The Influence of a Deep-Water Intrusion on the Distribution of *Chrysaora melanaster* in the Southeastern Bering Sea

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Abstract Scyphozoan jellyfish are conspicuous components of marine ecosystems, which during a bloom, can impact food web structure and economically important fisheries. Jellyfish biomass in the southeastern Bering Sea (SEBS) is primarily composed of *Chrysaora melanaster* and has varied widely over the past four decades, yet the underlying causes of these biomass fluctuations remain unclear. The present study investigated the spatial and seasonal dynamics of *C. melanaster* along the Alaska Peninsula in the SEBS using an adaptive resolution imaging sonar system and nets in June–July and September 2018. The abundance of *C. melanaster* was high in coastal waters near the Alaska Peninsula, with peak densities occurring east of Unimak Island in both sampling periods. The current pattern revealed by an acoustic Doppler current profiler showed that cold, deep water from Bering Canyon flowed onto the shelf east of Unimak Pass. Differences in the strength of this cross-isobath, deep-water intrusion were observed during the two sampling periods. This flow may have influenced the distribution of *C. melanaster* by constraining the mixed coastal water near of Unimak Island in June-July and by transporting medusae westward, into deeper water in September, after the deep-water intrusion weakened. The present study provides a new mechanistic understanding of how regional-scale ocean variability in the SEBS affects *C. melanaster* distribution.

Plain Language Summary Jellyfish can have detrimental effects on fisheries because they feed on fish eggs, fish larvae and zooplankton. The southeastern Bering Sea (SEBS) is a productive and economically important ecosystem. When jellyfish numbers increase, they can have a major impact on fisheries and food web structure. In the SEBS, jellyfish abundance was high north of the Alaska Peninsula, which appears to be a major source for SEBS scyphomedusae. The deep-water intrusion from Bering Canyon influenced coastal circulation patterns, which in turn affected jellyfish spatial distributions. This study showed that high-resolution sonar imaging systems are effective tools for sampling large jellyfish and provided a new mechanistic understanding of how ocean conditions affect jellyfish distribution in the SEBS.

1. Introduction

Scyphozoan jellyfish are conspicuous components of many marine ecosystems. When they bloom, they can have detrimental effects on fisheries because they feed on ichthyoplankton and zooplankton (Purcell, 2009; Tilves et al., 2016), and their spatial distributions and diets overlap with juvenile commercial fish and forage fish (e.g., Brodeur et al., 2008; Decker et al., 2018; Purcell & Arai, 2001). Thus, jellyfish can act as both predators and competitors of fish. In addition, jellyfish are also known for their rapid growth (Pitt et al., 2013), high fecundity (Lucas & Dawson, 2014), and ability to affect zooplankton and carbon flux (Stone & Steinberg, 2018), making them indicators of pelagic ecosystem status.

The southeastern Bering Sea (SEBS) is a productive and economically important ecosystem (National Research Council, 1996) and has been the subject of several coordinated research programs (Decker et al., 2014; Macklin et al., 2002). In the past few decades, dramatic changes have been observed in the...
environmental conditions and biota of the eastern Bering Sea pelagic ecosystem (e.g., Francis et al., 1998; Stabeno et al., 2017). One prominent change first observed in the mid-1990s was an increase in medusa biomass in fishery surveys, which was hypothesized to be driven by changes in ocean conditions (Brodeur et al., 1999). In the 1980s, medusa biomass, dominated by Chrysaora melanaster, was concentrated in the southeast margin of the Bering Sea, along the Alaska Peninsula (Brodeur et al., 1999). In the 1990s, the center of jellyfish biomass shifted to the northwestern part of the survey area (Brodeur et al., 2002, 2008; Decker et al., 2014).

The typical scyphozoan life cycle contains a free-swimming or pelagic medusa stage, in addition to a sessile (benthic) polyp stage (e.g., Arai, 2009; Shahrestani et al., 2017). Scyphozoan spatial distribution and abundance are often closely related to their life history and habitats (e.g., Doyle et al., 2007; Shahrestani et al., 2020). Previous studies examined jellyfish catch in fishery research trawls (Brodeur et al., 2002, 2008) and identified medusa concentrations on the northern side of the Alaska Peninsula. Likewise, fishermen refer to this region near Unimak Island as “Slime Bank” (Decker et al., 2014). It is likely that coastlines of the Alaska Peninsula and nearby islands provide habitat for C. melanaster polyps, which depend on hard surfaces to settle, and that increased medusa abundance follows increased polyp abundance in these areas (Brodeur et al., 2008; Decker et al., 2013). However, SEBS medusa source locations have not been confirmed with detailed sampling.

Changes in C. melanaster abundance may impact walleye pollock Gadus chalcogramma, which supports one of the largest single-species fishery in the world, because SEBS is the major spawning ground for pollock (Hinckley, 1987). Jellyfish have direct and/or indirect impacts on pollock by consumption of ichthyoplankton and competition for zooplankton prey (Ruzicka et al., 2020). Despite prominent changes in medusa biomass and distribution and the potential economic and ecosystem impacts of these changes, the drivers of these population fluctuations remain elusive. To better understand the impacts of changing ocean conditions on medusa populations, it is essential to understand processes occurring near the source, including early survival and dispersal.

The physical processes along the Alaska Peninsula are complex. Previous studies estimated that 30% of the Gulf of Alaska’s Alaska Coastal Current (ACC) flows into Unimak Pass (Aagaard et al., 2006; Stabeno et al., 2016). After a northward transit through Unimak Pass, this water mixes with the salty slope water near Bering Canyon and moves onto the SEBS shelf (Reed, 1998; Stabeno et al., 2016). As this water mass flows northeast of Unimak Island, it remains on top of the colder, cross-isobath, shelf water, forming a two-layer, thermally-stratified water column, which inhibits vertical mixing (Kachel et al., 2002). The water column in the central SEBS is typically characterized by thermo-stratification (Stabeno et al., 2012); however, it is not clear how the fine-scale vertical distribution of medusae relates to this stratification. Previous studies showed that C. melanaster was generally found in the upper 30 m (Brodeur et al., 2002; Decker et al., 2014).

In 2017–2018, the SEBS experienced moderately (2017) to anomalously (2018) warm conditions (Siddon & Zador, 2017, 2018), and the SEBS ecosystem underwent dramatic changes during this warm period. Sea-ice coverage and cold pool extent in the Bering Sea underwent an unprecedented decline, with a near-complete lack of sea ice in 2018. Latitudinal changes in the distributions of several commercial species, including walleye pollock (Gadus chalcogrammus), Pacific cod (Gadus macrocephalus), and several flatfish species, as well as jellyfish, were recorded during the warm conditions in 2017, relative to the occurrence of these species during the cool conditions in 2010 (Stevenson & Lauth, 2019). In addition, there was a 35% reduction in eastern Bering Sea Pacific cod biomass in 2017 and a 19% further reduction in 2018 (Siddon & Zador, 2017, 2018).

In the present study, an adaptive resolution imaging sonar (ARIS) was deployed to quantify C. melanaster spatial distribution and abundance in 2018. The objectives are (a) to determine C. melanaster horizontal distribution in relation to different water masses, (b) to quantify the fine-scale vertical distribution of C. melanaster with respect to vertical water column structure, and (c) to investigate the influence of dominant ocean currents on the medusa dispersal from the Alaska Peninsula coast into the SEBS.
2. Methods

2.1. Sampling and Study Area

Two research cruises were conducted in the SEBS during June 29 to July 3, 2018, onboard the R/V *Sikuliaq* and during September 2–7, 2018, onboard the R/V *Oceanus*. Sampling occurred between 54.47°N–56.76°N and 160.36°W–166.39°W, along the north side of the Alaska Peninsula (Figure 1). The study area has complex physical oceanographic and bathymetric characteristics (Figure 1). The survey composed of ~30 sampling stations along four transects: two relatively long, cross-shelf transects and two relatively short, along-shelf transects; stations were located 16–35 km apart on these transects (Figure 1 and Table S1). The southern cross-shelf transect followed the ~50-m isobath, ran parallel to the Alaska Peninsula, and surveyed shallow coastal water out to the deeper Bering Sea Canyon region. The northern transect was ~50 km north of the southern transect. Stations 1–3 and 25–30 were located west of Unimak Pass and near Bering Canyon, and had water depths >100 m. Two along-shelf transects were conducted ~275 km apart, with the eastern transect located along the 70-m isobath and the western transect on the 200-m isobath. This sampling scheme was designed to capture the north-south and coastal-oceanic gradients of medusa abundance and hydrography.

2.2. Hydrography and Ocean Current Observations

Temperature and salinity profiles were measured at each station with a Seabird SBE911+ (Sea-Bird Electronics Inc., Bellevue, WA, USA). A conductivity–temperature–depth instrument was deployed either to a maximum water depth of 500 m or within 5 m of the bottom. Data were recorded during the downward deployment, at a descent rate of 30 m min$^{-1}$. In total, 60 hydrographic casts were completed (Data Set S1).

Ocean currents were measured continuously by vessel-mounted acoustic Doppler current profilers (ADCPs). During the June–July cruise, the R/V *Sikuliaq* carried 300 kHz Workhorse (WH300) and 150 kHz Ocean Surveyor (OS150). In September cruise, the R/V *Oceanus* was equipped with 300 kHz Workhorse (WH300) and 75 kHz Ocean Surveyor (OS75). Data acquisition, calibration, and processing followed protocols from the University of Hawaii Data Acquisition System and Common Ocean Data Access System. To examine the consistency of the ADCP data, we statistically compared the results of the WH300, OS150, and OS75. The ADCPs on both cruises displayed remarkable similarities in terms of magnitudes of zonal (east-west direction) and meridional (north-south direction) velocities and their vertical structures. The statistical square root of the differences between two ADCPs range from 1 to 3 cm s$^{-1}$, which is reasonable after taking their different vertical bin lengths into account. The 300 kHz ADCP had enhanced vertical resolution (~2 m in bin length) and its total range (~100 m) can cover the whole water column in most of the survey area; therefore, we present data collected by the WH300 from both cruises.

The original ADCP data contain both tidal currents and subtidal flow. To determine ocean circulation, the ADCP data were detided by removing tidal currents (Data Set S2). The tidal parameters were obtained from an ADCP deployed on the M2 mooring during April–October 1998 as part of NOAA’s Ecosystems-Oceanography Coordinated Investigations (Kachel, 2010). The M2 mooring is located 70 km from our sampling station 18 (Figure 1). We assume that the tidal parameters (i.e., magnitude and phases) have not significantly changed from 1998 to 2018. These tidal parameters were used to estimate the tidal currents at each specific location and time of the ADCP profiles.
2.3. Medusa Data Collection

Medusa samples were collected at each station with a 1-m diameter, 500-μm mesh ring net. The net was towed obliquely through the water column, reaching depths of 5–10 m from the bottom in shallow water, or to depths of 200 m in deep water. A calibrated Sea Gear flowmeter was mounted near the net opening to record the volume filtered during each tow (Data Set S3). All C. melanaster (Morandini & Marques, 2010) and other medusa species were identified and enumerated immediately onboard the vessels in order to validate the images acquired by the ARIS 3000 (Sound Metrics, Bellevue, WA), a dual frequency sonar imaging camera, which is capable of recording near video images. See Shahrestani et al. (2020) for details. The ARIS 3000 was mounted on a towed-body frame with a forward-looking, fixed field of view (10 m, Figure 2). A battery pack and a computer unit, contained in two separate pressure housings, were also attached to the frame. The battery pack powered both the sonar and the computer. The computer recorded the ARIS data using preinstalled ARISscope Software (Sound Metrics). At each sampling station, the ARIS system was deployed vertically at a speed of 30 cm s⁻¹ from the surface to 5 m off the bottom or from the surface to 300 m, when water depth exceeded 300 m. These vertical profiles recorded fine-scale vertical distribution and occurrence of C. melanaster at each station. Vessel operations were continuous, and both the nets and ARIS 3000 were deployed around the clock.

ARIS data were processed with ARISFish Software (Sound Metrics, V2-6-3-1559), whereby the recorded footage was played back and each C. melanaster was manually located and marked in the water column (Figure 2). Using the ARISFish software, the geolocations and depth of each medusa detected were recorded. Sampling volumes were estimated by \( \frac{(w_1 + w_2)}{2} \times h \times d \), where \( w_1 \) and \( w_2 \) are the near field and far field width of sampling view, \( h \) is the depth of field, and \( d \) is the maximum sampling depth; all values in meters.

During the June–July cruise, 273,958 frames were recorded and 242,586 frames were collected during the September cruise (Data Set S4). ARIS sampling was not conducted at stations 10, 18, and 30 in June–July and stations 9 and 15 in September cruise due to instrument failure or unsafe weather conditions.

2.4. Medusa Data Analysis

The net-derived C. melanaster densities were calculated by dividing total medusa counts by the volume filtered, as recorded by a flowmeter (Data Set S3). The ARIS-derived densities (ind. m⁻³) were determined by dividing the total number of medusa detected by the volume sampled (m³). The volume sampled was the product of the ARIS frame area (m²) and depth (m) at each station. Depth-specific abundances (ind. m⁻³) were calculated as the total number of C. melanaster observed within a 1-m depth layer divided by the sample volume over 1 m depth (Data Set S4).

To examine horizontal and vertical spatial patterns of C. melanaster, densities and abundances determined by both ARIS and net sampling methods were plotted with Surfer 11 (Golden Software LLC). The base map of the study area was extracted from NOAA’s National Centers for Environmental Information (https://maps.ngdc.noaa.gov/viewers/wcs-client/). We used the ordinary kriging method to grid the base map, hydrography, and medusa data. Net-determined estimates of medusa densities were overlaid onto contour maps of ARIS-detected densities to illustrate the horizontal distributions of C. melanaster during both investigation periods.

ARIS-determined abundance data from each station were used to construct generalized additive models (GAMs, R Core Team, 2019) to quantify spatial patterns and examine the influence of environmental factors on C. melanaster distribution (Hastie & Tibshirani, 1990). The GAM is

\[
g(\mu) = \text{season} + s(\text{lon, lat, } k_1) + s(\text{temperature, } k_2) + s(\text{salinity, } k_3) + s(\text{offset (volume)}
\]

where \( g \) is a log link, \( \mu \) is the expected value, \( s \) is a smoothing function, and \( k_1, k_2, k_3 \) are the numbers of knots for smoothing functions. The season effect in the GAM quantifies the difference in C. melanaster abundance between our two cruises. We used near-surface water temperature and salinity at each sampling station. The negative binomial distribution and quasi-likelihood were used to estimate parameters (Wood, 2006), which allow overdispersion and could overcome the nonnormal distribution and nonhomogeneous variance. The generalized
A cross-validation procedure was applied to select the model with the smallest error, using the mgcv package in R.

To examine diurnal differences in vertical distribution, we used ARIS-derived depth-specific abundances from stations where *C. melanaster* were present to construct this GAM:

![Representative images of *Chrysaora melanaster* detected by ARIS in the southeastern Bering Sea: (a) medusa bell and tentacles detected at Station 9 on June 30, 2018, and (b) medusa tentacles detected at Station 5 on September 3, 2018. ARIS, adaptive resolution imaging sonar.](image)
where $g$ is a log link, $\mu$ is the expected value, $s$ is a smoothing function, and $k$ is the number of knots for smoothing functions. The diurnal term estimates daytime and nighttime differences in medusa vertical distribution. Note that continuous observations at a fixed location over a 24-h period were not conducted in this study. Given that intensive sampling was conducted within a relatively small geographic area, surveys conducted during the day and night can provide information on diurnal differences in medusa vertical distributions.

To examine differences in the vertical distributions of medusae on the two transects that ran parallel to the Alaska Peninsula (i.e., the northern and southern transects), ARIS-derived, depth-specific abundances (ind. m$^{-1}$) from stations where $C. melanaster$ occurred, were used to construct a GAM: $g(\mu) = \text{season} + \text{diurnal} + s(\text{depth, diurnal, } k) + \text{offset(volume)}$, where $g$ is a log link, $\mu$ is the expected value, $s$ is a smoothing function, and $k$ is the number of knots for smoothing functions. The objective of this test was to examine whether the vertical distribution of $C. melanaster$ changed as they were dispersed from the south to the north.

To examine the potential associations of $C. melanaster$ with different water masses in the study area, temperature–salinity (T–S) diagrams were constructed for observations that coincided with the presence of $C. melanaster$. Depth-specific, ARIS-derived medusa abundances (ind. m$^{-1}$) were overlaid on the T–S diagram using MATLAB, R2015b. Profiles of ARIS-derived abundance (ind. m$^{-1}$) were overlaid on vertical sections of temperature and salinity for each transect with Surfer 11 to visualize the association of $C. melanaster$ with different water masses.

3. Results

3.1. Hydrographic Conditions

The hydrographic conditions documented within the study area show distinct spatial and seasonal patterns (Figures 3 and S1–S3), which were related to topographic features and current patterns along the Alaska Peninsula. On the southern transect, stations 1–3 were located near the Bering Canyon and were...
characterized by deep-water depths, a relatively weak thermocline, low temperatures, and high salinities, indicating that this region was affected by slope water (Kachel et al., 2002) during both sampling periods (Figures 3 and S1–S3). A strong thermocline was present along the southern transect at approximately 30 m depth in June–July and 50 m depth in September from stations 9 to 12 (Figures 3 and S2). However, in June-July the thermocline was shallower in Alaska coastal waters (stations 13–15) than on the midshelf (stations 9–12) (Figure 3). Along the northern transect, stratification also occurred at stations 18–25, resulting in a strong thermocline at approximately 20 m depth in June–July and 50 m depth in September (Figures 3 and S2). The western portion of the study area was affected by slope water, as evidenced by high salinities at stations 26–28 (Figures S1 and S3; Table S1). The water mass sampled along the short transect (stations 13 and 16–18) had relatively low salinities, indicative of coastal water. Overall, the study area exhibited strong horizontal physical gradients, which indicated proximity both to oceanic slope waters and to warmer, less saline, coastal waters.

3.2. Circulation

In June–July 2018, the ADCP measurements near stations 4–15 showed persistent northeastward flow along the Alaska Peninsula coast (Figures 4a–4c). This along-shore current not only followed the coastal bathymetry, but also exhibited a weak onshore component toward the Alaska Peninsula, which was likely part of the ACC flow through Unimak Pass. The predominant flow turned northwestward near the 70-m isobath, indicated by strong currents observed at stations 18–21. The currents near the 100-m isobath (i.e., by stations 23 and 24) were weaker than those observed at the 70-m isobath. In the vertical dimension, the flows at 15 and 35 m were slightly stronger than those at 55 m, but overall, flows were consistent throughout the water column, indicating that vertical ocean circulation was primarily barotropic.

The flows near Bering Canyon revealed a convoluted spatial structure during both cruises. The energetic currents in the slope region displayed westward and northwestward flow near stations 1, 2, and 30. By contrast, we observed continuous eastward flows from stations 29 to 24, which crossed the 100-m isobath and...
represent the intrusion of slope water on to the shelf. This pattern was consistent with hydrographic profiles of stations 24 through 26, where vertical displacements of isohalines and isotherms were evident during both cruises (Figures 3 and S1–S3). These features were robust at various depths.

During the September cruise, coastal flows north of Alaska Peninsula showed distinct features at stations 4–15 (Figures 4d–4f). Circulation primarily moved parallel to coastal isobaths, but turned sharply away from the Alaska Peninsula near stations 17–19. Accordingly, strong northwestward currents were found at stations 20–25, especially near the 100-m isobath. These flows were most evident at the 35 and 55 m depth levels. The physical structure present in September differed from that of June–July, when strong currents occurred near the 70-m isobath (Figures 4a–4c).

The flow pattern near the Bering Canyon was also complex during the September cruise (Figures 4d–4f). Stations 1, 2, and 30 exhibited northward or southward currents, but these flows were much weaker in September relative to what we observed on the earlier cruise. Eastward flows also occurred near stations 27–29 during both cruises. However, in September, currents near stations 24–26 primarily flowed parallel to the 100-m isobath. These circulation characteristics co-occurred with strong horizontal gradients in salinity and temperature near station 25 (Figures S2 and S3), suggesting that geostrophic currents were the primary component in this region. These along-isobath flows present in September were fundamentally distinct from the cross-isobath flow measured during the June–July cruise (Figures 4a–4c).

### 3.3. Large Medusae in the SEBS

Chrysaora melanaster, Aequorea sp., Aurelia sp., and Cyanea sp. are four large jellyfish that commonly occur in the eastern Bering Sea (Hamner, 1983). Chrysaora melanaster, the largest and most abundant of these, dominates the jellyfish biomass on the SEBS shelf (Decker et al., 2014). Net sampling in the present study collected the same four species (Table 1). Chrysaora melanaster can reach 60 cm in diameter, and have tentacles up to 3 m in length (Morandini & Marques, 2010). These long tentacles and characteristic bell shape enable us to distinguish C. melanaster on ARIS images from the other three large jellyfish species that occur in the region (Figure 2). In this study, counts of C. melanaster were obtained from two types of ARIS images: those that contained both the bell and tentacles (Figure 2a) and those that contained only tentacles (Figure 2b). Repeated counts of the same individual were unlikely because only downcast videos were used to track individuals in the field of view, from the initial appearance to disappearance.

### 3.4. Horizontal Distribution of C. melanaster

The average densities of ARIS-detected C. melanaster throughout the water column were $0.78 \times 10^{-2}$ and $0.74 \times 10^{-2}$ ind. m$^{-3}$ in June–July and September 2018, respectively. During ARIS deployments, C. melanaster occurred at 22 out of 27 stations in June–July and at 21 out of 28 stations in September. Average densities of net-collected medusae in all size classes were $2.2 \times 10^{-2}$ and $3.6 \times 10^{-2}$ ind. m$^{-3}$ in June–July and

| Species                  | June–July 2018 | September 2018 |
|--------------------------|----------------|----------------|
|                          | Ind. (×10$^{-2}$ m$^{-3}$) | Dia. (mm)     | Ind. (×10$^{-2}$ m$^{-3}$) | Dia. (mm) |
| Chrysaora melanaster     | 2.16, 3.2      | 62.8 (83, 76.7) | 3.64, 4.1       | 65.7 (198, 54.4) |
| Aequorea sp.             | 0.02, 0.1      | 45.0 (1, −)    | 0.75, 1.9       | 34.1 (41, 22.9)  |
| Aurelia sp.             | 0.03, 0.2      | 30.0 (1, −)    | 0.64, 1.1       | 69.0 (34, 30.1)  |
| Cyanea sp.              | 0.02, 0.1      | 40.0 (1, −)    | 0.06, 0.3       | 57.5 (6, 21.9)   |

Note. Medusae in all size categories are included here. Mean bell diameters of medusae (in mm), with sample sizes and standard deviations, respectively, are in parentheses.

### Table 1

Abundance (Mean Ind. [×10$^{-2}$ m$^{-3}$], SD) of Medusae Collected With a 1-m, 500-µm Ring net at 27 Stations in June–July and at 31 Stations in September 2018 in the Southeastern Bering Sea
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September 2018, respectively (Table 1), which were not statistically different from those estimated by ARIS ($H = 3.35, p = 0.07$ and $H = 2.9, p = 0.09$).

*Chrysaora melanaster* showed distinct horizontal distribution patterns during both study periods (Figure 5). In June–July 2018, high densities of ARIS-detected *C. melanaster* occurred along the Alaska Peninsula east of Unimak Island (stations 8–12) and also on the middle shelf along the northern transect (stations 19 and 21). Medusa densities were relatively low at other shallow-water stations, from $0.06 \times 10^{-2}$ to $1.8 \times 10^{-2}$ ind. m$^{-3}$, and no medusae were observed at the five deep-water sites. In September, high concentrations of *C. melanaster* occurred primarily along the southern transect, specifically in the area east of Unimak Island, and few medusae were observed along the northern transect, compared to earlier sampling (Figure 5). Relatively low medusa densities were observed at the other inner shelf stations, from $0.04 \times 10^{-2}$ to $1.3 \times 10^{-2}$ ind. m$^{-3}$ and no *C. melanaster* were detected at the outer shelf stations in September.

Results of the GAM indicated that the spatial term, represented by latitude and longitude, had a significant effect on ARIS-determined medusa density ($\lambda^2 = 148.51, p < 0.01$). The spatial pattern of *C. melanaster* density differed significantly between the two periods ($z = -0.66, p < 0.01$). Note that *C. melanaster* was concentrated northeast of Unimak Island in both periods. This temporal difference was primarily driven by a wider distribution along the northern transect (at stations 18–25) during the September cruise than during the June–July cruise (Figure 5). This difference in the medusa spatial distribution was consistent with changes in flow fields observed during the two study periods (Figure 4). In June–July, the northeastward current flowed northwest along ~70-m isobath, but in September, this flow turned northwest along ~100-m isobath. Temperature ($\lambda^2 = 1.31, p < 0.25$) and salinity ($\lambda^2 = 0.60, p < 0.44$) showed no significant effects on *C. melanaster* density. The distribution of *C. melanaster* in our study area was centered in coastal water near the Alaska Peninsula and was associated with a front at the interface between coastal water and oceanic slope water (Figures 3 and S1–S3).

**Figure 5.** *Chrysaora melanaster* density (ind. ×10$^2$ m$^{-3}$) detected by nets (post map symbols) and ARIS (colored contour map) in June 29 to July 3, 2018 (upper, a, b) and September 2–7, 2018 (lower, c, d). The post maps in the left-hand panels indicate densities of all *C. melanaster* collected by the net, whereas, the right-hand panels (b, d) report densities of *C. melanaster* with bell diameters larger than 50 mm.
3.5. Medusa Vertical Distribution With Respect to Hydrography

Overall, the depth-specific ARIS-derived *C. melanaster* occurrence showed similar patterns with respect to water depth and water column properties throughout our study (Figures 3 and S1–S3). Our GAM analysis indicates that there is no difference in the vertical distribution of medusae detected during the June–July and September cruises ($z = 0.38, p = 0.71$). In general, *C. melanaster* were distributed across all water depths where they occurred in our study area.

In stratified water, particularly in the middle domain, *C. melanaster* concentrations were observed in both daytime and nighttime sampling during both study periods (Figures 3 and S1–S3). Based on results of the GAM, there was no difference in medusa vertical distribution in daytime and nighttime sampling ($z = -0.47, p = 0.64$). However, concentrations of medusae were commonly detected during vertical ARIS profiles. For example, vertical aggregations occurred at stations 11–12 and stations 21–22 during the daytime and at stations 8 and 19 during nighttime in the June–July cruise (Figures 3 and S2). Similarly, vertical concentrations also occurred at stations 8 and 20 during the day and stations 8 and 20–21 during nighttime sampling on the September cruise (Figures S2 and S3). Although these aggregations appeared to occur primarily near and below the pycnocline, *C. melanaster* was often distributed across all water depths (Figures 3 and S1–S3).

The vertical distribution of ARIS-detected *C. melanaster* did not differ significantly between the southern and northern transects, as indicated by the GAM ($z = 0.71, p = 0.48$). However, *C. melanaster* appeared to aggregate below the pycnocline, midway along the southern transect, and near the pycnocline along northern transect in September (Figures S2 and S3). A similar pattern was observed in June–July (Figures 3 and S2).

In our study area, *C. melanaster* occurred primarily in water with salinity $<32$ during both periods (Figure 6). The T–S diagram indicates that *C. melanaster* occurred in warm coastal waters, which is consistent with the vertical sections of medusa occurrence, temperature, and salinity (Figures S1–S3). In general, *C. melanaster* did not show a clear association with specific water temperatures in both periods.

3.6. Comparison Between ARIS-Derived and Net-Estimated Medusa Abundances

Results of the net sampling showed that >50% of the individuals collected had a bell diameter $<50$ mm (Figure 7, Data Set S5). The median size of *C. melanaster* was larger (45 mm) in September relative to June–July (35 mm, $W = 29,807.5, p = 0.001$), which was driven by more numerous medusae in the 25–50, 50–75, and 75–100 mm size categories in September (Figure 1). ARIS can detect *C. melanaster* with bell diameters $>50$ mm. In comparison to net-collected medusae with bell diameters $>50$ mm at stations where both ARIS and net were deployed, ARIS data produced similar density estimates as the nets ($0.77 \times 10^{-2}$ vs. $0.74 \times 10^{-2}$ ind m$^{-3}$, $F_{1,106} = 0.02, p = 0.88$. Data Set S5). As medusa density increases and becomes more concentrated, net samples recorded higher density estimates than ARIS (Figure 8). However, at low population densities, ARIS records medusa occurrences that are missed by the net. During the two sampling periods, ARIS detected medusae at 16 stations out of the total 25 stations at which the net sampling did not collect any *C. melanaster* $>50$ mm (Figure 8). By contrast, the net sampled medusae $>50$ mm at only 3 stations out of the total 11 stations at which the ARIS did not detect *C. melanaster*. ARIS recorded defined spatial patterns, with medusa densities concentrated northeast of Unimak Island.
The net-collected medusa densities showed overall distributions similar to the ARIS data, but the spatial patterns revealed by net sampling were more variable (Figure 5).

4. Discussion

The coastal region north of the Alaska Peninsula is important foraging area for seabirds and marine mammals (e.g., Jahncke et al., 2005; Stabeno & Hunt, 2002); the high abundance of euphausiids associated with this area plays a key role in sustaining upper trophic levels (Coyle & Pinchuk, 2002; Hunt et al., 2002; Ressler et al., 2012). Despite its ecological importance, the coastal area of the SEBS has been understudied relative to the central eastern Bering Sea, which is influenced by sea-ice processes and presence of the cold pool (Stabeno et al., 2012). In the current study, we characterized the coastal area along the Alaska Peninsula into three distinct zones: (1) the area on the Bering Sea side of Unimak Pass, which was influenced by coastal water and Bering Canyon water; (2) the region northeast of Unimak Island, which featured a stratified water column, with warm coastal water in the upper layer and cold cross-isobath deep water in the lower layer; C. melanaster was concentrated in this region; and (3) the eastern end of the southern transect, which was dominated by Bering Sea coastal water.

4.1. Physical Control of C. melanaster in the SEBS

Previous studies suggested that the spatial distribution of C. melanaster in the SEBS is influenced by northward transport (Chen et al., 2014). In the current study, the ADCP data reveal consistent along-shore flow on the north side of the Alaska Peninsula during both cruises (Figure 4), which provides a physical mechanism that can transport jellyfish away from their likely sources on the Peninsula. The spatial aggregations we observed along the Alaska Peninsula (Figure 5) were consistent with these ADCP observations (Figure 4). By contrast, ADCP measurements along the northern transect demonstrate a different flow profile. In June-July, we observed strong currents near the 70-m isobath. By contrast, in September, we observed intensified flow near 100-m isobath, with relatively strong advection toward the shelf break, from the 70-m to the 100-m isobaths (Figure 4). These flow patterns were consistent with a wider distribution of C. melanaster observed on the northern transect in September, relative to June–July (Figure 5). These observed physical features are consistent with drifter trajectories and other flow observations previously collected in this region (e.g., Stabeno et al., 2016).

The mechanisms by which oceanographic changes affect SEBS jellyfish population dynamics have been elusive, but our results provide evidence that circulation patterns strongly influence our study area. While water from Unimak Pass primarily flows northwestward along the continental slope (Stabeno et al., 2002), a portion of this flow runs northeastward onto the shelf, parallel to the Alaska Peninsula, and then turns northwestward, following the 70-m isobath (Stabeno et al., 2016). We observed complex flow patterns near Bering Canyon and an apparent cross-isobath intrusion of slope water near the 100-m isobath. During our June–July cruise, we documented cross-isobath transport (Figures 4a–4c), which usually occurs after the break down of frontal structure in fall (Danielson et al., 2011). This midsummer, onshore intrusion of cold, deep water had a clear impact on water column structure near Unimak Island, where it formed a two-layered, thermally-stratified water column, with well-mixed coastal waters in the top layer.

We hypothesized that cold, deep water originating from Bering Canyon affects the northwestern and cross-shelf transport of C. melanaster. Our findings document that in early summer, upwelling-favorable winds move...
deep, cold water into the area north of Unimak Island. This intrusion constrains the well-mixed coastal water on the inner shelf near Unimak Pass to flow northeastward along the Alaska Peninsula, which then turns northwesward along the 70-m isobath (Figures 4d–4f). As the deep-water intrusion weakens in late summer, some coastal water flows toward the shelf break, and turns northwesward at 100-m isobath. Historical observations have also shown intensified flows near both 70-m and 100-m isobaths (Coachman, 1986; Kinder & Schumacher, 1981). Therefore, a strong deep-water intrusion in early summer may have led to a more northwesward distribution of C. melanaster along the 70-m isobath. While a weakened deep-water intrusion in the late summer and fall appears to advect C. melanaster from the 70-m to 100-m isobath along the northern transect.

Previous studies provide limited information on the vertical distribution patterns of large jellyfish in the Bering Sea. C. melanaster occur primarily in the upper 200 m of the water column during both day and night at a station in the southwestern Aleutian basin (Decker et al., 2014). On the SEBS shelf, C. melanaster occur primarily between 15 and 40 m (Brodeur et al., 2002). Vertical distribution patterns of large jellyfish and their diel behavior may be influenced by the vertical distribution of their prey (Purcell & Sturdevant, 2001), which are often located near the pycnocline (Brodeur, 1998; Brodeur et al., 2002). However, our results indicate that C. melanaster are distributed throughout the water column in the middle and inner shelf regions of the study area (Figures 3 and S1–S3). We found no evidence of medusa aggregations at any specific water depth and no differences in vertical distribution between daytime and nighttime sampling.

4.2. ARIS as an Effective Tool for Estimating Large Medusa Abundance

The use of conventional nets has long been considered to be problematic in jellyfish studies (Graham et al., 2003). Plankton nets are not suitable for quantifying abundances of patchily distributed jellyfish, due to their reduced capture capacities and large sampling variability. Large-opening, midwater trawls have been used to study jellyfish distributions (Brodeur et al., 1999; Graham, 2001). However, large trawls require substantial effort and cost to operate, and they often damage gelatinous catch (Graham et al., 2003). Net samples are integrative by nature and thus, are not able to detect fine-scale spatial patterns. Acoustic sampling methods are increasingly used in situ to study large jellyfish ecology (e.g., Båmstedt et al., 2003; Makabe et al., 2012). However, acoustic approaches cannot provide information on species composition, and acoustically-derived biomass estimates require careful calibration. Video profilers and other optical cameras are increasingly being used to quantify jellyfish distributions (Bi et al., 2013; Graham et al., 2003; Mano et al., 2019) and to monitor jellyfish dynamics (Corgnati et al., 2016; Llewellyn et al., 2016); however, the use of optical underwater cameras to study large jellyfish can be compromised by the limited depth of field and small sampling volume of these instruments.

This study demonstrates that ARIS is an effective tool for sampling large medusae. The use of ARIS to sample large medusae has several advantages over sampling with a plankton net. ARIS samples large volumes of water. We found the ARIS sampled ~30 times more water by volume than a 1-m ring net. ARIS can effectively sample an entire water column and is a nonintrusive sampling approach that can resolve fine-scale vertical distributions. Whereas, integrative net sampling cannot resolve fine-scale spatial patterns and cannot adequately sample near the bottom, where medusae can occur. Finally, the distribution of large medusae is often patchy at multiple scales, which makes jellyfish difficult to sample effectively with conventional nets. ARIS can effectively resolve jellyfish distributions at a range of spatial scales (Shahrestani & Bi, 2018; Shahrestani et al., 2020). However, ARIS is not able to detect small medusae (<50 mm) and its image resolution declines with distance from the instrument.

4.3. Source-Sink Dynamics and Large-Scale Ocean Variability

Spatial distributions of scyphozoan jellyfish are often influenced by source-sink processes because the benthic life stage is key in regulating their population dynamics (Lucas, 2000, 2001; Makabe et al., 2015). Source-sink patterns have been observed in estuaries, where semienclosed systems provide hard substrate for benthic scyphozoan polyps (e.g., Breitburg & Burrell, 2014; Shahrestani & Bi, 2018) and retention of juvenile medusae (Costello et al., 2006; Shahrestani & Bi, 2018; Shahrestani et al., 2020). Source-sink dynamics have also been described for medusae in the SEBS, using trawl data for the period 1982–2004 (Chen et al., 2014).
Distributional shifts may have occurred from the combined effects of high jellyfish productivity and long jellyfish dispersal, resulting from a shift in the ocean circulation that began in 1991 (Chen et al., 2014). Such decadal shifts in circulation may influence shelf processes, including the deep-water intrusion from the Bering Canyon. We postulate that this physical process restricts the flow of coastal water in the Slime Bank region, resulting in the accumulation of medusae in coastal water near the Alaska Peninsula.

Our results suggest that the coastlines of the Alaska Peninsula and nearby islands are important sources of SEBS *C. melanaster* medusae. We hypothesize that these rocky coasts are likely habitat for benthic cnidarian polyps, as small medusae (<25 mm) were collected from nearby waters (Figures 5 and 7). Although, the exact locations and conditions for strobilation of *C. melanaster* polyps have not been determined empirically, local biotic and abiotic factors have been hypothesized to be important to the success of both the benthic and planktonic stages of *C. melanaster* (Brodeur et al., 2008). Although most of the small medusae collected in this study were likely produced in 2018, the large *C. melanaster* (>200 mm bell diameter, Figure 7) collected on our first cruise may have survived the 2017–2018 winter period. Overwintering *C. melanaster* could contribute to multiyear population increases (Purcell et al., 2018) in the SEBS, but this needs further study.

Determining spatial dynamics of medusae has been difficult because only a few large-coverage, annual surveys have been conducted for the purpose of targeting large jellyfish (Purcell, 2009). However, in the Bering Sea, shelf-wide fishery trawl surveys have been used to estimate relative biomass of large jellyfish on decadal time scales (Brodeur et al., 2002, 2008; Decker et al., 2014). Circulation modeling studies indicate that the Alaska Peninsula coast is an important source of scyphozoan medusae, and that other sources in the eastern Bering Sea, such as the Pribilof Islands, have also contributed to the jellyfish catch on surveys after 1991 (Chen et al., 2014). The current study sampled only a small portion of the Alaska Fisheries Science Center survey areas and used different sampling approaches, but both this study and the large-scale surveys document consistently high levels of jellyfish biomass north of the Alaska Peninsula. Future research should examine the influence of climate change and large-scale ocean variability on areas where potential medusa sources occur in the SEBS, including the impact of cross-shelf advection and coastal retention on early survival and spatial dynamics of *C. melanaster*. An understanding of the population dynamics of gelatinous predators, such as *C. melanaster*, is required for the successful management of the SEBS ecosystem.

5. Conclusions

To advance our understanding on how large-scale ocean variability affects jellyfish distribution in the SEBS, we hypothesize that the strength of a deep-water intrusion to the area north of Unimak Island determines the northwestward and cross-shelf transport of *C. melanaster* in the SEBS. In early summer, deep water from Bering Canyon constrains the mixed, coastal water on the inner shelf east of Unimak Pass. This deep water drives flow northwestward along 70-m isobath and influences the northwestward distribution of *C. melanaster*. When the deep-water flow weakens in late summer, a portion of this shelf water flows from the 70-m isobath to the 100-m isobath, and then turns northwestward along 100-m isobath. This further advects medusae and affects their cross-shelf distribution. Given the potential negative impacts of jellyfish blooms on fisheries and growing interests in the interannual and interdecadal variability of *C. melanaster* abundance and distribution, further tests of our proposed hypothesis are required to provide a full mechanistic understanding of the physical processes that influence *C. melanaster* and the SEBS ecosystem more broadly. Furthermore, the present study demonstrates that ARIS can effectively sample large medusae. This technology is quite versatile and adaptable for sampling large medusae, not only in deep water on large research vessels, as in this study, but also on small boats, which can sample in shallow water (Han & Uye, 2009; Shahrestani et al., 2020). Large medusa abundance derived by ARIS showed distributions that correspond to net-collected samples of *C. melanaster* north of Unimak Island and the Alaska Peninsula. These clearly-defined spatial patterns are consistent with the currents measured by the ADCP and corroborate our hypothesis.
Data Availability Statement

The data supporting the findings of this study are available at https://doi.org/10.5061/dryad.z34tmpgdb (Bi & Decker, 2021).

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