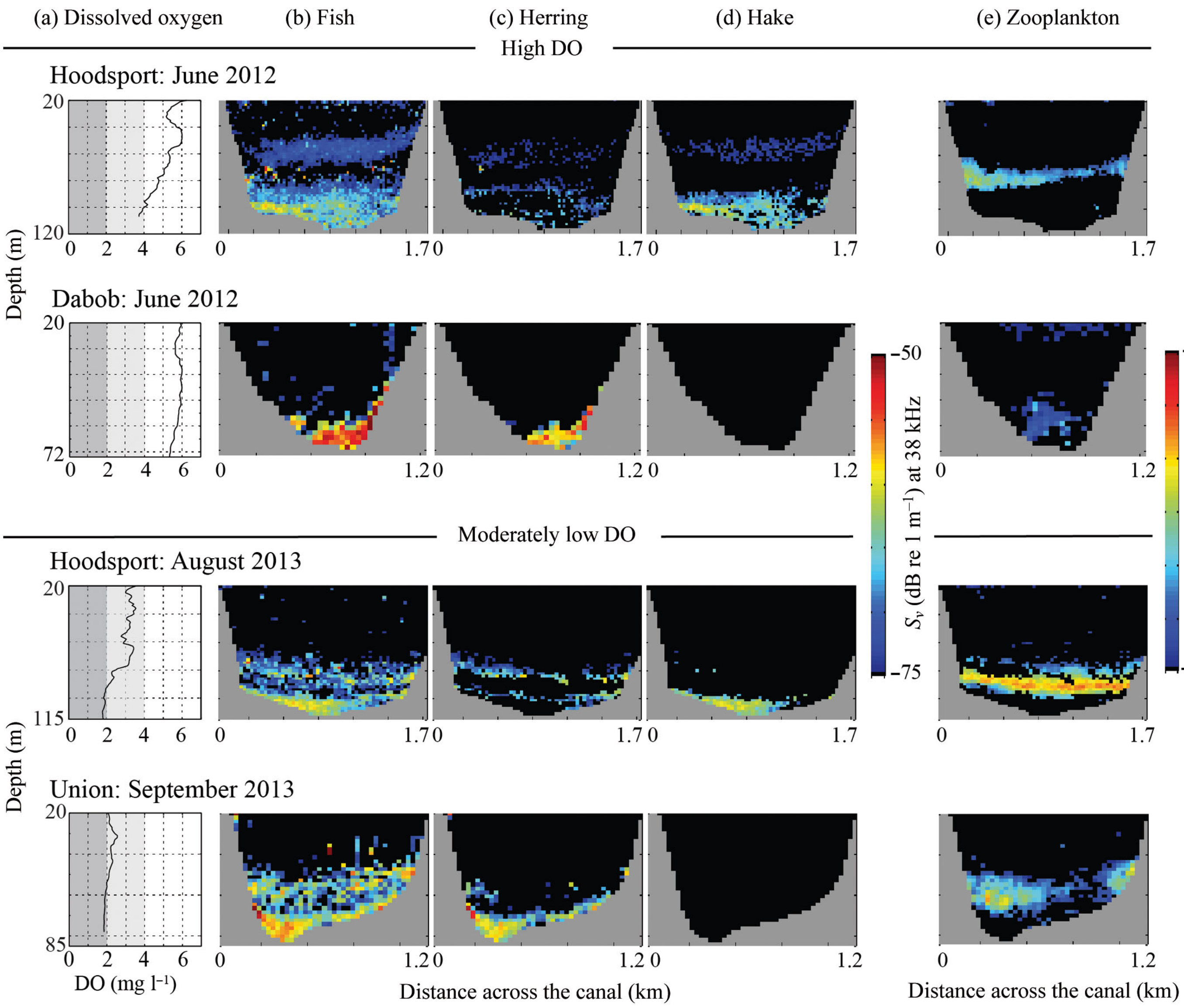


Fig. 4. Example distributions of pelagic communities during high and moderately low DO periods, showing high backscatter under both conditions. The sites with consistent DO characteristics throughout the water column were chosen, resulting in different combinations of the sites between 2 DO conditions. (a) DO concentrations: ranges of DO levels under hypoxia (DO <2 mg l^{-1}) and moderately low DO (2–4 mg l^{-1}) are shown in gray shadings with darker colors representing lower DO levels. (b–e) Daytime echograms of fish (including aggregations, single targets, and layers classified as fish), herring (including herring aggregations and layers classified as herring), and hake (including layers classified as hake) at 38 kHz and zooplankton at 200 kHz based on a transect of the sampling sites with representative DO conditions

Hoodsport), preventing us from separately testing the effect of hypoxia on horizontal and vertical distributions due to a small sample size.

DISCUSSION

We assessed the potential effects of moderately low DO on trophic links in Hood Canal by evaluating hypothesized differences in horizontal and vertical distributions of pelagic fish and their zooplankton prey over time and space. Contrary to our hypothesis, we found that planktivorous fish did not change their horizontal and vertical distributions during periods of, and in locations with, moderately low DO. Herring and hake were consistently observed in moderately low DO waters throughout the summer and fall. Consequently, there was no significant effect of moder-

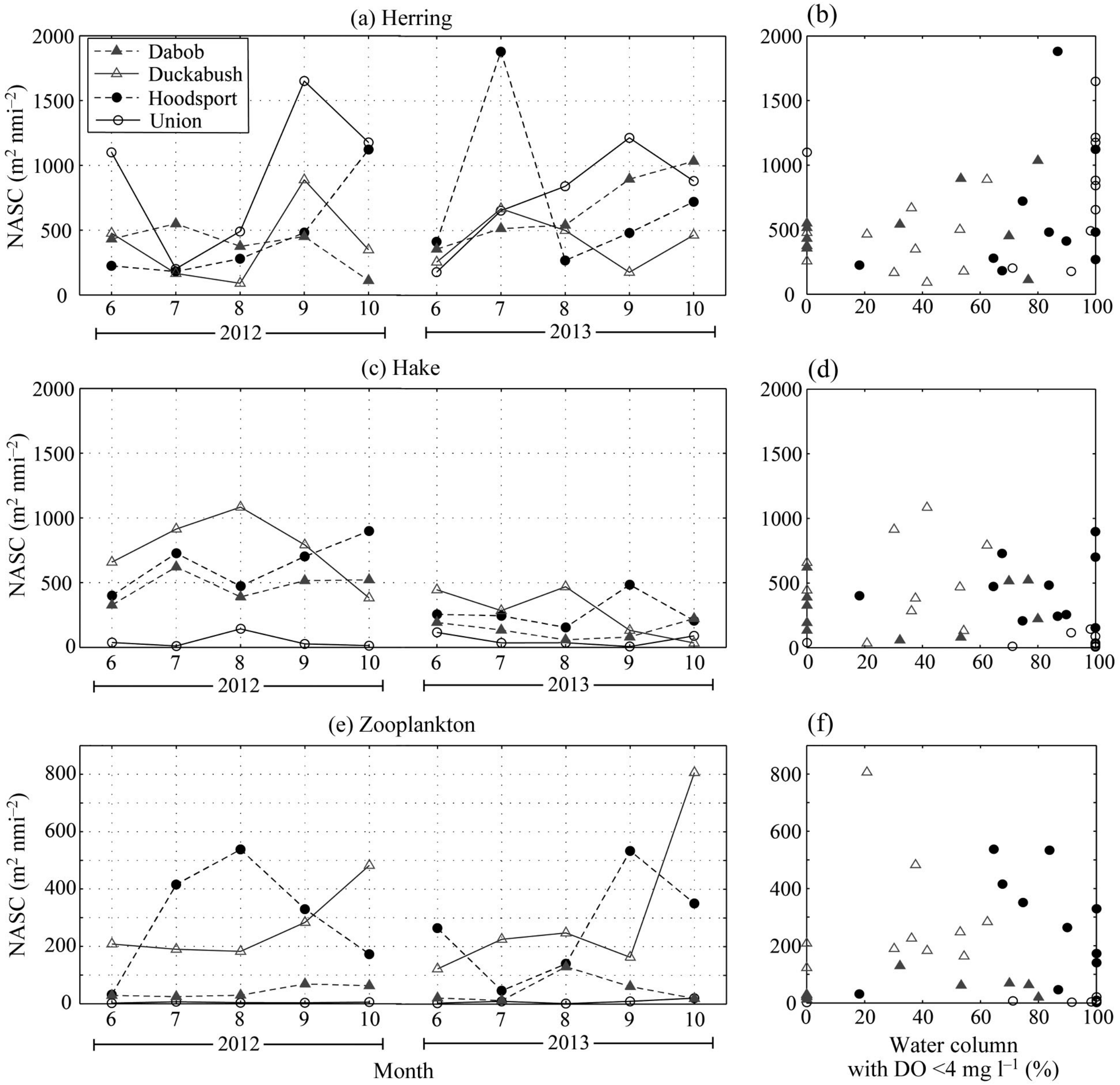


Fig. 5. (a,c,e) Seasonal changes of daytime nautical area scattering coefficient (NASC; m^2 nmi^{-2}) of herring and hake estimated at 38 kHz and zooplankton at 200 kHz at each site. Unclassified fish backscatter (i.e. single targets and other aggregations) were categorized into herring or hake based on the proportions of their NASC values at each site. (b,d,f) Percentage of water column with DO <4 mg l^{-1} vs. daytime NASC values

ately low DO on the overlap between fish and their primary prey.

The minimum DO level observed in this study, 1.7 mg l^{-1}, was below the DO thresholds that have been shown to induce behavioral changes in pelagic fish, but not in zooplankton. Numerous laboratory and field studies have shown that pelagic fish avoid waters with DO <2 mg l^{-1} or <4 mg l^{-1} (Ludsin et al. 2009, Vanderploeg et al. 2009). Thus, our finding of persistent distributions of pelagic fish regardless of DO levels was counter to our expectations. Laboratory experiments suggest that Pacific herring have a lethal DO threshold of 2.3 mg l^{-1} with 4–8 h of exposure (Froehlich et al. 2015). On the other hand, the DO tolerance of Pacific hake is not well understood. Related hake species have been observed in low DO environments, such as Chilean hake *Merluccius gayi* in waters with 0.4–2.1 mg l^{-1} (Vargas & Castro 2001) and juvenile Cape hake *Merluccius capensis* as low as 0.7 mg l^{-1} (Hamukuaya et al. 1998), whereas red hake *Urophycis chuss* were never observed at DO <2.0 mg l^{-1} (Howell & Simpson 1994).

Table 1. Summary of the linear mixed-effects model estimates of the effects of DO levels (percentage of the water column with DO <4 mg l^{-1}) on the daytime nautical area scattering coefficient (NASC) values of herring, hake, and zooplankton, and percentage of overlap area between herring/hake and zooplankton

Dependent variables	Estimate	SE	95% CI Lower	95% CI Upper
Herring NASC	2.45	2.17	−1.89	6.80
Hake NASC	−6.11	2.85	−11.81	−0.41
Zooplankton NASC	−0.05	4.87	−9.78	9.69
Overlap between herring and zooplankton	−0.02	0.09	−0.20	0.15
Overlap between hake and zooplankton	0.07	0.11	−0.16	0.29

In contrast, zooplankton are reported to have relatively high tolerances to hypoxia (Sameoto et al. 1987, De Robertis et al. 2001). Euphausiids were the dominant taxa sampled in the daytime backscatter layers and the major prey for herring and hake in Hood Canal, consistent with other studies (Tanasichuk et al. 1991, Robinson 2000). The critical oxygen partial pressure of the euphausiid *Euphausia pacifica* found in an oxygen minimum zone was 2.3 kPa (Childress 1975). This corresponds to critical oxygen saturation levels (O_{2crit}; the level at which oxygen demands to support standard metabolic rate can no longer be maintained) of 1.0 mg l^{-1} at 10°C, which is below the lowest DO level observed in this study. The apparent lack of change in horizontal and vertical distributions of zooplankton in this study is consistent with their reported oxygen tolerance. There is uncertainty in applying this O_{2crit} value to our study, because euphausiids inhabiting oxygen minimum zones would likely have lower lethal thresholds than ones in seasonally low DO regions such as Hood Canal (Childress & Seibel 1998, Seibel 2011).

Consistent daytime distributions of herring and hake in Hood Canal, despite moderately low DO concentrations, may be explained by several physiological and ecological factors: (1) decreased metabolic oxygen demand due to cool temperatures, (2) sustained availability and/or accessibility to their prey in moderately low DO waters, (3) increased predation

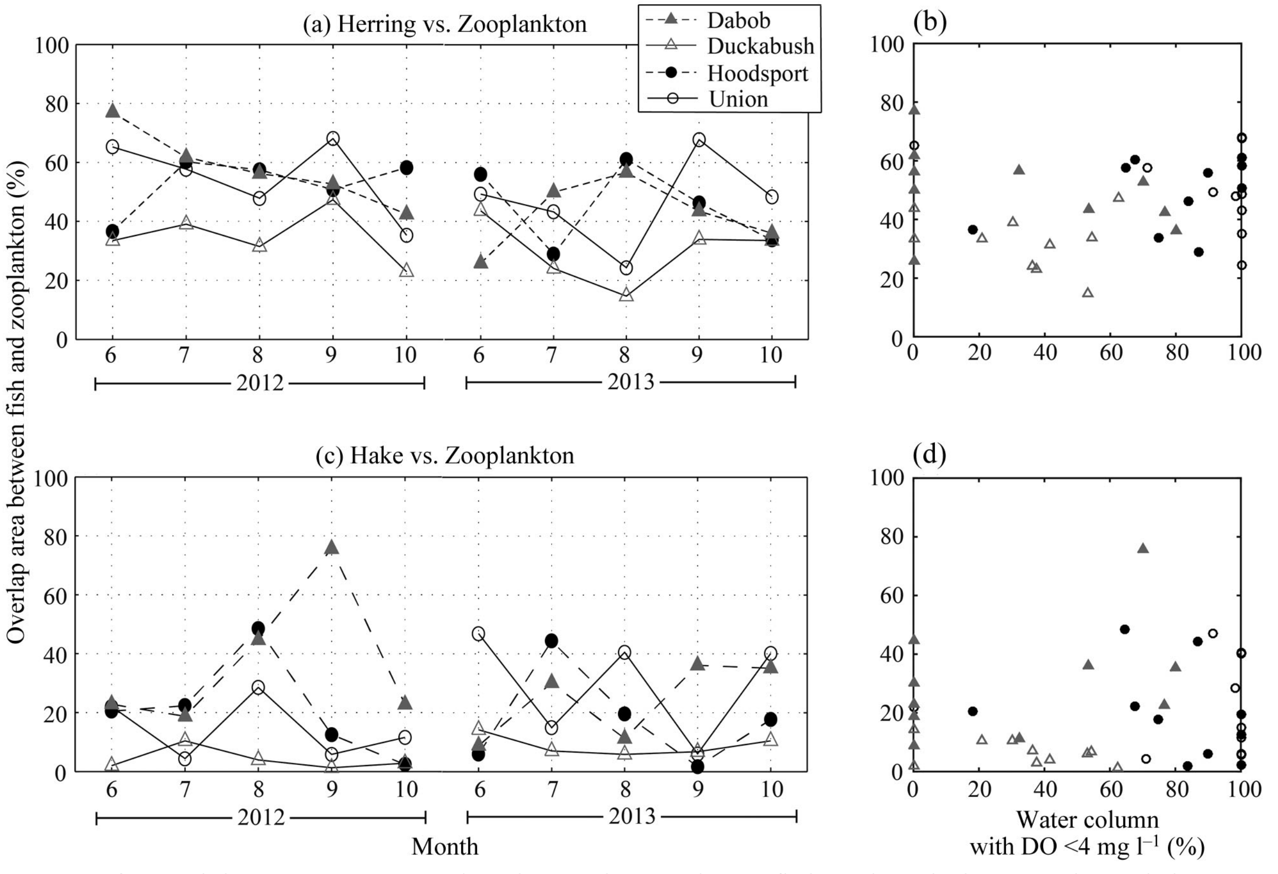
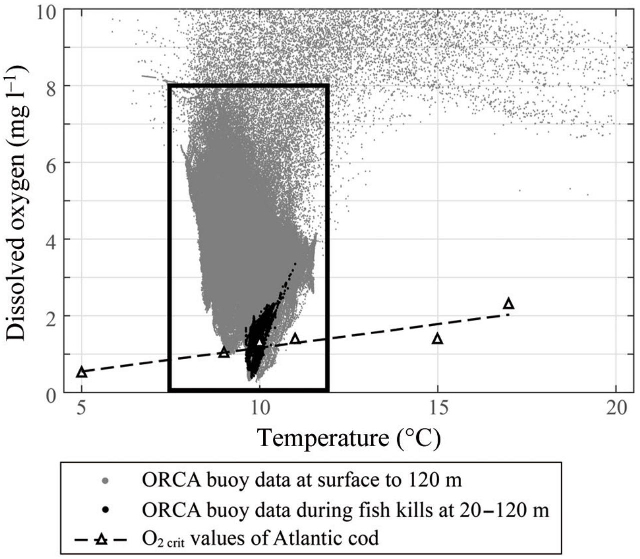


Fig. 6. (a,c) Seasonal changes in percentage of overlap area between herring/hake and zooplankton at each site. (b,d) Percentage of water column with DO <4 mg l^{-1} vs. percentage of overlap area between herring/hake and zooplankton

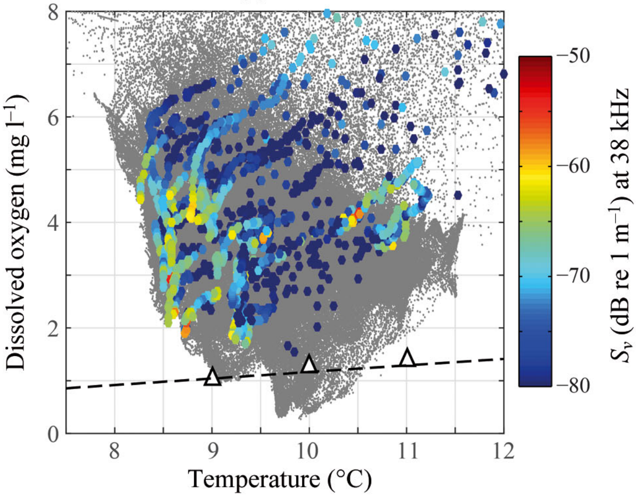
risk in shallower and high DO waters, and/or (4) phenotypic adaptation to chronic exposure. Physiological stress due to inhabiting moderately low DO waters may be mitigated by lower metabolic rates in colder water. Because metabolic rates of animals are temperature dependent, DO concentration alone cannot explain physiological stress posed by hypoxia (He et al. 2015). There is increasing evidence to suggest that both thermal and hypoxic tolerances of animals constrain inhabitable geographical ranges (Pörtner & Knust 2007, Deutsch et al. 2015). For fish, O_{2crit} is highly dependent on temperature, as illustrated by temperature-dependent increases for Atlantic cod *Gadus morhua* (Schurmann & Steffensen 1992) shown in Fig. 7a, as well as similar patterns observed for common eelpout *Zoarces viviparus* (Pörtner & Knust 2007) and midwater eelpout *Melanostigma pammelas* (Belman & Gordon 1979). Although there are no published laboratory data that allow calculation of O_{2crit} for Pacific herring or Pacific hake, we expect that their O_{2crit} values are also temperature dependent. Dense aggregations of Atlantic herring observed in waters of ~2.9 mg l^{-1} in a Norwegian fjord (Dommasnes et al. 1994) can be explained by low metabolic rates at cool temperature of 7–9°C, corresponding to the similar temperature and DO levels observed in this study.

Long-term monitoring of environmental conditions in Hood Canal through the ORCA buoy allowed us to examine how frequently oxygen and temperature values reached levels that would induce fish mortality (i.e. DO below O_{2crit}) in the past decade. Although distributional shifts should occur well before conditions reach lethal limits, O_{2crit} is a well-defined threshold providing a useful benchmark to compare with observed distributions. In Hood Canal, fish kills occurred during September 2006 and 2010 when DO concentrations fell below the O_{2crit} (Fig. 7a), causing mass mortality of benthic (e.g. lingcod *Ophiodon*

(a) 10-yr ORCA buoy data



(b) Fish



(c) Zooplankton

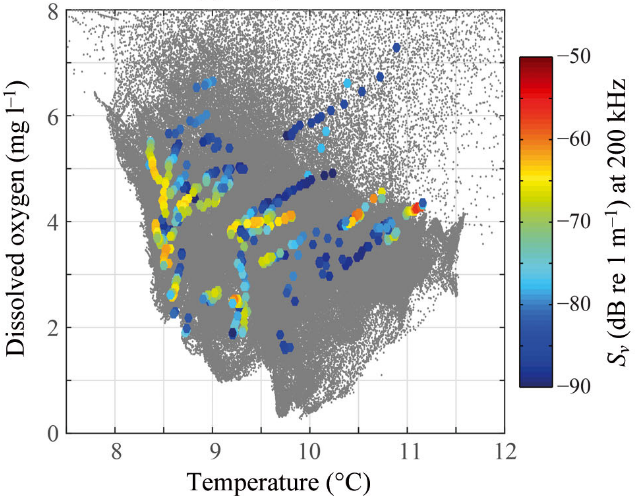


Fig. 7. (a) Temperature vs. DO concentrations collected at the ORCA buoy over 10 yr (gray dots), with data corresponding to the fish kill events during September 2006 and 2010 (black dots). The dotted line shows the laboratory-based critical oxygen saturation (O_{2crit}) values of Atlantic cod (Schurmann & Steffensen 1992). (b,c) Data ranges near the fish kill events and O_{2crit} values, corresponding to the box in (a). Acoustic backscatter values represent the median volume backscattering strength (S_v) of the entire transects at each site calculated in 2 m depth intervals, which were observed nearest to the depth of each CTD measurement. Note that due to the large sample sizes (fish: n = 2091; zooplankton: n = 514), some dots were plotted on top of one another

elongalus) and pelagic fishes including herring (Palsson et al. 2008). This observation supports the applicability of published O_{2crit} values to species at our study site. Assuming that O_{2crit} values for Atlantic cod shown in Fig. 7 apply to pelagic fish communities in our study site, these conditions occurred 1.6% of the time. Although the frequency of occurrence of such conditions was low, we expected behavioral changes to occur at DO levels higher than O_{2crit}. Thus, our observations of high fish density in conditions very close to O_{2crit} were unexpected, suggesting that other factors also influence horizontal and vertical distributions.

As a second possible explanation, there may be benefits of inhabiting moderately low DO waters that outweigh physiological stress induced by exposure to low DO concentrations. Persistent overlap between fish and zooplankton regardless of DO levels suggests that there is a benefit for fish to feed on zooplankton prey throughout the day when zooplankton form dense layers at depth. This set of conditions was observed at Hoodsport (Figs. 4 & 5), where deeper depths in the main channel potentially provide a refuge for zooplankton from visual predators during daytime. However, this predator–prey coherence was not consistent at Union, where high fish abundance was coupled with low zooplankton abundance throughout the field surveys (Fig. 5). It is possible that predation on zooplankton could suppress euphausiid abundances.

Alternatively, as a third potential mechanism, fish may remain at depth to avoid predators. It has been well documented that fish spend less time in habitats that have rich resources but a high mortality risk (Gilliam & Fraser 1987, Gotceitas & Colgan 1990). Herring and hake are key prey items for salmon (Healey 1980), lingcod (Beaudreau & Essington 2011), dogfish (Tanasichuk et al. 1991), marine mammals (Lance & Jeffries 2006), and seabirds (Lance & Thompson 2005). As many of these are visual predators, these animals have increased visual ranges and corresponding predation capabilities in shallower waters. Since all of these potential predators are present in Hood Canal, they could influence distributions of herring and hake, but our acoustic surveys and midwater trawls would not resolve behavior of highly mobile predators. Future field observations, including piscivorous predators to assess habitat-specific predation risks, foraging rates, and environmental stressors, would be needed to provide evidence in support of this hypothesis.

Lastly, fish may have temporarily or evolutionarily adapted to chronic exposure of moderately low DO concentrations to survive, because seasonal low DO is a common occurrence in Hood Canal (Newton 2002) and likely has been for hundreds of years (Brandenberger et al. 2011). Fish species frequently exposed to hypoxia show modifications to gill surface area (Sollid et al. 2003), respiration rates (Saint-Paul 1984), tissue oxygen demands (Hopkins & Powell 2001), and hemoglobin–oxygen affinity (Weber & Lykkeboe 1978). Similar adaptations may be utilized by herring and hake in Hood Canal. Because enhanced capacity to extract oxygen increases hypoxia tolerance, fish with these adaptive mechanisms will be favored in environments experiencing moderately low DO and hypoxia through natural selection.

It is possible that the lack of samples during very low DO concentrations masked behavioral and/or physiological sensitivity to hypoxic conditions in Hood Canal, and reflects our lack of knowledge in DO tolerance levels of Pacific herring and Pacific hake. An obvious next step would include laboratory experiments under various temperatures and DO concentrations to quantify species-specific O_{2crit} values. While our monthly acoustic surveys resolved distributions of pelagic communities over periods of kilometers and days, our survey design could not detect behavioral responses in short timescales, such as diel movement of weakfish and spot observed in a hypoxic estuary (Brady & Targett 2013). There is also potential misclassification of jellyfish as fish because of similar backscatter characteristics (Brierley et al. 2001, De Robertis & Taylor 2014). We attempted to minimize any misclassification by excluding the upper 20 m, but 2 jellyfish species captured by the midwater trawl, *Cyanea capillata* and *Phacellophora camtschatica*, have been observed at depths greater than 80 m in Hood Canal (Moriarty et al. 2012) and could contribute to backscatter measurements. Additionally, there may have been acoustic misclassification of age-0 herring and hake because criteria for fish classification was developed using older juvenile fish (Sato et al. 2015), while ontogenetic changes may affect backscatter properties of fish (Horne 2008). Despite these cautions and given that observed spatial distributions and predator–prey overlap of herring and hake were independent of moderately low DO and that age-0 fish abundances were relatively low, we believe that potential misclassification of acoustic backscatter to herring or hake did not bias patterns observed in the data.

The stability in observed distributions of pelagic communities suggests that the trophic structure of Hood Canal is resilient to moderately low DO under present conditions. Low O_{2crit} combined with cooler temperatures is likely an important mechanism allowing the overlap between fish and their zooplankton prey to be maintained. The extent and intensity of hypoxia will likely increase in nearshore and coastal waters in the future due to climate change and anthropogenic eutrophication (Altieri & Gedan 2015), corresponding to further expansion of areas experiencing moderately low DO conditions. Concurrently, increasing ocean temperatures due to global warming and stratification (Cox et al. 2000) will cause a decline in the solubility of oxygen (Broecker & Peng 1982). The combination of decreasing DO and increasing temperature will likely alter the trophic dynamics in coastal ecosystems. However, there is a potential for continued resilience to moderately low DO in some ecosystems, including Hood Canal, where hypoxia has likely been common over evolutionary timescales (Brandenberger et al. 2011) and deep-water renewal associated with upwelling (Barnes & Collias 1958) will likely keep temperatures low at depth.

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