# Oceanographic assessment of the planktonic communities in the northeastern Chukchi Sea

**Report for Survey year 2012** 

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# EXECUTIVE SUMMARY

Surveys of the planktonic communities over the Klondike, Burger and Statoil survey areas were completed during August 2012 and again as part of a broad scale effort in September/October of 2012. This year, the mesozooplankton surveys were augmented with concurrent assessments of microzooplankton and phytoplankton communities. Chlorophyll and nutrient concentrations together with phytoplankton composition indicate that the August sampling occurred after the seasonal phytoplankton bloom, with some elevated chlorophyll concentrations maintained the by winter-water cold pools over Burger and Statoil and the more northeastern stations. Microzooplankon abundance (range:  $11-83 \times 10^3 l^{-1}$ ) was dominated by small-sized heterotrophic dinoflagellates. Large-sized ciliate types dominated the biomass (range: 55-1946 mg  $m^{-2}$ ), which was comparable to and sometimes exceeded phytoplankton biomass. In total, 71 taxonomic categories of mesozooplankton, including 11 meroplanktonic larval categories, were recognized during the 2012 field year. The greatest taxonomic diversity occurred within the copepods (20 species, plus juvenile categories), followed by the cnidarians (11 species), with most species typical for the region and seeded from the Bering Sea. An average abundance of 2190 individuals  $m^{-3}$  and 66.0 mg DW  $m^{-3}$  was captured by the 150-µm net, and an average of 393  $m^{-3}$  and 72.1 mg DW  $m^{-3}$  was captured by the 505– $\mu$ m net over the Klondike, Burger and Statoil survey grids. The contribution by meroplankton to both abundance and biomass was low in 2012. Holozooplankton abundance was lower than determined in previous years, although the biomass was generally higher, driven predominantly by the copepod *Calanus glacialis*. In 2012, Klondike zooplankton could generally be separated from Burger and Statoil based on community structure, but a temporal evolution of the community structure was not obvious. Differences in community structure among study years were also apparent, and in 2012 much of this pattern appeared to be driven by water temperature, and to a lesser degree salinity and chlorophyll-a. Differences in the timing of ice-melt, water temperatures, transport of water masses, nutrients and chlorophyll-a are believed to drive the large inter-annual differences observed in the planktonic communities over the past 5 years.

# INTRODUCTION

#### Purpose of Study and Rationale

Chukchi Lease Sale 193 occurred in February 2008, followed by the completion of the first year of a 5-year multidisciplinary environmental studies program initiated by ConocoPhillips in cooperation with Shell Exploration & Production Company, and Statoil USA Exploration & Production Inc. The 2012 field effort represents a fifth year of data collection that will aid in the preparation of a NEPA document required prior to exploratory drilling. Pelagic biological oceanography forms one aspect of the baseline studies program, because the productivity of the water column determines the flux of energy to the seafloor, as well as production transferred through zooplankton to higher trophic levels such as fish, seabirds and marine mammals. Alterations to water column productivity as a result of inter-annual variability, long-term climate change or human activity, could have direct impact on the ecosystem, including the more visible vertebrates. The data collected through this program, combined with historical and region-wide data, will provide us with direct observations of community composition and biomass, providing the only means to compare temporal and spatial variation in biological communities to environmental change.

#### **Objectives of Study**

The major objective of this study is to describe the spatial and seasonal characteristics of the plankton (phytoplankton, microzooplankton and mesozooplankton) communities, with specific detail in the three adjacent study areas: Burger, Klondike and Statoil. Planktonic communities are strongly coupled to the underlying physical oceanography, with major differences in water-masses generally reflected in the plankton. The study areas are near the historical transition between Alaska Coastal waters and Bering Shelf waters, both of which have unique assemblages of zooplankton. Simultaneous measurement of the physical, chemical, and biological oceanographic setting is therefore essential to forming an understanding of the patterns and the range of seasonal and interannual variability characteristic of the region.

## Brief History of Planktonic Biological Oceanography in Chukchi Sea

The Chukchi Sea represents a complex ecosystem at the Pacific Ocean's gateway into the Arctic where water masses of Pacific origin interact with those of the central Arctic Ocean and its continental-shelf seas. Large quantities of Pacific nutrients, phytoplankton and mesozooplankton enter the region through the Bering Strait, in a complicated mixture of water masses (i.e. Alaska Coastal, Bering Shelf, and Anadyr Water), each with unique assemblages and quantities of zooplankton (Springer *et al.*, 1989; Coyle *et al.*, 1996; Hopcroft *et al.*, 2010a). It has been estimated that 1.8 million metric tons of Bering Sea mesozooplankton are carried into the Chukchi Sea annually (Springer *et al.*, 1989) and that this, along with the entrained phytoplankton and microzooplankton communities, are responsible for the high productivity of the Chukchi Sea in comparison to adjoining regions of the Arctic Ocean (e.g. Plourde *et al.*, 2005).

During the ice-free season, the southern Chukchi mesozooplankton fauna is primarily Pacific in character (Questel *et al.*, 2013). During summer, the Pacific inflow is diluted by Coastal Arctic waters carried along by the East Siberian Current and water carried in from the deeper

waters of the Canada Basin or Chukchi Plateau (Grebmeier *et al.*, 1995). Nonetheless, Pacific species are carried northward as far as the eastern side of Wrangel Island (Hopcroft *et al.*, 2010a), as well as to the shelf break in the northeastern Chukchi Sea (Lane *et al.*, 2008, Nelson *et al.*, 2009). The influx of these "rich" Pacific waters determines the reproductive success of both the imported and resident zooplankton communities (Plourde *et al.*, 2005; Hopcroft and Kosobokova, 2010). Both inter-annual and long-term variations in climate affect the relative transport of these various water masses and hence the composition, distribution, standing stock, and production of zooplankton and their predators within the Chukchi Sea (Questel *et al.*, 2013).

A regional and basin-wide review of arctic zooplankton, their composition, seasonal life cycles, and trophic interactions was completed nearly two decades ago (Smith and Schnack-Schiel, 1990). A more recent effort emphasizing the Russian literature for the Bering Sea and parts of the southern Chukchi has also been completed (Coyle *et al.*, 1996), as well as a review of zooplankton in Arctic polynyas (Deibel and Daly, 2007). The most current review is specific to the Chukchi and Beaufort Seas and has an extensive review of the literature for zooplankton as well as other groups (Hopcroft *et al.*, 2008). Prior to the lease sale, we lacked comprehensive estimates of the abundance, biomass and relative composition of the zooplankton throughout the Chukchi Sea. This gap has recently been addressed through publications by RUSALCA (Russian American Long-term Census of the Arctic), SBI (Shelf-Basin Interactions) and Arctic Ocean Biodiversity (ArcOD) programs, as well as the initial results of CSESP program (Questel *et al.*, 2013), although we still wrestle with understanding the forces that shape inter-annual variability.

It is now clear that the spatial distribution of mesozooplankton communities in the Chukchi Sea is largely tied to the different water masses present in this region (Lane *et al.*, 2008; Hopcroft *et al.*, 2010a; Questel *et al.*, 2013). While copepod crustaceans generally dominate zooplankton communities in most ocean regions, both larvaceans and meroplankton contribute significantly to community abundance and biomass (Lane *et al.*, 2008; Hopcroft *et al.*, 2009, 2010a,b). Similarly, a relatively diverse group of jellyfish, and a single species of chaetognaths remain important predatory components of the zooplankton community (Ashjian *et al.*, 2003; Lane *et al.*, 2008; Hopcroft *et al.*, 2005, 2009, 2010a,b, 2011). Arguably, the greatest strength of this study has been the observation of the seasonal progression of the planktonic communities, and a consistent sampling framework to highlight the extent of spatial and inter-annual variability within these communities. The surveys in 2011 and 2012 provide a greatly expanded spatial domain to further solidify our understanding of the patterns in this ecosystem.

In contrast to the mesozooplankton, much less is known about phytoplankton and microzooplankton communities and their seasonal, spatial or interannual variability in the Chukchi Sea, where there have only been a few published studies on the composition and distribution of phytoplankton (Hill *et al.*, 2005; Sukhanova *et al.*, 2009) or microzooplankton (Sherr *et al.*, 2009). Studies on microzooplankton on the eastern Bering Sea shelf have shown that their biomass is substantial and can exceed that of phytoplankton during the summer, and that microzooplankton have significant grazing impacts on both small and large phytoplankton (Howell-Kübler *et al.*, 2014). Microzooplankton are now known to be the major consumers of phytoplankton in almost all pelagic ecosystems, including subarctic and arctic ecosystems (Calbet and Landry 2004; Levinsen and Nielsen 2002; Sherr *et al.*, 2009). They are also important prey for copepods and euphausiids (Stoecker and Capuzzo 1990; Levinson *et al.* 2000;

Olson *et al.*, 2006; Campbell *et al.*, 2009; Lessard *et al.*, unpublished data), as well as an important food resource for larval fish (Lessard *et al.*, 1996; Figueiredo *et al.*, 2007, Montagnes *et al.*, 2010). As microzooplankton are critical trophic links between phytoplankton and mesozooplankton, a microzooplankton and phytoplankton component was added to the CSEP plankton surveys for the 2012 survey year.

# **METHODS**

#### Survey Design

The 2012 schedule consisted of a 2 week cruise from August 14-27 (WWW1202), followed by 2 consecutive cruises from August 30 - September 16 (WWW1203), and September 17-October 4 (WWW1204); the combined survey area on the later cruises being greatly expanded from initial years, but similar to that of 2011 (Fig. 1). Throughout, we will often refer to the first cruise as the 'August' cruise, and the latter two cruises combined as the 'September' or 'expanded survey'. The core sampling areas occurred within a 30 x 30 nautical mile (NM) box at the Klondike and Burger study areas, with a grid of 5x5 stations, at ~7.5 NM spacing, plus a somewhat irregular rectangle of 22 stations at similar spacing within the Statoil study area. The expanded sampling domain was ~120 NM across. In 2012 an oblique cross-shelf survey line was added for the Distributed Biological Observatory (DBO) effort that passed through both Burger and Statoil. Bottom depth over these core survey areas was similar and relatively constant, varying between approximately 35 and 45 m, and slightly deeper or shallower in parts of the expanded grid. Inorganic macro-nutrients, phytoplankton (as chlorophyll-*a*) were sampled on each cruise, concurrent with collection of CTD measurements, while zooplankton collections were taken at ~50% of the stations.

## **Collection Procedures**

Chlorophyll-*a* concentration, a proxy for phytoplankton biomass, was assessed from samples collected with 4-L Niskin bottles on a Seabird SBE19/SBE55 CTD rosette (Weingartner *et al.*, 2013a) during upcasts at 6 depths per station: 0, 5, 10, 20, and 30 m, plus 3m above the sea floor. Samples were filtered under low pressure onto 47-mm Whatman GF/F filters and frozen at -20  $^{\circ}$ C shipboard and -40  $^{\circ}$ C in the lab for post-cruise analysis (Parsons *et al.*, 1984). Nutrient samples were taken from the same Niskin bottles as chlorophyll, passed through 0.4  $\mu$ m cellulose-acetate filters and frozen immediately. Samples were analyzed post-cruise for nitrate, nitrite, ammonium, phosphate and silicate concentrations (Whitledge *et al.*, 1981; Gordon *et al.*, 1993).

Phytoplankton and microzooplankton samples for microscopy were collected from the Niskin bottles at the same depths as the chlorophyll samples. At each station, equal subsamples from the three upper and three lower depths were combined to obtain an integrated 'upper' sample and an integrated 'lower' sample. The samples were preserved with 5% Lugols iodine solution in amber bottles and stored at room temperature. Post-cruise, the samples were analyzed for abundance and biomass of major phytoplankton and protozooplankton taxa.

Smaller mesozooplankton were collected at alternate stations by paired 150– $\mu$ m-mesh ring nets of 60-cm diameter hauled vertically from within 3 m of the bottom to the surface at a speed of 0.5 m s<sup>-1</sup>. The volume of water filtered was measured by one-way General Oceanic

flowmeters in each vertical net. To target larger, more mobile zooplankton, a set of 60-cm diameter  $505-\mu m$  Bongo nets were deployed in a double oblique tow with the ship moving at an average speed of 2 kts. General Oceanic flowmeters, installed in each Bongo net, were used to estimate the volume of water filtered. Upon retrieval, one sample was preserved in 10% buffered formalin, and the other in 95% ethanol (required for molecular sequence identification). When present, large cnidarians and ctenophores were removed, measured, photographed, identified and then discarded prior to sample preservation.

## Sample Processing

Chlorophyll-*a* was extracted for frozen filters in 95% acetone, and concentrations determined fluorometrically post-cruise (Parsons *et al.*, 1984) using a Turner Fluorometer. Measurements were used to calibrate *in vivo* fluorescence profiles measured at stations. Integral chlorophyll concentration was calculated by assuming each depth at a station represented the concentration to the midpoint depth between each sampling interval. Frozen nutrient samples were measured post-cruise using an Alpkem Rapid Flow Analyzer (Whitledge *et al.*, 1981) and conformed to WOCE standards (Gordon *et al.*, 1993).

Aliquots of the Lugols-preserved samples were settled in Utermöhl chambers for 24hr, after which the supernatant was removed and DAPI (a fluorescent nuclear stain) was added. The settled cells (flagellates >10  $\mu$ m, ciliates, dinoflagellates and diatoms) were identified to the lowest taxa possible. Dinoflagellates were distinguished based on morphology and their distinctive nucleus; heterotrophic and autotrophic dinoflagellates were categorized based on species identifications. Cells were enumerated and sized using a digitizing system (Roff and Hopcroft, 1986) connected to a Zeiss inverted light and epifluorescent microscope. Biovolumes were converted to carbon biomass using the equations of Menden-Deuer and Lessard (2000).

Formalin-preserved zooplankton samples were processed for quantitative determination of species composition, and prediction of biomass, at 13 stations for Klondike and Burger and at 11 stations for Statoil. Alternate samples were analyzed within the expanded grid yielding an additional 46 samples outside the primary surveys, plus 7 additional locations along the DBO line. During taxonomic processing, all larger organisms (primarily shrimp and jellyfish) were removed, enumerated, and measured. The sample was then divided with a Folsom splitter until the smallest subsample contained about 100 specimens of the more abundant taxa. Specimens were identified to the lowest taxonomic category possible, developmental staged noted (where appropriate), enumerated, and measured (Roff and Hopcroft, 1986). Increasingly larger fractions were examined to identify, measure and enumerate the larger-bodied, less abundant taxa, that contribute disproportionately to community biomass. This was particularly the case for the 505– µm net which typically captures greater taxonomic diversity. A minimum of 300, and typically 400-600, individual organisms, were identified from each sample. Larval fish were excluded from the analysis, and passed to the fisheries ecology team for detailed identification.

Where earlier copepodite stages of species within a genera could not be distinguished, they were grouped with the sibling species. Adults were always identified to the species level, with the exception of *Calanus*. Distinguishing *C. marshallae* from *C. glacialis* has proven problematic, we therefore assumed they were represented primarily by the latter species (Nelson *et al.*, 2009). The larger *C. hyperboreus* was distinguished by size (e.g. Unstad and Tande, 1991; Hirche *et al.*, 1994). The weight of each specimen was predicted from species-specific relationships, or from those of a morphologically similar species of holozooplankton (Table 1).

Where necessary, ash-free dry weight (AFDW) was converted to dry weight (DW) assuming 10% ash (Båmstedt, 1986), and dry weight was assumed to be 18% of wet-weight (Davis and Weibe, 1985). We assumed carbon to be 40% of DW for *Oikopleura vanhoeffeni*, as is typical of many copepods (Båmstedt, 1986).

## Data Analysis

In addition to a descriptive summary, community patterns were explored using the Primer (V6) software package which has been shown to reveal patterns in zooplankton communities (e.g. Clarke and Warwick 2001; Wishner *et al.*, 2008). Data sets were power transformed (4<sup>th</sup> root), and the Bray-Curtis similarity index among stations was calculated employing all taxonomic categories that contributed at least 3% to any sample in that dataset. Significant groups within the hierarchical clustering were established with the SIMPROF routine, and these clusters were superimposed on the 2D and 3D plots of the multi-dimensional scaled (MDS) datasets, as well as spatial plots of the data. Relationships linking zooplankton community patterns with normalized physical data (above and below the thermocline; represented by 12 m and 25 m, respectively, for calculations) and integral chlorophyll were explored with Primer's BEST routine.

## **Quality Control Procedures**

In the field, mesozooplankton samples were collected in duplicate, thus discrepancies in the flowmeter readings were readily apparent. The flowmeters used on the vertical nets were rigged to not spin during descent, but can be problematic - when measured values were unreasonably large or small they were constrained to station depth.

In the lab, replicate samples were not routinely analyzed. Replicates served as insurance in the event that one sample was compromised. Data files were inspected for valid taxa and taxa-specific length measurements. Where necessary, specimens were compared to the voucher set housed at UAF. Periodic cross-comparison occurred among the co-authors processing samples.

**Table 1.** Relationships employed to predict weight from length for the holozooplankton encountered in the study region. Where species-specific relations were not employed we used relationships from: \* *T. japonica*, \*\* *Oithona nana*, <sup>+</sup> *F. pellucida*, <sup>++</sup>*Pseudocalanus*. DW- dry weight, AFDW- ash-free dry weight, CW- carbon weight, BL-total body length, TL-trunk length, PL- prosome length, CL- carapace length, SD- shell diameter

Species	Regression	Units	Source
Acartia longiremis	CW=1.023-10 <sup>-8</sup> PL <sup>2.906</sup>	μm, μg	Hansen <i>et al.</i> , 1999
Calanus glacialis/marshallae	log <i>DW</i> =4.034·log <i>PL</i> -11.561	μm, μg	Liu & Hopcroft, 2007
Calanus hyperboreus	DW = 0.0027 · PL <sup>3.718</sup>	mm, mg	Ashjian et al., 2003
Centropages abdominalis	log DW = 3.00·log PL-7.89	μm, μg	Uye, 1982
Eucalanus bungii	LogDW=3.091.logPL-0.0026	mm, µg	Hopcroft <i>et al.</i> , 2002
Eurytemora herdmani	logDW = 2.96.logPL-7.60	μm, μg	Middlebrook & Roff, 1986
Metridia longa	$DW = 0.0101 \cdot PL^{3.100}$	mm, mg	Mumm, 1991
Metridia pacifica	logDW = 3.29.logPL-8.75	μm, μg	Liu & Hopcroft, 2006b
Neocalanus plumchrus/flemingerii	log <i>DW</i> =3.56·log <i>PL</i> -2.32	mm, mg	Liu & Hopcroft, 2006a
Neocalanus cristatus	LogDW=4.001.logPL-11.776	μm, μg	Kobari <i>et al</i> ., 2003
Paraeuchaeta spp.	AFDW=0.0075-PL <sup>3.274</sup>	mm, mg	Mumm, 1991
Pseudocalanus spp.	log <i>DW</i> =-2.85·log <i>PL-</i> 7.62	μm, μg	Liu & Hopcroft, 2008
Oithona similis**	logAFDW=3.16.logPL-8.18	μm, μg	Hopcroft et al., 1998
Oncaea spp.**	InDW=2.90.InPL-16.81	μm, μg	Satapoomin, 1999
Oikopleura vanhoeffeni	logC=3.20·logTL-8.93	μm, μg	Deibel, 1986
Fritillaria borealis <sup>+</sup>	logDW=3.21.logTL-9.11	μm, μg	Fenaux, 1976
Other calanoids <sup>++</sup>	logDW=-2.85.logPL-7.62	μm, μg	Liu & Hopcroft, 2008
Microsetella norvegica	CW=2.65·10 <sup>-6</sup> BL <sup>1.95</sup>	μm, μg	Uye <i>et al.</i> , 2002
Other harpacticoids	DW=8.148.10 <sup>-8</sup> BL <sup>2.736</sup>	μm, μg	Ara, 2001
Themisto abyssorum/pacifica*	DW=0.0049·BL <sup>2.957</sup>	mm, µg	Ikeda & Shiga, 1999
Themisto libellula	DW=0.006-BL <sup>2.821</sup>	mm, µg	Auel & Werner, 2003
Apherusa glacialis	DW=2.556·BL <sup>3.0960</sup>	mm, µg	Werner & Auel, 2005
Gammarus spp.	DW=0.824·BL <sup>3.378</sup>	mm, µg	Werner & Auel, 2005
Onisimus spp.	DW=8.558·BL <sup>2.890</sup>	mm, µg	Werner & Auel, 2005
Ostracods	AFDW=0.0228-BL <sup>2.3698</sup>	mm, mg	Mumm, 1991
Thysanoessa inermis/raschii	Log DW=2.50·logCL-1.162	mm, mg	Pinchuk & Hopcroft, 2007
Eualus gaimardii, other decapods	WW=8.56 BL <sup>2.995</sup>	mm, µg	Weslawski, 1987
Mysids	WW=0.20 BL <sup>3.678</sup>	mm, µg	Chipps & Bennett, 2000
Evadne & Podon	logDW=4.0·logBL-10.5	μm, μg	Uye, 1982
Tomopteris	DW=0.005·BL <sup>2.25</sup>	mm, mg	Matthews & Hestad, 1977
Clione limacina	InWW=2.53·logBL-6.89	mm, mg	Davis & Wiebe, 1985
Limacina helicina	AFDW=0.0390-SD <sup>3.5032</sup>	mm, mg	Mumm 1991
Eukrohnia hamata	DW=0.00032·BL <sup>3.00</sup>	mm, mg	Matthews & Hestad, 1977
Parasagitta elegans	DW=0.000064·BL <sup>3.30</sup>	mm, mg	Matthews & Hestad, 1977
Aglantha digitale & other jellies	DW=0.00194-PL <sup>3.05</sup>	mm, mg	Matthews & Hestad, 1977
Decapod zoea	logDW=2.35-logCL+1.74	mm, µg	Lindley, 1998
Decapod megalopa	logDW=2.58·logCL+2.04	mm, µg	Lindley, 1998
Barnacle nauplii	logDW=3.356.logBL-9.060	μm, μg	Muxagata <i>et al.</i> 2004
Barnacle cyprids	logDW=2.763.logBL-6.985	μm, μg	Muxagata <i>et al.</i> 2004
Bivalve larvae	DW=0.000000306-BL <sup>2.88</sup>	μm, μg	Fotel <i>et al.</i> 1999
Polychaete larvae	logDW=2.06·logBL-5.372	μm, μg	Hansen, 1999

## RESULTS

## Nutrients and chlorophyll-a

Nitrate was virtually absent from surface waters (i.e. 0-10 m) even during the first 2012 cruise. It generally increased toward the seafloor, although the increase was limited at Klondike and particularly pronounced at Burger and Statoil, especially in their northeastern corners (Fig. 2). While the patterns were similar for phosphate and silicate, surface concentrations were not fully depleted over Burger or Statoil, particularly so for silicate (Fig 3,4). Chlorophyll concentrations were consistent with the nitrate patterns, being extremely low in the upper 10m, showing mid-depth maxima over northern Burger and eastern Statoil (Fig.5). The expanded domain on the September-October cruises looks like a simple continuation of patterns observed over the smaller domain on the first cruises: nitrate was depleted in all surface waters (Fig 6), while phosphate and silicate were not fully depleted in surface waters over Burger or Statoil (Fig 7, 8), and concentrations generally increased moving toward the northeast, although the pattern was somewhat patchy. Hanna Shoal, rises to 25 m at several stations creating a depression in nutrient concentrations either due to upward mixing of nutrients, or perhaps some interpolation errors. Chlorophyll remained low in surface waters on the September-October cruises, with the exception of the southeastern corner of the expanded survey area (Fig. 9), and subsurface maxima seemed to be confined to just northeast of Burger and Klondike.

Once integrated, it is clear that during the August cruise concentration were low over Burger and highest over northern Burger and eastern Statoil (Fig. 10). Chlorophyll increased over Klondike on the expanded cruise, but generally declined over the formerly enhanced regions of Burger and Statoil, it was also low on the northeastern parts of Hanna shoal. As in previous years, mean concentrations at Klondike were lower than at Burger or Statoil, on the first cruise, but relatively similar on the September cruise (Table 2). Over the expanded study area, chlorophyll averaged 17.4 mg m<sup>-2</sup>.

Cruise	Klondike	Burger	Statoil
August	16.3 / 19.1	47.9 / 38.0	65.8 / 54.9
September/October	15.7 / 16.1	13.3 / 15.7	19.3 / 17.9

*Table 2.* Average integral chlorophyll-*a* concentrations (mg m<sup>-2</sup>) at the Klondike, Burger and Statoil survey grids during 2012. First values are determined from extracted filters, second values are estimated from *in situ* fluorescence.

Alignment of extracted chlorophyll (Chl) data with *in situ* fluorescence (Fl) profiles determined during CTD casts (Weingartner *et al.*, 2013a) allowed calibration of the *in situ* values (log Fl = 0.613 log Chl - 0.564,  $r^2$ =0.73). Predicting chlorophyll- *a* from the *in situ* profiles at 1 m depth intervals generally produced values similar to those using extracted samples alone (Table 2), although they yielded lower averages when values were higher. Examination of the fluorescence profiles revealed a strong and often narrow subsurface chlorophyll maximum between 20 and 30 m (particularly in August) that was occasionally captured by bottles, thereby yielding intermittent and somewhat anomalous mid-depth chlorophyll spikes. The fluorescence profiles also helped better define a 2-layered pattern of chlorophyll where upper values were relatively low in concentration and phaeopigment content, while depths below the pycnocline were often higher in both concentration and the percentage of phaeopigments (particularly in September/October).

#### Phytoplankton and Microzooplankton

Consistent with chlorophyll trends, phytoplankton carbon biomass over the grid area was lower in the upper 10 m than below, with a few exceptions (Fig. 11). Phytoplankton biomass at most stations was dominated by coccolithophorids and small unidentified nanoflagellates (Fig. 12). The pennate diatom, *Cylindrotheca closterium*, was widespread and achieved high biomass in the subsurface at two stations in August (Figure 12) in Burger and Statoil where nutrients were relatively high. Another pennate diatom, the toxigenic *Pseudo-nitzschia*, was widespread at very low concentrations, but was the dominant diatom at the most inshore (DF001) station on the DBO line. Centric diatoms typical of the spring bloom were largely absent, indicating that the bloom had been largely consumed and/or exported to the benthos.

Microzooplankton biomass, like phytoplankton biomass, was also low in the surface water and increased with depth (Fig. 13). Even though heterotrophic dinoflagellates dominated microzooplankton abundances, ciliates dominated the biomass (Fig. 14), due to their larger average size. Microzooplankton biomass was comparable, sometimes exceeding, phytoplankton biomass at all stations sampled (Fig. 15).

#### Mesozooplankton

In total, 71 taxonomic categories of zooplankton, including 11 meroplanktonic larval categories, were observed during the 2012 field year. An average abundance of 2190 individuals m<sup>-3</sup> and 66.0 mg DW m<sup>-3</sup> was captured by the 150– $\mu$ m net, and an average of 393 m<sup>-3</sup> and 72.1 mg DW m<sup>-3</sup> captured by the 505–µm net over the Klondike, Burger and Statoil survey grids (Table 3). The equivalent numbers, including the expanded survey grid, were very similar: 2100  $m^{-3}$  and 74 mg DW  $m^{-3}$  captured by the 150- $\mu$ m net, and 399  $m^{-3}$  and 83.9 mg DW  $m^{-3}$  captured by the 505–µm net. The greatest diversity was observed within the copepods (20 species, plus juvenile categories), followed by the cnidarians (11 species). The relative contribution and ranking of taxa varied depending on the net considered, and whether abundance or biomass was used for such assessment. For the 150-µm nets, abundance was dominated by the *Pseudocalanus* copepod species complex, followed by *Calanus glacialis* and the cyclopoid copepod Oithona similis, all in nearly equal numbers. The copepod nauplii and barnacle larvae (nauplii and cyprids) all averaged more than 100 m<sup>-3</sup>. These were followed only by the copepod Acartia spp. that exceeded 50 m<sup>-3</sup>, with the larvaceans, polychaete larvae and Aglantha at usually low abundances. Biomass in the 150-um nets was overwhelmed by Calanus glacialis, followed by the chaetognath Parasagitta elegans, the larvacean Oikopleura vanhoeffeni, Pseudocalanus copepods, and barnacle larvae. It is notable that several ice-associated copepods – Jashnovia tolli and Cyclopina sp. - and coldwater preferring species Microcalanus pygmaeus and Microsetella norvegica occurred in moderate numbers scattered across the sampling domain.

The top abundance ranking zooplankton for the 505– $\mu$ m nets was unusually similar to that of the 150  $\mu$ m net, led by the copepod *Calanus glacialis* (over 90% of the holozooplankton), barnacle larvae, the larvacean *Oikopleura vanhoeffeni*, the *Pseudocalanus* species complex and the chaetognath *Parasagitta elegans*. Biomass in the 505– $\mu$ m nets was dominated by the copepod *Calanus glacialis* and the chaetognath *Parasagitta elegans*, with only the larvacean *Oikopleura vanhoeffeni*, net *Parasagitta elegans*, with only the larvacean *Oikopleura vanhoeffeni*, *Neocalanus* copepods, and the predatory pteropod *Clione limacina* 

*Table 3.* Zooplankton species observed during 2012, in the Klondike, Burger and Statoil surveys along with their average abundance and biomass across the samples examined. Data is presented for both vertical 150– $\mu$ m and the oblique 505– $\mu$ m samples. 'Trace' refers to taxa observed only once or twice during analysis and of insignificant biomass. The copepod *Calanus hyperboreus* was present, but observed only in the greater Hanna Shoal survey area.

	150–µm net		505–µm net	
_	Abundance	Biomass	Abundance	Biomass
	(Ind. m <sup>-3</sup> )	(mg DW m⁻³)	(Ind. m <sup>-3</sup> )	(mg DW m <sup>-3</sup> )
Copepoda				
<i>Acartia</i> spp.	36.93	0.060	0.00	0.000
Acartia longiremis	27.63	0.134	0.74	0.004
Acartia hudsonica	0.00	0.000	0.00	0.000
Eurytemora pacifica	1.59	0.006	0.00	0.000
Calanus glacialis/marshallae	405.30	49.883	327.43	62.958
Centropages abdominalis	1.45	0.008	0.02	0.000
Eucalanus bungii	0.26	0.033	0.07	0.016
Jashnovia tolli	0.05	0.002	0.00	0.000
Metridia pacifica	0.74	0.008	0.01	0.001
Microcalanus pygmaeus	0.50	0.001	0.00	0.000
Neocalanus flemingerii	1.30	0.578	0.00	0.000
Neocalanus plumchrus	0.82	0.273	1.98	0.965
Neocalanus cristatus	0.40	2.036	0.56	2.965
Pseudocalanus spp. (juvenile)	35.03	0.179	0.00	0.000
Pseudocalanus minutus	24.90	0.410	7.59	0.156
Pseudocalanus acuspes	46.62	0.515	2.26	0.035
Pseudocalanus newmanii	29.06	0.164	0.00	0.000
Pseudocalanus mimus	0.00	0.000	0.02	0.000
Pseudocalanus spp. (male)	35.03	0.179	0.00	0.000
Cyclopina sp.	1.77	0.002	0.00	0.000
Oithona similis	434.22	0.664		
Triconia (Oncaea) borealis	7.48	0.019		
Harpacticoida	0.66	0.009	0.00	0.000
Microsetella norvegica	4.73	0.016	0.00	0.000
Calanoida nauplii	291.24	0.381		
Cyclopoida nauplii	5.95	0.002		
Larvaceans				
Oikopleura vanhoeffeni	40.74	2.982	9.23	1.840
Fritillaria borealis	3.22	0.000	0.00	0.000
Pteropods				
Limacina helicina	3.97	0.188	0.02	0.042
Clione limacina	0.18	0.875	0.07	0.968
Euphausiids				
Euphausiid nauplii	0.05	0.000	0.00	0.000
Euphausiid calytopsis	0.06	0.000	0.00	0.000
Euphausiid furcillia	0.17	0.011	0.16	0.011
Euphausiid juvenile	0.04	0.058	0.03	0.013
Thysanoessa inermis	0.01	0.019	0.02	0.071
Thysanoessa longipes	0.00	0.000	0.00	0.000
Thysanoessa raschii	0.00	0.011	0.03	0.083

Table 3 continued	150–µm net		505–µm net	
	Abundance	Biomass	Abundance	Biomass
Shrimps and Mysids				
Hippolytidae (juvenile)	0.09	0.123	0.09	0.090
Pandalidae (juvenile)	0.00	0.115	0.00	0.049
Eualus gaimardii	0.00	0.065	0.01	0.103
Mysis oculata	0.00	0.000	0.00	0.025
Mysis/Neomysis spp.	0.00	0.000	0.00	0.013
Amphipods				
Apherusa glacialis	0.01	0.218	0.00	0.000
Hyperia galba/medusarum	0.11	0.003	0.02	0.066
Hyperoche medusarum	0.01	0.004	0.00	0.007
Themisto libellula	0.00	0.000	0.02	0.080
Themisto abyssorum/pacifica	0.01	0.030	0.02	0.026
Gammaridae	0.15	0.226	0.16	0.279
Ctenophores				
Ctenophora	0.03	0.039	0.00	0.000
Mertensia ovum	0.51	0.801	0.20	0.377
Cnidarians				
Aeginopsis laurentii	0.24	0.000	0.00	0.000
Aglantha digitale	0.64	0.627	0.06	0.382
Bougainvillia supercilliaris				
Catablema vesicarium	0.01	0.082	0.00	0.008
Halitholus cirratus	0.00	0.007	0.00	0.000
Melicertum octopunctata	0.01	0.003	0.00	0.005
Sarsia tubulosa	0.00	0.003	0.00	0.001
Miscellaneous Cnidaria	0.01	0.007	0.00	0.000
Aurelia aurita	0.00	0.000	0.00	0.001
Cyanea capillata	0.02	0.066	0.00	0.042
Chrysaora melanaster			Observed	
Chaetognaths				
Parasagitta elegans	28.88	10.677	5.93	11.758
TOTAL Holozooplankton	1916	63.9	352	71.7
Bivalvia larvae	6.59	0.002		
Gastopod larvae	0.72	0.001	0.00	0.000
Barnacle cyprid	76.55	1.656	1.49	0.029
Barnacle nauplii	152.57	0.111	39.03	0.188
Decapoda zoea	0.08	0.015	0.09	0.011
Paguriidae zoea	0.15	0.082	0.12	0.099
Crangonidae zoea	Trace		Trace	
Decapoda megalopa	0.02	0.024	0.03	0.049
Polychaeta larvae	44.27	0.256	0.01	0.000
Asteroid bipinnaria	0.00	0.000	0.00	0.000
Echinoid/Ophiuroid larvae	1.18	0.0003		
Total Meroplankton	274	2.1	40.8	0.4
TOTAL Zooplankton	2190	66.0	393	72.1

contributing more then 0.5 mg DW m<sup>-3</sup>. Collections in 2012 are notable in that overall abundance and diversity were low, but dominated by later stages of large-bodied copepod species (*Calanus glacialis*). This explains the remarkable similarity in abundance and biomass values for this species between the 150– $\mu$ m and 505– $\mu$ m nets.

Summarizing by major taxonomic groups: in terms of abundance, copepods and their nauplii, followed by meroplankton (on the first cruise), appear to dominate numerically across all cruises for the 150– $\mu$ m nets (Fig. 16). Based on the 505– $\mu$ m net, large-bodied copepod numbers were persistent across all cruises. Larvaceans and all predatory groups remained low in numbers across all cruises. In terms of biomass, copepods again dominated both nets, with notable contribution by chaetognaths, and secondarily by larvaceans in the 150– $\mu$ m nets (Fig. 17).

Changes in the relative contributions of the different groups were apparent when viewed at the station level, although the continuous dominance of copepods obscured some of these differences (Fig. 18-21). For the 150-µm nets, in August copepods appear more dominant in southern Klondike and southwestern Burger, while meroplankton became more important over northern Burger Statoil, and meroplankton and nauplii were important in the northern half of the sampling region (Fig. 18). In September/October, regional patterns were less clear: copepods were generally even more dominant, meroplankton was reduced, but nauplii still remained notable contributors. In terms of biomass, in the 150-µm nets, in August chaetognaths appear more prominent in Klondike and southwestern Burger, while larvaceans became more visible over Statoil (Fig. 19). In September/October, chaetognaths remained most important in the southwest, while larvaceans became more important in the in the central and northern regions. In terms of numerical contribution for the 505-um nets, in August Klondike and southern Burger were overwhelmed by copepods with meroplankton relatively abundant over much of Statoil and northern Burger (Fig. 20). In September/October copepods dominated the central region, with chaetognaths and larvaceans notable in the southeastern region. In terms of biomass, while copepods remained dominant, chaetognaths and at times larvaceans made notable contributions to total biomass, with very limited contributions of other taxonomic groups (Fig. 21).

Looking more closely at the species and genus level, faunal differences between the cruises and survey areas are poorly resolved with a few exceptions. For the 150–µm nets, the strongest signals were in the copepods: *Neocalanus* spp., and *Eucalanus bungii* where more abundant over Klondike and Southern Hanna Shoal study area, while *Acartia, Centropages, Metridia* and *Microsetella* showed the opposite pattern, and *Calanus hyperboreus* was confined to northern Hanna Shoals (Fig 22-25). Barnacle nauplii were only abundant at Burger and Statoil on the first cruise. For the 505–µm nets, regional patterns are also limited, but reveal the same patterns for *Neocalanus* spp., and *Eucalanus bungii*, and suggest increasing abundances of *Calanus glacialis* over Statoil, while euphausiids tended to increase during the second cruise (Fig. 26-28).

#### **Broad-scale patterns**

The greater Hanna Shoal survey with the  $150-\mu m$  nets suggests that the most abundant small-bodied copepods were broadly distributed over the study area, but somewhat less so in the southwestern corner (Fig. 29). *Calanus glacialis* was more abundant in the northern half of the survey and *Calanus hyperboreus* was confined to the waters adjoining the arctic basin (Fig 30). As suggested previously, the Pacific oceanic copepods *Neocalanus* spp. and *Eucalanus bungii* were restricted to the southeastern study area, including Klondike, while the cold-affinity *Microsetella* had the opposite pattern (Fig 31). The neritic *Acartia longiremis* was mostly

concentrated in the central region, while the ice-associated *Cyclopina* was most common in areas near where ice had persisted, and the polar oceanic *Microcalanus pygmaeus* was patchily distributed, but most consistently at the stations adjoining the arctic basin (Fig. 32). Of the other groups, larvaceans were uncommon in the southwest, *Limacina* was patchy, and meroplankton was broadly distributed, but more abundant in the northeastern half of the study area (Fig. 33). Hydromedusae were present in low abundance, mostly in the northern half of the study area, while the chaetognath *Parasagitta elegans*, was broadly distributed and most abundant over Hanna Shoal. Euphausiids were largely restricted to the southwestern corner of the study area (Fig. 34).

The 505–µm nets used in the greater Hanna Shoal survey were dominated almost completely by the copepod *Calanus glacialis*,, with lower abundance observed in the southwestern part of the study area (Fig 35). Although *Calanus hyperboreus* was not observed in these samples, they may have simply escaped detection given their low numbers suggested by the 150–µm nets. The large-bodied Pacific oceanic copepods *Neocalanus* spp. and *Eucalanus bungii* were largely restricted to the southwestern study area, although some animals appear to be present along the inner DBO line where the Alaska Coastal Current enhances northward transport (Fig. 36). *Metridia pacifica* was notably absent from all but one sample where it was present in extremely low numbers. Euphausiids (primarily early life stages) were also concentrated in the southwestern study area, while chaetognaths were broadly distributed, as were generally low numbers hydrozoans (Fig. 37) and amphipods (not shown).

#### Community patterns

Cluster analysis of stations using Bray-Curtis similarity suggested approximately 15 distinct clusters (and several outliers) within the 150– $\mu$ m abundances, with 2 major clusters emerging at the ~70-75% similarity level (Fig. 38). The two Klondike surveys, along with Southern Hanna Shoal formed one of these major clusters, with the two Klondike surveys somewhat distinct from one another within this cluster. During September/October Klondike was more intertwined with the Southern Hanna Shoal stations, and several stations fell within the other major cluster. Burger stations tended to cluster together during the August cruise, although Statoil was more dispersed. Burger and Statoil were highly intertwined with each other as well as the Central Shoal and Northern Shoal on the September/October cruise. The most inshore DBO stations did not cluster well with each other or other stations, although station 3-5 clustered together. In general, these groupings were also supported by multidimensional scaling (MDS) of the data (Fig. 39), that tends to better illustrate the relationship among stations. The 2D MDS stress value suggested that a 3D representation of the stations (stress=0.13) was superior to the 2D representation. The temporal trajectory often apparent between cruises in previous years was relatively indistinct in the 150– $\mu$ m abundance data during 2012.

The 505–µm nets clustered less tightly in general than the 150–µm data. Cluster analysis suggested only 4-7 distinct clusters, with only 2 major clusters and several outliers. The two Klondike surveys, along with Southern Hanna Shoal formed one of these major intertwined clusters. The other major cluster considered of Burger and Statoil from both surveys highly intertwined with each other as well as the Central Shoal and Northern Shoal. Most of the southern DBO stations (i.e. stations 1-5) fell within the Klondike cluster, although the two most inshore stations clustered most poorly to the rest of the group. These groupings were supported by MDS (Fig. 39), with stress values also suggesting that a 3D representation of the stations

(stress=0.16) was superior to the 2D representation. Temporal trajectories were also not apparent with the 505– $\mu$ m abundance data during 2012.

In 2012, zooplankton community patterns were strongly linked to environmental conditions with water column temperature being the strongest single variable. This was true for both the 150– $\mu$ m nets (Spearman r=0.63 for deep, 0.61 for average, and 0.47 for upper waters), as well as the 505– $\mu$ m (r=0.54 for average, 0.53 for deep, and 0.44 for upper waters), while salinity was correlated but less strongly (in the 150– $\mu$ m nets, r=0.54 for deep, and 0.34 for surface waters; in the 505– $\mu$ m nets, r=0.50 for deep, and 0.38 for surface waters). The best correlations to nutrients or chlorophyll were only half of the best correlations to temperature, but still notable. Two variable models offer some improvement (i.e. in the 150– $\mu$ m nets, 0.64 for temperature and salinity together; in the 505– $\mu$ m nets, 0.67 for temperature and chlorophyll, or 0.56 for temperature and salinity together), as did the three variable models (in the 150– $\mu$ m nets, 0.66 for combinations of temperature and salinity; in the 150– $\mu$ m nets, 0.60 for combinations of temperature, salinity and chlorophyll).

The strong influence of temperature is readily apparent when it is superimposed upon the MDS (Fig. 42). This approach suggests that in the 150– $\mu$ m nets, the dominant small-bodied copepods *Acartia longiremis* and *Pseudocalanus* tend to be more abundant in the colder waters, while *Oithona similis* is uninfluenced by temperature, and *Microsetella norvegica* is strongly associated with colder waters (Fig 43). Of the large-bodied copepods, both nets indicate *Calanus glacialis* is more abundant in colder waters, while the subarctic *Eucalanus bungii* and *Neocalanus*, as well as euphausiids, are largely restricted to warmer waters (Fig. 44, 45,46). For the other non-crustaceans, abundances tended to be higher in the colder waters (Fig. 47).

#### Inter-annual comparisons: 2008-2012

A comparison by sampling month across the five years shows August 2012 to have been relatively typical in terms of copepod abundance in the 150–µm net, but under-represented in larvaceans and perhaps meroplankton (Fig. 48). The 505–µm net indicated that August 2012 was the best year in the last five for copepods, while typical for larger meroplankton (i.e. decapod larvae). In terms of biomass, August 2012 was clearly the year with highest copepods biomass in both nets, but with relatively typical biomass of many other groups such as chaetognaths (Fig. 49). In contrast, September 2012 was relatively unremarkable in terms of total copepod numbers for the 150–µm net, as well as relatively low for most other groups compared to previous years (Figure 50). The copepods collected by the 505–µm net were 2-8 times more abundant than that observed in prior years, with low abundances in most other groups. In terms of biomass, September 2012 had the highest copepod biomass observe in the 150–µm net for the 5-year period, while most other groups had relatively typical values (Fig. 51). The copepod biomass in the 505–µm net during September 2012 was 2-8 times higher than that observed in prior years. With the exception of chaetognaths, where biomass equaled that of 2010, the biomass of other groups in the 505–µm net was typical or below average.

Looking at the species-level details, in the 150–µm nets abundances of the major zooplankton copepod genera were comparable most previous years with the exception of 2010 (Fig. 52). Notable exceptions are for *Calanus glacialis* which was unusually abundant and the larvacean *Fritillaria* which was unusually rare. In the 505–µm nets, the large copepod *Calanus glacialis* was highly abundant and *Neocalanus* numbers were somewhat elevated (Fig 53),

*Oikopleura* and euphausiid numbers we relatively typical (Fig 54), and the hydromedusae *Aglantha* was surprisingly rare (Fig 55). From examination of copepod size-spectra we can see the clear modes associated with the final three stages of *Calanus glacialis* at 1700, 2300 and 3200  $\mu$ m prosome-length in both mesh sizes of nets (Fig 56, 57), that are as much as 1.5-2 orders of magnitude above the poorest year observed for *Calanus* (i.e. 2008).

# DISCUSSION

#### Chlorophyll and Nutrients

During all the 2012 surveys, low nitrate and chlorophyll concentrations persisted in surface waters. With the exception of Klondike and other southwestern stations, a large pool of nutrients existed at depth (20m and greater) that was not generally being exploited by the phytoplankton community. While nitrate was depleted in surface waters, it is usual that both phosphate and silicate were not fully depleted. Despite the relatively recent of seasonal sea-ice, chlorophyll levels at Burger and Statoil were relatively moderate on the first cruise and declined to the low levels typical of the study area by September. This suggests the seasonal bloom had either preceded sampling and/or was being depressed by some environmental factor such as the extremely cold conditions over most of the sampling region (Weingartner et al., 2013). Those authors found different transport rates and water masses in the survey areas, that were likely responsible for the distinct difference observed at Klondike. A compilation of chlorophyll values from the 1974-1995 period (Dunton et al., 2005) suggest large spatial gradients of chlorophyll occur throughout the Chukchi Sea, with their value in our study area approximately 80-200 mg m<sup>-2</sup>. Our 2012 observations overlap these values, but generally fall below these estimates. Finally, 2012 provides the first opportunity to determine the ratio of chlorophyll to carbon (see below) and thereby better quantify the amount of food available to the zooplankton.

## Phytoplankton and Microzooplankton composition

By the time of the August survey, the spring bloom was clearly over, as evidenced by the low chlorophyll-*a* concentrations and near absence of typical ice algae (e.g. *Fragiliariopsis*) and centric diatom species characteristic of the spring bloom (e.g. *Thalassiosira, Chaetoceros*). Diatoms dominated phytoplankton biomass at only a few stations in August where the solitary pennate diatom *Cylindrotheca*, was present at relatively high concentrations in the subsurface likely due to high subsurface nutrient levels. The toxigenic diatom, *Pseudo-nitzschia*, was also present in significant numbers at the inner stations of the DBO line. Throughout the survey grid and over time, phytoplankton numbers and biomass were mainly dominated by small flagellates, including coccolithophorids. Coccolithophorids are calcifying phytoplankton that may be sensitive to ocean acidification. Coccolithophorid blooms have been observed to occur irregularly in the Bering Sea since 1997 (Iada et al., 2012), but coccolithophorids have only been recorded in very low numbers in the Chukchi Sea (<1 ml<sup>-1</sup>, Booth and Horner, 1997). We found it to occur in moderately high numbers up to 850 ml<sup>-1</sup>, higher than found in the massive 1997 Bering Sea bloom (295 ml<sup>-1</sup>, Stockwell *et al.*, 2001). With only one season of data, it is not known if coccolithophorid blooms are a new or unusual occurrence in the Chukchi Sea.

Unlike mesozooplankton, the abundance and biomass of the ecological and taxonomic types of microzooplankton are more closely tied to nutrient levels and phytoplankton prey size and biomass rather than water mass biogeography. Although less abundant than the mostly small size  $(<30 \ \mu\text{m})$  heterotrophic dinoflagellates, large ciliates (>20-75  $\mu\text{m}$  in length) dominated total microzooplankton biomass. The composition of the microzooplankton reflects the low biomass levels and small size of the phytoplankton in post bloom summer conditions and feeding preferences. During diatom blooms, large heterotrophic dinoflagellate species tend to dominate microzooplankton biomass due to their unique abilities to feed on diatoms (Hansen, 1991; Lessard, 1991) while filter-feeding ciliates, adapted to feed on small prey, tend to dominate in the summer (Nielson and Kiorboe, 1994). Total microzooplankton biomass was comparable to, sometimes exceeding, phytoplankton biomass at all stations, providing a significant prey resource for mesozooplankton in the Chukchi shelf region. This knowledge of the microzooplankton biomass allows us to appreciate that suspension-feeding mesozooplankton have twice the biomass of food available to them as would be suggested by knowledge of chlorophyll concentration alone.

#### Mesozooplankton composition

As was found in the initial 3 years of the program (Questel *et al.*, 2013), most copepod species in this study were common to the subarctic Pacific Ocean and/or the Bering Sea rather than specific to the Arctic (Brodsky, 1950, 1957). This is due to the generally northward advection of waters through the Bering Strait (e.g. Weingartner *et al.*, 2005, Woodgate *et al.*, 2012). The genus *Calanus* provides a notable exception to this habitat affinity, with a Pacific genotype of the Arctic endemic *Calanus glacialis* now thought to be maintained in the Bering Sea (Nelson *et al.*, 2009). Oceanic Pacific species were largely confined to the southwestern corner of the study region (including Klondike), while more neritic species were broadly distributed. It is notable that 2012 saw frequent occurrence of two arctic ice-associated copepods (*Jashnovia, Cylcopina*) and several species of strong cold-water preference (*Microcalanus, Microsetella*) widely distributed across the study area. Unlike 2011, large oceanic arctic species like *Calanus hyperboreus* were rare or confined to water adjoining the deep basin. Overall, the community showed limited diversity and a less even mix of major zooplankton groups that are typical of the summer ice-free period (e.g. Wing, 1974; English and Horner, 1977; Springer *et al.*, 1989; Kulikov, 1992; Hopcroft *et al.*, 2010).

Our 2012 estimate of an average abundance of 2190 individuals m<sup>-3</sup> and 66.0 mg DW m<sup>-3</sup> captured by the 150-um net, and an average of 393 m<sup>-3</sup> and 72.1 mg DW m<sup>-3</sup> captured by the 505-µm net over the Klondike, Burger and Statoil survey grids (Table 3), are comparable to previous studies from the Chukchi Sea, albeit abundances are somewhat low and biomass somewhat high. In waters to the south and west of the Klondike and Burger survey areas an average of 5760 individuals m<sup>-3</sup> and 42 mg DW m<sup>-3</sup> were recently determined using identical techniques with a 150-µm vertical net (Hopcroft et al., 2010). There is also a broad range of older biomass estimates for the region,  $\sim 2 \text{ g DW m}^{-2}$  (*ca.* 50 mg DW m<sup>-3</sup>) for herbivorous zooplankton in summer north and south of the Bering Strait (Springer et al., 1989), 2.5-5.5 g DW  $m^{-2}$  on the US side of the Chukchi Sea (but only 1.3 g DW  $m^{-2}$  spanning both sides of the Chukchi - Turco, 1992a, b). Furthermore, 14.8 g WW m<sup>-2</sup> (Kulikov, 1992) and 356 mg WW m<sup>-3</sup> (14.2 g WW m<sup>-2</sup> - Pavshtiks, 1984) for all mesozooplankton spanning the Chukchi Sea are also somewhat lower, if we assume DW is 10-15% of WW (Wiebe et al., 1975). A recent estimate of ~2000 individuals  $m^{-3}$  and ~200 mg DW  $m^{-3}$  to the south using a 335-µm (Matsuno *et al.*, 2011) can be reconciled with our observations in terms of abundance but not biomass, perhaps due to differences in methodology. Our 2012 findings exceed the range of recent observations (3-58 mg DW m<sup>-3</sup>) to the north of the study area near the shelf break (Lane et al. 2008; Llinás et al., 2009),

as well as values for the upper 50 m (42 mg DW m<sup>-3</sup>) further into the adjoining basin (Kosobokova and Hopcroft, 2010), but are encompassed by the wide range reported recently for the slope region (Matsuno *et al.*, 2012).

In terms of composition, the species observed in this study have all been reported previously for this region, but not consistently within a single publication. Our 505–µm data is directly comparable to data from the ISHTAR (Inner Shelf Transfer and Recycling) program (Springer *et al.*, 1989; Turco, 1992a,b), who noted the predominance of *Calanus marshallae/glacialis*, *Pseudocalanus* spp., *Acartia longiremis* and *Oikopleura* among the herbivorous grazers. Our copepod community composition is consistent with recent studies to the south (Matsuno *et al.*, 2011) and north (Matsuno *et al.*, 2012) of our study area. Non-crustacean groups have been recorded with variable taxonomic resolution and identification proficiency in other studies. It is notable that other filter-feeding grazers typical of the study area, such as larvaceans and pteropods, were uncommon in 2012 during this period of pronounced *Calanus glacialis* dominance.

The dominant predators in terms of abundance and biomass were the chaetognaths, almost exclusively *Parasagitta elegans*, consistent with other studies from the region (e.g. Cooney, 1977; Neimark, 1979; Springer *et al.*, 1989; Kulikov 1992; Lane *et al.*, 2008; Hopcroft *et al.*, 2010). As with the filter-feeders, other predators were relatively rare in 2012, in particular the hydrozoan *Aglantha digitale*.

## Community patterns

The spatial distribution of zooplankton communities in the Chukchi Sea has been frequently tied to the different water masses in this region. Patterns were first recognized by Russian researchers as early as the 1930s (Stepanova, 1937a,b), and are to a large extent a continuation of patterns observed in the northern Bering Sea (see review by Coyle *et al.*, 1996). These patterns were reiterated by later Russian studies (e.g. Pavshtiks, 1984) that identified at least three water types in the region. Although the first few years of the ISHTAR program were restricted to sampling in US waters, the oceanic Anadyr waters, continental shelf and low-saline near-shore waters were also encountered and implicated in zooplankton distribution (Springer *et al.*, 1989). Cross-basin studies by the international BERPAC (Bering-Pacific) program also identified three zooplankton clusters within the Chukchi Sea, but failed to articulate their species assemblages or associate them with specific water masses (Kulikov, 1992). Recent sampling in the Chukchi to the south and west by the RUSALCA program, and by Japanese programs also confirms strong ties to water masses (Hopcroft *et al.*, 2010; Matsuno *et al.*, 2011, 2012), as does a recent fisheries-driven survey (Eisner *et al.*, 2013).

Distribution maps of the more dominant species show that small neritic copepod genera (e.g. *Acartia, Pseudocalanus, and Oithona*) are widespread. The tendency for *Acartia* and *Pseudocalanus* to be more associated with colder waters is somewhat perplexing, as different patterns have existed in prior years, indicating we do not yet understand what drives regional differences. In contrast, our studies in 2011 and 2012 are consistent in showing that species of strong subarctic Pacific affinity (e.g. *Eucalanus, Neocalanus*, and euphausiids) become abundant in the southwestern parts of the study area during summer, but progressively decline across Burger and Statoil due to changes in water mass characteristics. The non-copepod groups are still more poorly understood due to their patchier distributions. While we had anticipated the occurrence of more species of Arctic Basin affinity to the north of Hanna Shoal (Lane *et al.*,

2008), several species appear to be dispersed onto the shelf. Several different mechanisms for this are possible, with the late ice retreat in 2012 appearing to have favored the persistence of several ice-associated species.

Despite the relative proximity of the survey areas to each other, as in previous years we were generally able to distinguish these areas based on community structure. Klondike remained most distinct form the other core study areas. In 2012, however, Burger and Statoil were relatively distinct during August, but relatively similar to each other in September/October. Seasonal shifts in community structure were limited in 2012 compared to previous years. This was likely associated with the long persistence of winter water and melt water over much of the northwestern half of the study region, and the limited penetration of Bering Sea summer water into the southwest (Weingartner *et al.*, 2013).

## Inter-annual comparison

The most striking zooplankton community feature of 2012 was the persistent dominance of the copepod *Calanus glacialis* in all samples, even over the expanded study domain. From examination of copepod size-spectra we can see the clear modes associated with the final three developmental stages of *Calanus glacialis* (at ~1700, 2300 and 3200  $\mu$ m prosome-length) in both mesh sizes of nets (Fig 46, 47): these are as much as 1.5-2 orders of magnitude above the poorest year observed for *Calanus*. Simultaneously, several other common groups and species showed lower than normal contributions to community structure. It is believed that the interannual variability observed for the planktonic communities from 2008-2012 is related to a combination of physical parameters observed at the study area and the intensity of physical transport from the Bering Strait

Although cooler conditions experienced in 2012 appeared to favor *Calanus* – consistent with observations in the Bering Sea (Baier and Napp 2003), other species may have experienced reduced growth and reproduction related to the colder than normal environment. As examples, *Aglantha* as been a upper-ranked species in other years (Hopcroft *et al.*, 2012), but recruitment of the holoplanktonic medusae *Aglantha* was reduced and most specimens were small compared to normal and the medusoid phase of many benthic cnidarians were uncommon. In contrast, the ctenophore *Mertensia ovum*, remained at typically abundance levels. Several meroplankton groups also had reduced abundances in 2012. Lastly, cladocerans normally transported within warmer, fresher Alaska Coastal Current waters failed to appear during 2012.

# CONCLUSIONS

Significant differences in water temperatures and timing of the phytoplankton blooms from 2008-2012 caused variations among both seasonally and spatially averaged mesozooplankton community values. We think that both the intensity of mesozooplankton transport from more southern waters, and their productivity while en route to the study region are also important. Nonetheless, 2011 demonstrates transport from other directions may also have significant impacts, and 2012 suggests local conditions may favour the development large populations of cold-water species such as *Calanus glacialis*. In addition to confirming the known predominance of crustacean zooplankton as resources for higher trophic levels, these surveys are establishing the unappreciated importance of microzooplankton and lesser-studied groups in the northeastern Chukchi Sea.

A major strength of this program is the use of a consistent sampling design capable of capturing differences in timing and magnitude of the planktonic communities and other ecosystem components. Sampling during five years of the ice-free period in the northeastern Chukchi Sea has allowed us to recognize the high level of inter- and intra-annual variability of the plankton community over the study region, and is providing insight into what shapes the abundance of different species annually. This design also lays a solid foundation for assessing any potential perturbation associated with exploration and production activities in the northeastern Chukchi region.

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*Fig. 1* Locations of the CSESP survey area in the northeastern Chukchi Sea. Survey areas Klondike, Burger, and Statoil are approximately -NM<sup>2</sup>.



*Fig. 2.* Nitrate concentrations observed throughout the water column [0, 5, 10, 20, 30 m & Bottom (~40m)] over the Hanna Shoal study area during the August cruise 2012 (WWW1302).



*Fig. 3.* Phosphate concentrations observed throughout the water [0, 5, 10, 20, 30 m & Bottom (~40m)] over the Hanna Shoal study area during the August cruise 2012 (WWW1302).



*Fig. 4.* Silicate concentrations observed throughout the water column [0, 5, 10, 20, 30 m & Bottom (~40m)] over the Hanna Shoal study area during the August cruise 2012 (WWW1302).



*Fig. 5.* Chlorophyll–*a* concentrations observed throughout the water column [0, 5, 10, 20, 30 m & Bottom (~40m)] over the Hanna Shoal study area during the August cruise 2012 (WWW1302).



*Fig. 6.* Nitrate concentrations observed throughout the water column (0, 5, 10, 20, 30 & 40 m) over the expanded Hanna Shoal study area during the September/October cruises 2012 (WWW1303-4).



*Fig. 7.* Phosphate concentrations observed throughout the water column (0, 5, 10, 20, 30 & 40 m) over the expanded Hanna Shoal study area during the September/October cruises 2012 (WWW1303-4).



*Fig. 8.* Silicate concentrations observed throughout the water column (0, 5, 10, 20, 30 & 40 m) over the expanded Hanna Shoal study area during the September/October cruises 2012 (WWW1303-4).


*Fig. 9.* Chlorophyll–*a* concentrations observed throughout the water column (0, 5, 10, 20, 30 & 40 m) over the expanded Hanna Shoal study area during September/October cruises 2012 (WWW1303-4).



*Fig. 10.* Integrated Chlorophyll–*a* concentrations observed during August (WWW1202) and September/October cruises, 2012 (WWW1203-4).



*Fig.* 11. Average phytoplankton biomass ( $\mu$ g l<sup>-1</sup>) in the upper and lower water column layers during August (\*) and September/October 2012.



*Fig. 12.* Contribution of the major phytoplankton taxa groups to total phytoplankton biomass in the upper and lower water column in each survey area in August (\*) and September/October, 2012.



*Fig. 13.* Average protozooplankton biomass ( $\mu g l^{-1}$ ) in the upper and lower water column layers during August (\*) and September/October, 2012.



*Fig. 14.* Contribution of ciliates and heterotrophic dinoflagellates to protozooplankton biomass in the upper and lower water column layers during August (\*) and September/October, 2012.



*Fig. 15.* Integrated biomass of phytoplankton and protozooplankton in the upper and lower water column layers during August (\*) and September/October, 2012.



*Fig. 16.* Contribution of the major groups to the community abundance at each survey area during 2012 as determined for both plankton nets. Error bars are standard error of the means.



*Fig.* **17.** Contribution of the major groups to the community biomass at each survey area during 2012 as determined for both plankton nets. Error bars are standard error of the means.



*Fig. 18.* Relative contribution of major taxonomic groups to the community abundance captured by the  $150-\mu m$  net at each station during 2012.



*Fig. 19.* Relative contribution of major taxonomic groups to the community biomass captured by the 150 $-\mu$ m net at each station during 2012.



*Fig. 20* Relative contribution of major taxonomic groups to the community abundance captured by the  $505-\mu m$  net at each station during 2012



*Fig. 21* Relative contribution of major taxonomic groups to the community biomass captured by the 505–µm net at each station during 2012.



*Fig.* 22 Abundance of the dominant copepod species or genera during each survey area in 2012 as captured by the 150– $\mu$ m net. The black or white line through the box is the sample median; grey line is the mean, limits of the box are the 25<sup>th</sup> and 75<sup>th</sup> percentile. Whiskers are the 10<sup>th</sup> and 90<sup>th</sup> percentiles and the single points are the 5<sup>th</sup> and 95<sup>th</sup> percentiles. Features may be absent where number of samples where the tax occurred in the samples was low.



*Fig. 23* Abundance of the sub-dominant copepod species and nauplii during each survey area in 2012 as captured by the 150– $\mu$ m net. The black or white line through the box is the sample median; grey line is the mean, limits of the box are the 25<sup>th</sup> and 75<sup>th</sup> percentile. Whiskers are the 10<sup>th</sup> and 90<sup>th</sup> percentiles and the single points are the 5<sup>th</sup> and 95<sup>th</sup> percentiles. Features may be absent where number of samples where the tax occurred in the samples was low.



*Fig.* 24 Abundance of the dominant cnidarian, chaetognath, larvaceans, pteropod and ctenophore during each survey area in 2012 as captured by the 150– $\mu$ m net. The black or white line through the box is the sample median; grey line is the mean, limits of the box are the 25<sup>th</sup> and 75<sup>th</sup> percentile. Whiskers are the 10<sup>th</sup> and 90<sup>th</sup> percentiles and the single points are the 5<sup>th</sup> and 95<sup>th</sup> percentiles. Features may be absent where number of samples where the tax occurred in the samples was low.



*Fig.* 25 Abundance of the dominant meroplankton during each survey area in 2012 as captured by the 150– $\mu$ m net. The black or white line through the box is the sample median; grey line is the mean, limits of the box are the 25<sup>th</sup> and 75<sup>th</sup> percentile. Whiskers are the 10<sup>th</sup> and 90<sup>th</sup> percentiles and the single points are the 5<sup>th</sup> and 95<sup>th</sup> percentiles. Features may be absent where number of samples where the tax occurred in the samples was low.

## 150-µm



*Fig.26* Abundance of the dominant copepods during each survey area in 2012 as captured by the 505– $\mu$ m net. The black or white line through the box is the sample median; grey line is the mean, limits of the box are the 25<sup>th</sup> and 75<sup>th</sup> percentile. Whiskers are the 10<sup>th</sup> and 90<sup>th</sup> percentiles and the single points are the 5<sup>th</sup> and 95<sup>th</sup> percentiles. Features may be absent where number of samples where the tax occurred in the samples was low.

505-µm

## 505-µm



*Fig.* **27** Abundance of the dominant crustacean zooplankton during each survey area in 2012 as captured by the 505– $\mu$ m net. The black or white line through the box is the sample median; grey line is the mean, limits of the box are the 25<sup>th</sup> and 75<sup>th</sup> percentile. Whiskers are the 10<sup>th</sup> and 90<sup>th</sup> percentiles and the single points are the 5<sup>th</sup> and 95<sup>th</sup> percentiles. Features may be absent where number of samples where the tax occurred in the samples was low.



*Fig. 28* Abundance of the dominant non-copepod zooplankton during each survey area in 2012 as captured by the 505– $\mu$ m net. The black or white line through the box is the sample median; grey line is the mean, limits of the box are the 25<sup>th</sup> and 75<sup>th</sup> percentile. Whiskers are the 10<sup>th</sup> and 90<sup>th</sup> percentiles and the single points are the 5<sup>th</sup> and 95<sup>th</sup> percentiles. Features may be absent where number of samples where the tax occurred in the samples was low.



*Fig. 29.* Abundance of all copepods, and their most abundant species, over the Greater Hanna Shoal study area in 2012 as assessed using the 150– $\mu$ m mesh nets. Area of bubbles is proportional to abundance (individuals m<sup>-3</sup>). Color fills represent bathymetry in meters.



*Fig. 30.* Abundance of *Calanus* copepod species and copepod nauplii over the Greater Hanna Shoal study area in 2012 as assessed using the 150– $\mu$ m mesh nets. Area of bubbles is proportional to abundance (individuals m<sup>-3</sup>). Color fills represent bathymetry in meters.



*Fig. 31.* Abundance of Pacific copepods *Eucalanus bungii* and *Neocalanus* spp., and the subpolar *Microsetella norvegica* over the Greater Hanna Shoal study area in 2012 as assessed using the 150– $\mu$ m mesh nets. Area of bubbles is proportional to abundance (individuals m<sup>-3</sup>). Color fills represent bathymetry in meters.



*Fig. 32.* Abundance of the neritic *Acartia longiremis*, the ice-associated *Cyclopina*, and the polar oceanic *Microcalanus pygmaeus* copepods over the Greater Hanna Shoal study area in 2012 as assessed using the 150– $\mu$ m mesh nets. Area of bubbles is proportional to abundance (individuals m<sup>-3</sup>). Color fills represent bathymetry in meters.



*Fig. 33.* Abundance of larvaceans, the pteropod *Limacina helicina*, and meroplankton over the Greater Hanna Shoal study area in 2012 as assessed using the  $150-\mu m$  mesh nets. Area of bubbles is proportional to abundance (individuals m<sup>-3</sup>). Color fills represent bathymetry in meters.



*Fig. 34.* Abundance of hydrozoan medusae, the chaetognath *Parasagitta elegans*, and euphausiids over the Greater Hanna Shoal study area in 2012 as assessed using the 150– $\mu$ m mesh nets. Area of bubbles is proportional to abundance (individuals m<sup>-3</sup>). Color fills represent bathymetry in meters.



*Fig. 35.* Abundance of all copepods, and their Calanus species, over the Greater Hanna Shoal study area in 2012 as assessed using the 505– $\mu$ m mesh nets. Area of bubbles is proportional to abundance (individuals m<sup>-3</sup>). Color fills represent bathymetry in meters.



*Fig. 36.* Abundance of three large-bodied Pacific copepods over the Greater Hanna Shoal study area in 2012 as assessed using the 505– $\mu$ m mesh nets. Area of bubbles is proportional to abundance (individuals m<sup>-3</sup>). Color fills represent bathymetry in meters.



*Fig.* 37. Abundance of euphausids, the chaetognath *Parasagitta elegans* and hydrozoan medusae over the Greater Hanna Shoal study area in 2012 as assessed using the 505– $\mu$ m mesh nets. Area of bubbles is proportional to abundance (individuals m<sup>-3</sup>). Color fills represent bathymetry in meters.



*Fig. 38.* Station similarity as determined by hierarchical clustering of fourth-root transformed zooplankton abundance for the 150– $\mu$ m net. Red lines connect stations that are not statistically unique (P<0.05). Stations are color-coded by survey area to aid interpretation. Expanded Hanna Shoal cruises distinguished by the suffix "2." Stations numbers are last two digits of sample ID number.



*Fig. 39.* Multidimensional scaling of zooplankton community abundances for the 150– $\mu$ m net based on clustering performed in Fig. 38. Axes are arbitrary, spacing of samples represents the best 2-D projection of the distance in similarity among samples. Stations are color-coded by survey area to aid interpretation.



*Fig. 40.* Station similarity as determined by hierarchical clustering of fourth-root transformed zooplankton abundance for the  $505-\mu m$  net. Red lines connect stations that are not statistically unique (P<0.05). Stations are color-coded by survey area to aid interpretation. Expanded Hanna Shoal cruises distinguished by the suffix "2." Stations numbers are last two digits of sample ID number.



*Fig. 41.* Multidimensional scaling of zooplankton community abundances for the 150– $\mu$ m net based on clustering performed in Fig. 39. Axes are arbitrary, spacing of samples represents the best 2-D projection of the distance in similarity among samples. Stations are color-coded by survey area to aid interpretation.



*Fig. 42.* Mean water column temperature overlain on zooplankton community MDS patterns for the  $150-\mu m$  and  $150-\mu m$  nets. Symbols area is proportional to temperature, and colors are correspondingly ramped form red (warmest) to blue (cooldest).



*Fig. 43.* Abundances of the dominant small-bodied copepods overlaid on zooplankton community MDS patterns for the 150– $\mu$ m nets. Symbols area is proportional to abundances, while colors are ramped from coldest (blue) to warmest (red)



*Fig. 44.* Abundance of the dominant large-bodied copepods and the euphausiids overlaid on zooplankton community MDS patterns for the 150– $\mu$ m nets. Symbols area is proportional to abundances, while colors are ramped from coldest (blue) to warmest (red)


*Fig. 45.* Abundance of the dominant large-bodied copepods and the euphausiids overlaid on zooplankton community MDS patterns for the 150– $\mu$ m nets. Symbols area is proportional to abundances, while colors are ramped from coldest (blue) to warmest (red)



*Fig. 46.* Abundance of the dominant large-bodied copepods and the euphausiids in the  $505-\mu m$  nets overlaid on average water column temperature for the September/October 2012 cruises.



*Fig.* **47.** Abundances of the larvaceans, meroplankton, hydrozoans and the chaetognath *Parasagitta elegans* overlaid on zooplankton community MDS patterns for the 150– $\mu$ m nets. Symbols area is proportional to abundances, while colors are ramped from coldest (blue) to warmest (red).



*Fig. 48* Contribution of the major groups to the community abundance during August at each survey area spanning the 2008–2012 season as determined for both plankton nets. Error bars are standard error of the means.



*Fig. 49.* Contribution of the major groups to the community biomass during August at each survey area spanning the 2008–2012 season as determined for both plankton nets. Error bars are standard error of the means.



*Fig. 50.* Contribution of the major groups to the community abundance during September at each survey area spanning the 2008–2012 season as determined for both plankton nets. Error bars are standard error of the means.



*Fig. 51.* Contribution of the major groups to the community biomass during September at each survey area spanning the 2008–2012 season as determined for both plankton nets. Error bars are standard error of the means.



*Fig. 52a.* Abundance of the dominant copepod and larvacean species within each survey area spanning the 2008-2012 seasons as captured by the 150– $\mu$ m net. The black or white line through the box is the sample median; grey line is the mean, limits of the box are the 25<sup>th</sup> and 75<sup>th</sup> percentile. Whiskers are the 10<sup>th</sup> and 90<sup>th</sup> percentiles and the single points are the 5<sup>th</sup> and 95<sup>th</sup> percentiles.



*Fig. 52b.* Abundance of the dominant copepod and larvacean species within each survey area spanning the 2008-2012 seasons as captured by the 150– $\mu$ m net. The black or white line through the box is the sample median; grey line is the mean, limits of the box are the 25<sup>th</sup> and 75<sup>th</sup> percentile. Whiskers are the 10<sup>th</sup> and 90<sup>th</sup> percentiles and the single points are the 5<sup>th</sup> and 95<sup>th</sup> percentiles.



*Fig. 52c. Abundance* of the dominant copepod and larvacean species within each survey area spanning the 2008-2012 seasons as captured by the 150– $\mu$ m net. The black or white line through the box is the sample median; grey line is the mean, limits of the box are the 25<sup>th</sup> and 75<sup>th</sup> percentile. Whiskers are the 10<sup>th</sup> and 90<sup>th</sup> percentiles and the single points are the 5<sup>th</sup> and 95<sup>th</sup> percentiles.



*Fig. 52d.* Abundance of the dominant meroplankton within each survey area spanning the 2008-2012 seasons as captured by the 150– $\mu$ m net. The black or white line through the box is the sample median; grey line is the mean, limits of the box are the 25<sup>th</sup> and 75<sup>th</sup> percentile. Whiskers are the 10<sup>th</sup> and 90<sup>th</sup> percentiles and the single points are the 5<sup>th</sup> and 95<sup>th</sup> percentiles.



*Fig. 53.* Abundance of the dominant copepod species within each survey area spanning the 2008-2012 seasons as captured by the 505– $\mu$ m net. The black or white line through the box is the sample median; grey line is the mean, limits of the box are the 25<sup>th</sup> and 75<sup>th</sup> percentile. Whiskers are the 10<sup>th</sup> and 90<sup>th</sup> percentiles and the single points are the 5<sup>th</sup> and 95<sup>th</sup> percentiles.



*Fig. 54.* Abundance of the dominant larvacean species and euphausiids (juveniles plus adults) within each survey area spanning the 2008-2012 seasons as captured by the 505– $\mu$ m net. The black or white line through the box is the sample median; grey line is the mean, limits of the box are the 25<sup>th</sup> and 75<sup>th</sup> percentile. Whiskers are the 10<sup>th</sup> and 90<sup>th</sup> percentiles and the single points are the 5<sup>th</sup> and 95<sup>th</sup> percentiles.



*Fig. 55.* Abundance of the dominant cnidarian, ctenophore and chaetognath species within each survey area spanning the 2008-2012 seasons as captured by the 505– $\mu$ m net. The black or white line through the box is the sample median; grey line is the mean, limits of the box are the 25<sup>th</sup>

and  $75^{\text{th}}$  percentile. Whiskers are the  $10^{\text{th}}$  and  $90^{\text{th}}$  percentiles and the single points are the  $5^{\text{th}}$  and  $95^{\text{th}}$  percentiles.



*Fig. 56.* Average size-spectra of the copepod community captured by the 150– $\mu$ m net for each survey year. Data is sorted into 50– $\mu$ m wide bins, gaps reflect an absence of data in that bin within the samples examined.



*Fig. 57.* Average size-spectra of the copepod community captured by the 505– $\mu$ m net for each survey year. Data is sorted into 50– $\mu$ m wide bins, gaps reflect an absence of data in that bin within the samples examined.