*Exxon Valdez* Oil Spill
Long-Term Monitoring Program (Gulf Watch Alaska) Final Report


Long-term Monitoring of Plankton Populations on the Alaskan Shelf and in the Gulf of
Alaska using Continuous Plankton Recorders

*Exxon Valdez* Oil Spill Trustee Council Project 16120114-A
Final Report

Sonia Batten

Sir Alister Hardy Foundation for Ocean Science
c/o 4737 Vista View Cr, Nanaimo, BC
Canada, V9V 1N8


Robin Brown

North Pacific Marine Science Organization
P.O. Box 6000, 9860 West Saanich Road,
Sidney, BC
Canada V8L 4B2

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**Study History:**  The first Continuous Plankton Recorder project supported by the *Exxon Valdez* Oil Spill Trustee Council (Project 02624-BAA), built on a large-scale plankton sampling program that was initially funded by the North Pacific Marine Research Initiative in 2000 and 2001. Recognizing the relevance to the planned Gulf Ecosystem Monitoring program, the *Exxon Valdez* Oil Spill Trustee Council awarded one year of funding for two transects in 2002, one north-south and one east-west across the Gulf of Alaska. The North Pacific Research Board then provided funding for the east-west transect from 2003. Funding for the north-south transect was continued through the *Exxon Valdez* Oil Spill Trustee Council Gulf Ecosystem Monitoring program for four more years (until 2008) via projects 030624 and 040624. After the Gulf Ecosystem Monitoring program ended, the value of the plankton data to herring restoration efforts was acknowledged with an additional year of funding as Restoration Project 070624 and, subsequently, as a contract under the Integrated Herring Research Program for 3 years (2010-2012), project 12100624. At about this time, a funding consortium for the North Pacific Continuous Plankton Recorder survey was established under the auspices of the North Pacific Marine Science Organization, so that several agencies (including the North Pacific Research Board and Department of Fisheries and Oceans, Canada) contributed to the survey's costs and reducing the amount requested from the *Exxon Valdez* Oil Spill Trustee Council. From 2012, the Continuous Plankton Recorder project became part of the Long-Term Monitoring Program of the *Exxon Valdez* Oil Spill Trustee Council (Gulf Watch Alaska) with 4 years of funding under the contract described in this final report, beginning in 2013. Annual reports have been submitted for each year of this contract. We have continued to work closely with Herring Research and Monitoring Principal Investigators throughout this contract and a paper resulting from that collaboration was published earlier this year (Batten et al. 2016).

**Abstract:**  Five years of large-scale plankton data (2012-2016) have been collected using a Continuous Plankton Recorder towed behind a commercial ship on its route into Cook Inlet. Sampling occurred monthly between spring and autumn each year. The time series is now 17 years in length. The last three years of the five years summarized here sampled plankton during unusual, and persistent, warm conditions resulting in plankton communities on the Alaskan shelf that were biased towards smaller zooplankton. Large diatoms were also low during this warm period, caused by increased grazing by higher numbers of zooplankton or unfavorable nutrient conditions. Warm water copepods were more numerous than average. The plankton communities were thus different with lower diatoms and increased smaller warm water species (and for an extended period of time) from those sampled in other years, even warm years, since 2000. We speculate that first year growth in juvenile herring may be poor in 2014-2016 given previously documented relationships showing that the first year growth of Prince William Sound herring was greater in years with higher abundances of smaller sized plankton, particularly the large diatoms.

**Key words:**  Biological oceanography, Continuous Plankton Recorder, Cook Inlet, Gulf of Alaska, monitoring, phytoplankton, plankton, Prince William Sound, zooplankton

**Project Data:**  Data exist as abundances per sample for 418 zooplankton and phytoplankton taxonomic entities together with sample location, time and date of collection (with position reported as the mid-point of each 18.5 km sample). Data from over 1,000 processed samples from 2012-2016 (and > 4,000 samples from previous years) are available from Sonia Batten, email soba@sahfos.ac.uk, through the Gulf of Alaska Data Portal: http://portal.aoos.org/gulf-of-alaska.php#metadata/87f56b09-2c7d-4373-944e-94de748b6d4b/project, or through the DataONE catalog: https://doi.org/10.24431/rw1k112.

The data custodian is

Carol Janzen, Alaska Ocean Observing System, 1007 W. 3rd Ave. #100, Anchorage, AK 99501, 907-644-6703. janzen@aoos.org.

Some data can also be viewed and plotted at http://pices.int/projects/tcprsotnp/default.aspx.

Temperature data from temperature loggers mounted on the Continuous Plankton Recorder are also available, either from Sonia Batten or from the project website above.

There are no limitations on the use of the data, however, it is requested that the authors be cited for any subsequent publications that reference this dataset. It is strongly recommended that careful attention be paid to the contents of the metadata file associated with these data to evaluate data set limitations or intended use.

**Citation:**

Batten, S.D. and R. Brown. 2018. Long-term monitoring of plankton populations on the Alaskan shelf and in the Gulf of Alaska using Continuous Plankton Recorders. Long-Term Monitoring Program (Gulf Watch Alaska) Final Report, (*Exxon Valdez* Oil Spill Trustee Council Project 16120114-A), *Exxon Valdez* Oil Spill Trustee Council, Anchorage, Alaska.

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**EXECUTIVE SUMMARY**

The *Exxon Valdez* Oil Spill Trustee Council (EVOSTC) support has enabled a further five years (2012-2016) of large-scale plankton data to be collected using a Continuous Plankton Recorder (CPR) towed behind a commercial container ship on its route from Washington State into Cook Inlet. Sampling occurred monthly, six times between spring and autumn each year. Methodology was unchanged from previous projects. Plankton were filtered onto a slowly moving band of 270 μm mesh as the ship towed the instrument along the transect. The mesh was subsequently cut into discrete 18.5 km sections (containing about 3m$^3$ of filtered seawater) and the plankton retained in each sample analyzed using a microscope to give taxonomically resolved abundances. Ship's log information was used to allocate each sample mid-point a time, date and geographic location. All shelf samples were analyzed, and then archived. A temperature logger was also attached to the CPR to record in situ temperature along the transect.

The last three years of the five year project summarized here sampled plankton during unusual, and persistent, warm conditions. This began with anomalous warm water offshore in summer 2013 (also known colloquially as "the Blob"), which was visible in temperature data collected on the shelf in autumn 2013 and was succeeded by a strong El Niño so that conditions remained warm right through the remainder of the sampling period (2016). Data shown in this report reveal that the plankton communities on the shelf were affected by this anomaly. Comparison with the existing time series begun in 2000 also revealed differences from the previous warm period in the mid-2000s. For example, prior to 2013 warm years had resulted in increased abundances of large diatoms, but abundances in 2014-2016 were below the long-term average. Zooplankton were quite abundant, higher than average in the summer, but were biased towards smaller taxa. Warm water copepods were more numerous than average. The plankton communities were thus different (and for an extended period of time) from those sampled in other years, even warm years, since 2000. We speculate that the large diatoms were low during this warm period, either through increased grazing by the higher numbers of zooplankton or unfavorable nutrient conditions caused by the oceanographic conditions, including increased water column stability. We also suggest that first year growth in juvenile herring may be poor in 2014-2016 given previously documented relationships between plankton indices and herring growth that showed a significant positive relationship between diatom abundances and first year growth.


**INTRODUCTION**

The *Exxon Valdez* Oil Spill Trustee Council support has contributed to a larger effort to use CPRs to collect lower trophic level samples from the North Pacific and describe changes occurring in the plankton in the North Pacific. The Pacific CPR program was initiated following a recommendation from the North Pacific Marine Science Organization (PICES 1998) that the CPR be used to address the lack of consistent, seasonal, large-scale plankton data. CPRs have been deployed for over 70 years in the North Atlantic from Ships-of-Opportunity, providing a wealth of time series data (Reid et al. 2003). Prior to the start of

the Pacific CPR program, the North Pacific had only a few regional zooplankton time series, and the CPR offered the most cost-effective way to sample larger areas on a seasonal basis.

As the study history above indicates, a CPR survey has been in place in the region since 2000 using commercial ships to tow CPRs on two regular routes in the North Pacific. EVOSTC final reports for projects 02624-BAA, 030624, 040624, 070624 and 12100624 give details of previous findings based on EVOSTC support. This report updates the survey results but has been more integrative during the last five years through the inception of the EVOSTC Long-term Monitoring Program in 2012.

The spill-affected area is an oceanographically complex subarctic shelf ecosystem and the valuable marine resources that are found here (e.g., herring, salmon, marine birds, and mammals) experience naturally-induced variability on several scales, as well as being impacted by catastrophic events such as the oil spill. Natural, rather than human-related, processes known to influence this region are many; on seasonal and interannual time scales the strength of the Alaskan shelf and Alaskan Coastal currents are mediated by freshwater run-off and winds (Royer 1979, Stabeno et al. 2004, Weingartner et al. 2005), persistent coastal downwelling in contrast to most eastern Pacific boundary regions, and eddy-mediated cross-shelf transport of organisms and nutrients (Okkonen et al. 2003, Ladd et al. 2005). More quasi-decadal time scale influences are the change in sign of the Pacific Decadal Oscillation (PDO, Mantua et al. 1997). Historically, the PDO has been a useful indicator of weather patterns that persist for a decade or more but has more recently been switching state approximately every 5 years. Positive (negative) PDO values are associated with warmer (cooler) than normal conditions in the Northeast Pacific. A second, medium time-scale influence is the North Pacific Gyre Oscillation (NPGO), a climate pattern that emerges as the second dominant mode of sea surface height variability in the Northeast Pacific Ocean (Di Lorenzo et al. 2008, http://www.o3d.org/npgo/). When the NPGO index is positive the westerly winds over the eastern North Pacific are often stronger than normal, influencing the circulation processes. Moderate to strong El Niño and La Niña events are also felt on the Alaskan Shelf (Weingartner et al. 2002). Regime shifts, which may be triggered by the climate processes described above, have periodically occurred with lower frequency, such as the 1976 shift, which changed Alaskan fisheries from shrimp to fish dominated (Francis and Hare 1994). More recently, anomalous warming across a wide expanse of the Northeast Pacific occurred late in 2013 and persisted through 2014 (Bond et al. 2015). Nicknamed "the Blob" and succeeded by a strong El Niño in 2015, the Alaskan shelf has been influenced by these strong warming events for at least three consecutive years (Di Lorenzo and Mantua 2016).

Plankton have short life-cycles and limited mobility, so they often respond rapidly to changes in their environmental conditions. They also support many of the marine food webs that terminate in valuable marine resources, and this provides the rationale behind the CPR program. Results presented here integrate the plankton observations with physical forcing data collected during Gulf Watch Alaska to try to understand temporal variability in the plankton, particularly during the recent unusually warm conditions. We have recently shown that the variability in plankton populations (abundance of appropriately sized prey at time of first feeding) can explain much of the variability in growth of Prince William

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Sound herring larvae (Batten et al. 2016) as one example of how oceanographic variability propagates through the food web from plankton to fish.


**OBJECTIVES**

The fundamental goal of this project is to provide continued large spatial scale data on plankton populations to extend the existing time series and integrate the data with more regional, locally more intensive, sampling programs. Specifically:

*Objective 1*.    Collect samples on the transect from Cook Inlet to Puget Sound in spring 2012 and continue approximately monthly through August/September 2013 (6 transects sampled with the CPR). Repeat this schedule each year to 2016. Process all shelf samples and every 4th oceanic sample.

*Objective 2*.    Process a subset of samples (25%) within 3 months of collection at the Institute of Ocean Sciences (DFO, Canada) and report results from this processing (e.g., estimated mesozooplankton biomass and comparisons with data from previous years) in progress reports and on the project website as soon as practicable. Make available full, quality controlled data from 2013 by August 2014, and in a similar fashion in subsequent years (e.g., August 2015 for data collected within 2014).


**METHODS**

Methodology used remains unchanged from that described in the proposal, and from previous EVOSTC funded CPR projects.

**Plankton sample collection**

A full description of the CPR instrument and sampling is given in Batten et al. (2003), and Richardson et al. (2006) describe data analysis methods.

The CPR was supplied to the ship with sufficient internal cassettes preloaded with filtering mesh and formaldehyde preservative to cover the sampling transect. Each cassette was deployed for a maximum of ~800 km (450 nautical miles), after which the crew recovered the CPR, changed the cassette and redeployed it (normally within 30 minutes of recovery, unless activities of the ship prevented this). The ship's officers kept a log of deployment and recovery positions and any course changes.

Water and plankton enter the front of the CPR through a small square aperture (1.27 cm), pass along a tunnel, and then through the silk filtering mesh (with a mesh size of 270 µm), which retains the plankton and allows the water to exit at the back of the machine. The movement of the CPR through the water turns an external propeller which, via a drive shaft and gear-box, moves the filtering mesh across the tunnel at a rate of approximately 10 cm per 18.5 km of tow. As the filtering mesh leaves the tunnel it is covered by a second band of mesh so that the plankton are sandwiched between these two layers. This mesh and plankton sandwich is then wound into a storage chamber containing buffered 40% formaldehyde preservative (which dilutes in the seawater to a concentration of about 4%, sufficient to fix and preserve the plankton). As the ship approaches port in Anchorage the

CPR is recovered for the final time and stored onboard until the ship docks. At this time the mechanisms are offloaded and collected by technicians from Kinnetic Laboratories in Anchorage, who have been previously trained in CPR servicing. The samples are unloaded and sent to the laboratory in British Columbia for processing while the gear is serviced, reloaded with filtering mesh and returned to the ship for the next transect. The towed mesh is processed according to standard CPR protocols; first cut into separate samples (each representing 18.5 km of tow and about 3 m$^3$ of seawater), which are randomly apportioned amongst the analysts for plankton analysis. Every fourth sample in the open ocean is analyzed with the remainder being archived, but over the Alaskan shelf consecutive samples are processed. The ship's log is used to determine the mid-point latitude and longitude of each sample (shown in Fig. 1), along with the date and time.
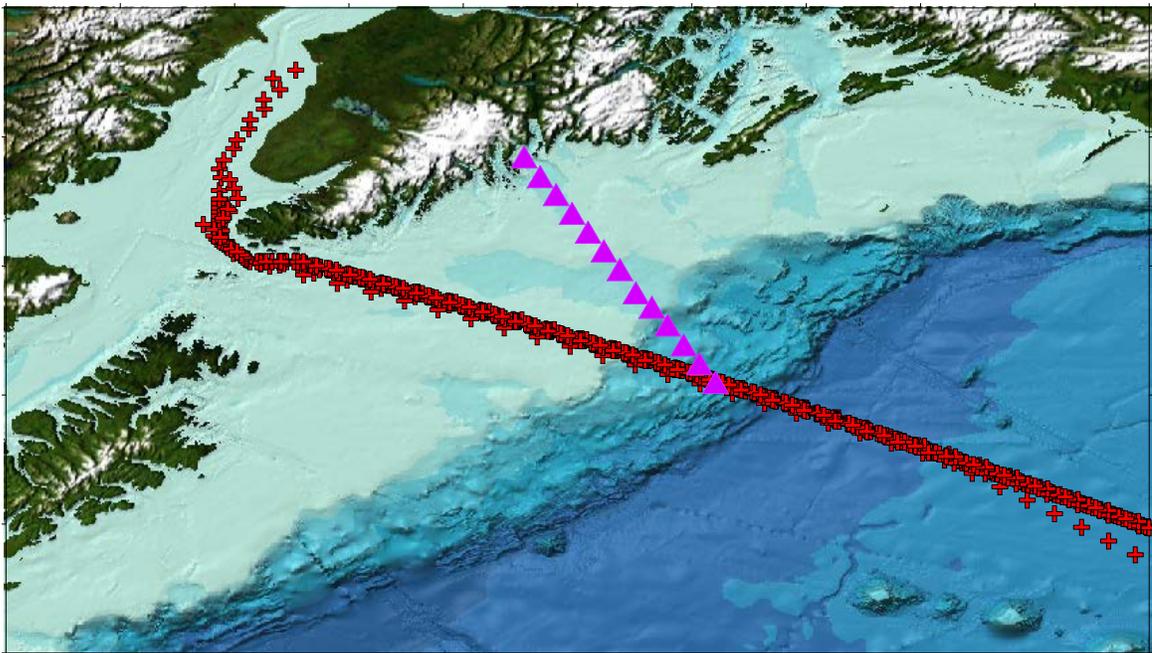


Figure 1. Location of all samples collected in the northern Gulf of Alaska during this project's duration (2013-2016, red +). Note the consistency of the transect; there are 24 separate monthly transects but they overlap almost entirely. Seward Line stations are shown as purple Δ.

**Taxonomic analysis**

The first step was the assessment of phytoplankton color (the greenness of the sample, or Phytoplankton Colour Index, PCI), which was determined by comparison with standard color charts. This is a semi-quantitative representation of the total phytoplankton biomass and includes the organisms that are too fragile to survive the sampling process intact but which leave a stain on the mesh. Hard-shelled phytoplankton are then semi-quantitatively counted under a purpose-built microscope by viewing 20 fields of view (diameter 295 μm)

evenly spaced across each sample under high magnification (x 450) and recording the presence of all the taxa in each field. Abundance is then gauged as presence in the number of fields, e.g., presence in 20 fields is assumed to reflect a more abundant organism than presence in 2 fields. Small zooplankton are then identified and counted from a sub-sample by tracking across the filtering mesh with the microscope objective (a 2 mm diameter field of view = 2% of the sample width) whilst all zooplankton larger than about 2 mm are removed from the mesh and counted without sub-sampling. Identification in all cases is carried out to the most detailed practicable taxonomic level and is a compromise between speed of analysis and scientific interest. For example, since copepods make up the majority of the zooplankton most copepods are identified to species level whilst rarer groups, or those not preserved well by the sampling mechanism (such as chaetognaths), are identified to a lower level. A list of taxa and their abundance category on each sample is thus generated, and from this summary indices (such as zooplankton biomass, diatom abundance) can also be calculated.

Full, quality controlled data are normally available 9-12 months after collection. In order to get a more rapid 'first look' at each transect a portion of the samples were processed within 2 months of the ship's return. Every 16th off-shelf sample and every 4th shelf sample was processed rapidly. This represents 25% of the total samples that are eventually processed. Quality control was carried out following a routine procedure developed for the Atlantic CPR survey: After all samples on a transect have been processed, adjacent samples are compared and counts that differ significantly from both adjacent samples are sent back for re-counting of the taxa concerned. Once the count has been checked and required corrections are made, the final data are entered into the database.

### Collection of temperature data

A small self-powered, self-logging temperature recorder (Vemco Minilogger™) was attached to the tail section of the CPR. This unit recorded temperature at the depth of the CPR every 10 minutes and the ship's log was then used to estimate a position for each temperature record. From August 2016, a CTD was added to also record salinity, depth of sampling and chlorophyll a fluorescence, and these data will be more valuable in the next phase of the project.


### RESULTS

### Sampling

The objectives described above were met fully, with 6 transects being sampled each year (Table 1). Spacing between sampling was typically monthly as planned, though occasionally shorter than this (for example, when the ship went into dry dock in early September 2015 and the last 2 transects had to be towed closer together). Sometimes 6 weeks occurred between samplings to accommodate the technicians' schedule or to lengthen the field season (e.g., July to August 2016).

Table 1. Dates for each transect sampled during this project.

| YEAR | TRANSECT NUMBER | DATES | YEAR | TRANSECT NUMBER | DATES |
|---|---|---|---|---|---|
| **2013** | 1 | 11th-14th April | **2015** | 1 | 4th-6th April |
| | 2 | 11th-13th May | | 2 | 7th-9th May |
| | 3 | 13th-16th June | | 3 | 6th-8th June |
| | 4 | 14th-15th July | | 4 | 30th July-1st Aug |
| | 5 | 16th-17th Aug | | 5 | 20th-23rd Aug |
| | 6 | 15th-16th Sept | | 6 | 30th Aug-1st Sept |
| **2014** | 1 | 22nd-24th March | **2016** | 1 | 14th-16th April |
| | 2 | 24th-26th April | | 2 | 14th-16th May |
| | 3 | 24th-26th May | | 3 | 16th-18th June |
| | 4 | 26th-28th June | | 4 | 16th-18th July |
| | 5 | 26th-28th July | | 5 | 27th-29th Aug |
| | 6 | 28th-30th August | | 6 | 29th Sept-1st Oct |

Although data from 2012 were collected under the previous contract, for consistency with other Gulf Watch Alaska reports we are including 2012 data here, too.

**Temperature Data**

Physical data were collected by other Gulf Watch Alaska principal investigators in the Environmental Drivers component (see EVOSTC final project reports) along the Seward Line (Hopcroft et al., 2018), within Cook Inlet (Doroff and Holderied, 2018), at GAK1 (Weingartner and Danielson, 2018) and in Prince William Sound (Campbell, 2018). These data give a more complete picture of oceanographic conditions during the 5-year period; however, data from the temperature loggers on the CPR provide *in situ* temperature conditions for the plankton described previously. Fig. 2 shows the along-transect temperatures for May and September, although timing of the transect does vary between years within these months (see Table 1 for dates) and the 2014 and 2015 September transects were actually during the last few days of August.
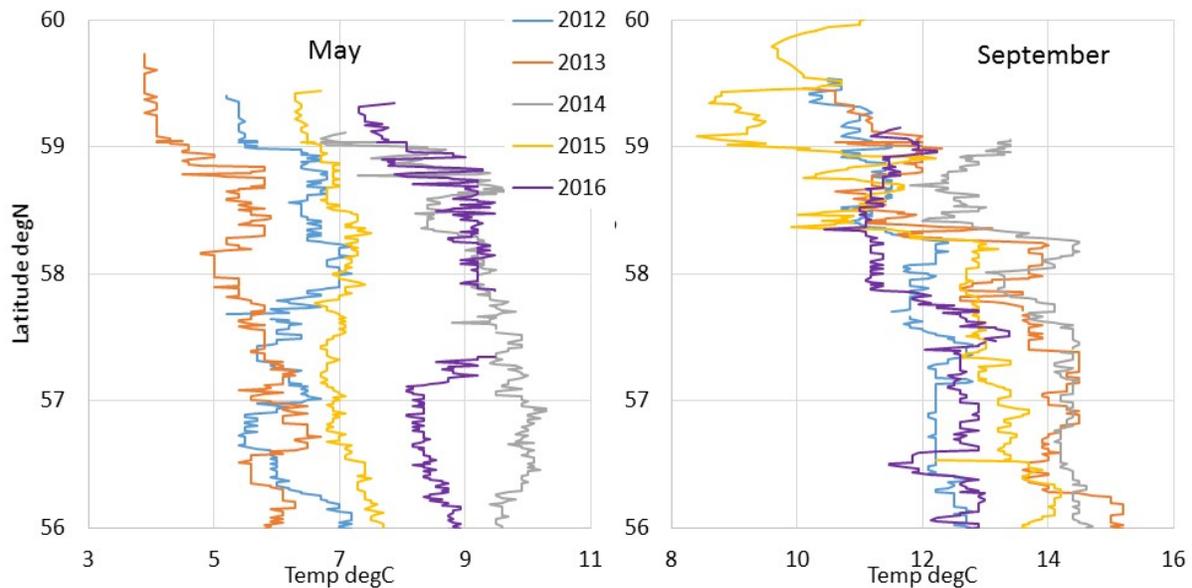
Figure 2. Along-transect temperature from loggers on the CPR for May (left) and September (right). The ship crosses the shelf break at about 58°N. Note that 2014 and 2015 September data were actually from 29-31 August.

These data show that there was a considerable range of temperatures in spring during the five years, with May of 2014 and 2016 being especially warm and May 2013 being coldest on the shelf, though similar to 2012 in the oceanic Gulf of Alaska. September temperatures show less extreme interannual variability with the warmest years being 2013 and 2014. This emphasizes the dramatic impact of "the Blob," which appeared in late summer 2013; spring 2013 was one of the coolest of the last 5 years but September was one of the warmest.

**Time series results**

Four summary plankton variables are shown in Fig. 3, for the shelf region in Fig. 1: total diatom abundance (an index of the large diatoms captured by the CPR), total mesozooplankton abundance (an index of the number of zooplankton organisms in the size range ~200 μm to ~1 cm), total mesozooplankton biomass (total dry weight, estimated from taxon-specific values and the abundance of each taxon), and average copepod community size (a community composition index, based on the adult female length of each copepod taxon recorded). The monthly mean data from 2012-2016 are superimposed on the mean time series values for all data collected from 2004-2015 (2016 data are provisional at this time). These indices are also contributed each year to the NOAA Ecosystem Considerations report and the Fisheries and Oceans Canada State of the Pacific Ocean report.

The long-term averages show that there are typically two peaks in diatoms each year, in spring and autumn, with spring abundances higher than the autumn peak. Mesozooplankton abundance and biomass have similar seasonal patterns being highest in spring and declining through summer and autumn; however the decline in biomass is

steeper than the decline in abundance. As the copepod community size index shows, spring is dominated by large copepods, which have a high individual biomass. Summer and autumn see smaller species dominating (many of the large species enter a dormant overwintering phase at depth by summer and disappear from surface waters); thus, while there are still numerous organisms present in summer (sometime more than in spring), overall biomass is much less than in spring. Further data analysis that places these 5 years of sampling into longer-term context and explores the interannual relationships between plankton and physical variables has been undertaken and published in the combined Gulf Watch Alaska and Herring Research and Monitoring special issue of Deep Sea Research II (Batten et al. 2018).
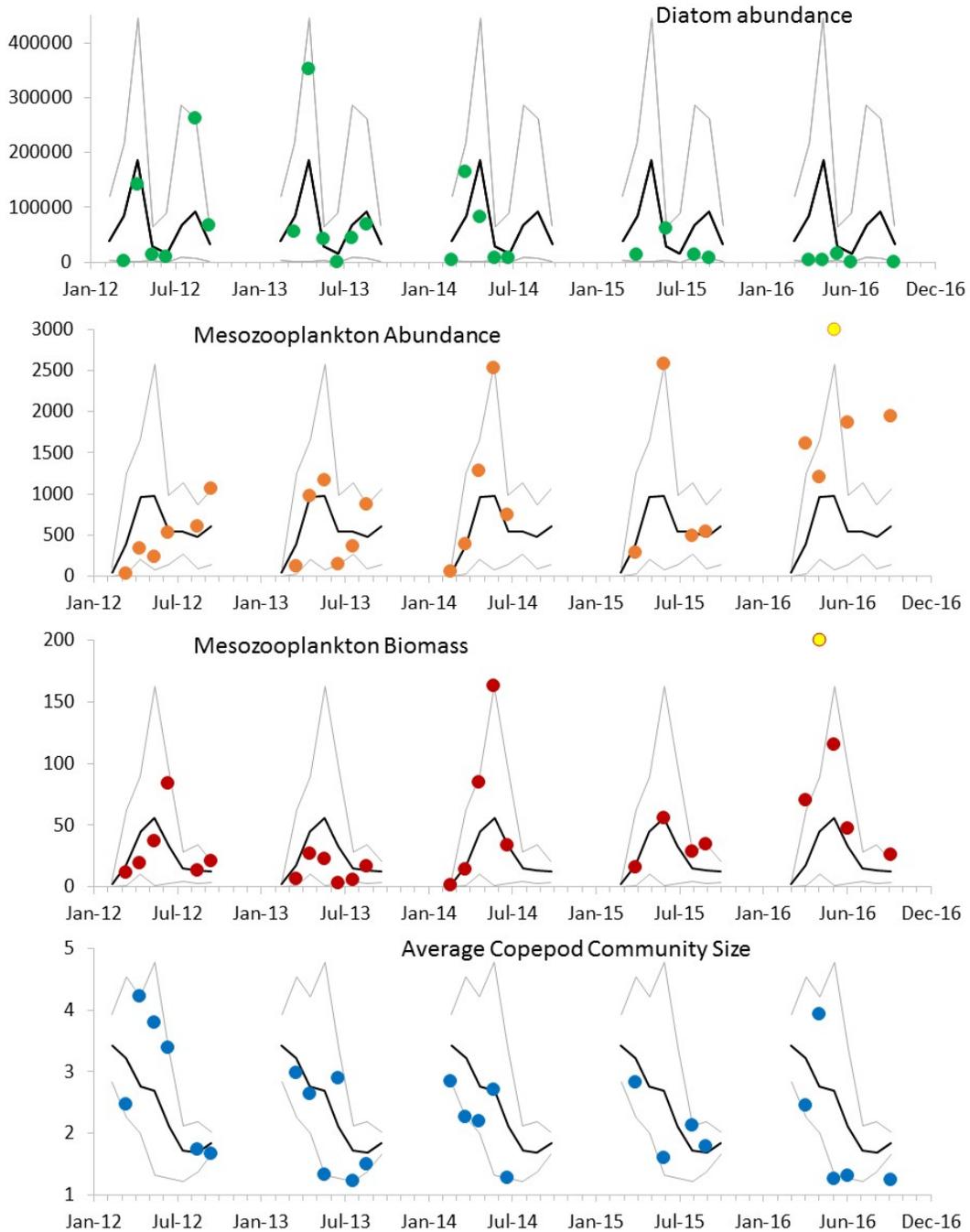
Figure 3. Monthly mean values (dots) per sample for all shelf samples, 2012-2016 for 4 plankton indices; Abundance = number organisms per sample, Biomass = mg dry weight per sample, Size = mm. Black line is the monthly mean, 2004-2015 and thin grey lines are the monthly minimum and maximum 2004-2015, in each case. 2016 data are provisional and the yellow points indicate values that are currently larger than the y-axis maximum. See text for details on indices.

Most copepods in CPR samples are identified to species, certainly to genus, and so changes in the abundance of specific taxa can be indicative of changing oceanographic conditions. Given that anomalous warmth was a strong feature of the last part of the sampling period, we have further examined copepod taxa that tend to have a more southerly distribution, i.e., occur in warmer water. Mean annual abundances are shown in Fig. 4 for 1) the large copepod *Calanus pacificus* (copepodites CV-CVI), which, while ubiquitous in the North Pacific, is associated with warm water, and 2) a suite of 4 rarer taxa that tend to occur on the Alaskan shelf only in warm conditions (*Mesocalanus tenuicornis, Corycaeus* spp., *Clausocalanus* spp. and *Acartia danae*). Abundances of both indicators were higher in 2014-2016, second only to 2005, which was also a warm year (Fig. 4).
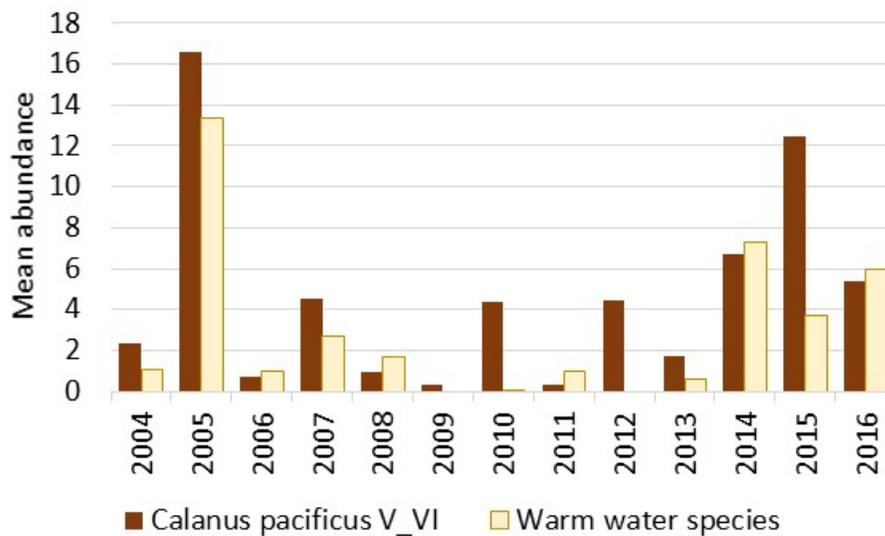


Figure 4. Annual mean sample abundances for copepods that indicate warm conditions; *C. pacificus* (dark bars, copepodite stages V-VI) and a suite of 4 southern species (light bars, see text for species names). 2016 data are provisional.

## DISCUSSION

The five years of sampling described here ended during a period of unusually warm conditions across much of the Northeast Pacific. First noted late in 2013 (Fig. 2), the warmth persisted through 2014 (Bond et al. 2015) and was then succeeded by a strong El Niño in 2015, and the event has now been termed a "marine heat wave" (Di Lorenzo and Mantua 2016). CPR data shown in Figs. 3 and 4 suggest that the plankton was impacted by these unusual conditions; diatom abundances were low, particularly in 2015 and 2016, mesozooplankton abundance showed the highest recorded values of the time series in the summers of 2014, 2015 and 2016, but average copepod size was small during these warm

years and warm water species were more abundant than usual. An earlier period of warm conditions occurred in the mid-2000s when CPRs also sampled the region, allowing an opportunity to compare results with this most recent event.

Total mesozooplankton biomass on the Alaskan shelf was strongly positively correlated with diatom abundance between 2000-2013 (Batten et al. Appendix 1) so that the warm years of 2003 and 2005 had high diatom abundances and high zooplankton biomass while the reverse was true in the cold year 2008. However, in the warm years of 2014 and 2015 (and likely 2016 when data are finalized) diatoms were unexpectedly low but these two years had the highest numbers of small copepods recorded in the time series. These copepods were also biased earlier in the year than average. It is possible that the data for these two years show top-down control of the large diatoms by copepod grazing pressure, which was not seen in other warm years with high diatoms and high zooplankton abundance/biomass such as 2005.  This could be because of a difference in the diatoms and/or zooplankton species present. An alternative explanation is that the unusual "heat-wave" conditions caused an unfavourable nutrient regime, which reduced the productivity of large diatoms. The taxa recorded by the CPR in spring 2014 and 2015 did show a bias towards diatoms with longer, narrow cells (e.g., *Proboscia* spp., *Thalassiothrix* spp., and pennate species). Only 2004 had a higher proportion of such cells and spring community composition analyses also show 2004 and 2014 as very similar (Batten et al. Appendix 1). In 2015 there were again low diatoms overall and high numbers of copepods still. Cells with this narrow morphology have a high surface area to volume (SA:Vol) ratio that would facilitate the uptake of nutrients; studies have shown that smaller cells that also have a higher SA:Vol take up nutrients faster (Friebele et al. 1978, Geider et al. 1986). If nutrients were scarce these high SA:Vol cells would have an advantage over the rounder cell types. Stratification indices from the Seward Line sampling suggest only moderate stratification in 2014-2016 (Batten et al. Appendix 1). Nutrient data from the Seward Line (Hopcroft et al. 2018) are only available from May and September and are very sensitive to timing of the spring and autumn blooms. However, they also found reduced chlorophyll levels and smaller cells in May of the warm years.

It is also clear, however, that the high numbers of copepods in 2014-2016 must have been eating something - if not the large diatoms then perhaps some part of the plankton community not well resolved by the CPR. There will also likely be impacts on other parts of the ecosystem whether large diatoms were low because of unfavourable nutrient conditions or grazed by the zooplankton. Batten et al. (2016) showed that the first year growth of Prince William Sound herring was greater in years with higher abundances of smaller sized plankton, particularly the large diatoms ($r^2$=0.76, p=0.0005). If this strong correlation between first year herring growth and diatom abundance from 2000-2009 (growth is measured from scales of 4-6 year old fish, see EVOSTC Project 13120111-N for further details) so growth measurements from fish hatched in 2010 and later are not yet available) is applied to the diatom abundances recorded here in Fig. 2, then 2015 should have the lowest growth of all years in the 30-year time series of herring growth measurements dating back to 1979, and 2014 would be the 4th lowest. While first-year growth is only one factor in the success of PWS herring stocks, it is likely that the unusual

oceanographic conditions, which subsequently altered the plankton communities, would have some impact.

It is also worth noting that the "heat wave" has persisted from late in 2013 through 2016 and may continue into the next phase of the project beginning in 2017. Fig. 3 shows that for three consecutive years, small zooplankton were numerous and large diatoms were low, and Fig. 4 shows that warm water species were high in numbers. Persistence of these values for this length of time is also unprecedented in the current 17-year time series. Whether or not, and how rapidly, the plankton could return to more typical communities remains to be seen.

## CONCLUSIONS

The last years of the project sampled plankton during unusual, and persistent, warm conditions resulting in plankton communities on the shelf that were biased towards smaller zooplankton. Large diatoms were also low during this warm period, possibly due to increased grazing or reduced nutrient conditions. Warm water copepods were more numerous than average. The plankton communities were thus different (and for an extended period of time) from those sampled in other years, even warm years, since 2000. We speculate that first year growth in juvenile herring may be poor in 2014-2016 but this can be examined only after the scale growth data become available.

## ACKNOWLEDGEMENTS

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# Interannual variability in lower trophic levels on the Alaskan Shelf

Sonia D. Batten[a,*], Dionysios E. Raitsos[b], Seth Danielson[c], Russell Hopcroft[c], Kenneth Coyle[c], Abigail McQuatters-Gollop[d]

[a] Sir Alister Hardy Foundation for Ocean Science, c/o 4737 Vista View Cr, Nanaimo, BC, Canada V9V 1N8
[b] Plymouth Marine Laboratory, Prospect Place, The Hoe, Plymouth PL1 3DH, United Kingdom
[c] Institute of Marine Science, University of Alaska Fairbanks, 120 O'Neill, P.O. Box 757220, Fairbanks, AK 99775-7220, USA
[d] Centre for Marine and Conservation Policy, Plymouth University, Drake Circus, Plymouth PL4 8AA, United Kingdom

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## ABSTRACT

This study describes results from the first 16 years of the Continuous Plankton Recorder (CPR) program that has sampled the lower trophic levels (restricted to larger, hard-shelled phytoplankton and robust zooplankton taxa) on the Alaskan shelf. Sampling took place along transects from the open ocean across the shelf (to the entrance to Prince William Sound from 2000 to 2003 and into Cook Inlet from 2004 to 2015) to provide plankton abundance data, spring through autumn of each year. We document interannual variability in concentration and composition of the plankton community of the region over this time period. At least in part and through correlative relationships, this can be attributed to changes in the physical environment, particularly direct and indirect effects of temperature. For example; spring mixed layer depth is shown to influence the timing of the spring diatom peak and warmer years are biased towards smaller copepod species. A significant positive relationship between temperature, diatom abundance and zooplankton biomass existed from 2000 to 2013 but was not present in the warm years of 2014 and 2015. These results suggest that anomalous warming events, such as the "heat wave" of 2014–2015, could fundamentally influence typical lower trophic level patterns, possibly altering trophic interactions.

## 1. Introduction

The south Alaskan Shelf region that encompasses the large inlets of Cook Inlet (CI) and Prince William Sound (PWS) and the outer shelf of the northern Gulf of Alaska is a productive, dynamic, subarctic shelf system supporting numerous valued marine resources such as commercially-harvestable fish (e.g. herring, salmon, groundfish), large marine mammals (e.g. belugas, humpback whales), and seabirds. Lower trophic level productivity underpins this ecosystem but our understanding of plankton variability in this region is still somewhat limited.

It is recognized now that forcing of marine ecosystems occurs at multiple temporal and spatial scales. It is challenging to attempt to understand the impacts of climate change on marine organisms and detect trends in data when there is high interannual variability in both the physical forcing and biological responses. For example, restoration projects for injured resources following the Exxon Valdez oil spill in PWS in 1989 have struggled with teasing apart the impacts of this one-off catastrophic event from naturally-induced variability (EVOS Trustee Council, 2010). Natural, rather than human-related, processes known to influence this region are numerous. For example, on seasonal and

interannual time scales the strength of the Alaskan shelf and Alaskan Coastal currents are mediated by freshwater run-off and winds (Royer, 1979; Stabeno et al., 2004; Weingartner et al., 2005), persistent coastal downwelling in contrast to most eastern Pacific boundary regions, and eddy-mediated cross-shelf transport of organisms and nutrients (Okkonen et al., 2003; Ladd et al., 2005). More quasi-decadal time scale influences are the change in sign of the Pacific Decadal Oscillation (PDO), which is based on the analysis of Mantua et al. (1997) and is the first mode of ocean surface temperature variability in the North Pacific Ocean. Historically it has been a good indicator of weather patterns that persist for a decade or more but has more recently been switching state approximately every 5 years. Positive (negative) PDO values are associated with warmer (cooler) than normal conditions in the NE Pacific. A second medium time-scale influence is the North Pacific Gyre Oscillation (NPGO), a climate pattern that emerges as the second dominant mode of sea surface height variability in the Northeast Pacific Ocean (Di Lorenzo et al., 2008, http://www.o3d.org/npgo/). When the NPGO index is positive the westerly winds over the eastern North Pacific are often stronger than normal, influencing the circulation processes. Moderate to strong El Niño and La Niña events are also evident on the

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Alaskan Shelf (Weingartner et al., 2002). Regime shifts, which may be triggered by the climate processes described above, have periodically occurred with lower frequency, such as the 1976 shift which changed Alaskan fisheries from shrimp to fish dominated (Francis and Hare, 1994). More recently, anomalous warming across a wide expanse of the Northeast Pacific occurred late in 2013 and persisted through 2014 (Bond et al., 2015). Nicknamed "the Blob" and succeeded by a strong El Nino in 2015, the Alaskan shelf has been influenced by these strong warming events for at least two consecutive years (DiLorenzo and Mantua, 2016).

With short generation times, limited mobility and lack of a commercial harvest, plankton often respond to changes in their environment more rapidly and less ambiguously than higher trophic levels, so that a relatively short time series of plankton information can provide insights into the responses of the shelf ecosystem to some of the processes described above. Primary productivity is strongly seasonal in this region, owing primarily to the relatively high latitude and low light levels in winter. Mueter et al. (2009) report that although there are clear peaks in satellite-derived chlorophyll-$a$ levels in spring and autumn (owing to the spring bloom and replenishment of nutrients by autumn storms respectively) there is in fact a single broad peak of productivity in the Gulf of Alaska through summer that is heavily grazed by zooplankton and so results in low phytoplankton standing stocks in summer. There has been significant interannual variability in chlorophyll-$a$ concentrations over the previous decade and more, with positive anomalies in years with reduced cloud cover, lower SST and reduced downwelling-favourable winds (Waite and Mueter, 2013). These observations do not necessarily represent variability in primary productivity but may suggest that strong cyclonic circulation does not favour high chlorophyll-$a$ concentrations throughout the Gulf of Alaska.

Previous studies of zooplankton on the shelf (Coyle and Pinchuk, 2003) and in PWS (Cooney et al., 2001) suggest a strong seasonal community dominated by copepods (with significant contributions from other taxa such as cnidarians on the shelf, euphausiids, pteropods and larvaceans seasonally in PWS). While small-medium sized copepod species dominated in terms of abundance at all times of year, the biomass in spring and early summer was dominated by larger copepods that spend the winter in diapause at depth. Negative salinity anomalies, followed by temperature, were the strongest influencers of the zooplankton community (Coyle and Pinchuk, 2003).

The Continuous Plankton Recorder (CPR) was designed to be towed behind commercial ships and to sample plankton from near surface waters over large spatial scales (Batten et al., 2003a). This study describes results from the first 16 years of the Continuous Plankton Recorder (CPR) program that has sampled the lower trophic levels of the south-central Alaska Shelf, on a seasonal basis from spring to autumn. Although restricted to larger, hard-shelled phytoplankton and robust zooplankton taxa, this dataset is complementary to previous studies which have been more geographically focussed but with reduced temporal coverage. The CPR data are now sufficient to examine the interannual variability of the plankton populations with respect to changing oceanographic conditions of the region.

## 2. Methods

### 2.1. Sampling

The CPR was towed behind a volunteer commercial vessel making the sampling cost-effective, but with limited ability to control the timing of the sampling and no ability to determine the transect position. The original transect operated from 2000 between ports in California, USA and PWS, with sampling normally stopping at Hinchinbrook Entrance. Owing to changes in shipping activities the transect was changed in 2004 to a route from the mouth of Juan de Fuca Strait (at the border of British Columbia, Canada, and Washington State, USA) to Anchorage, with sampling normally stopping in CI between about 59-
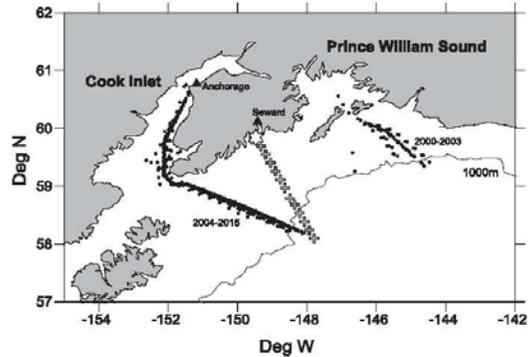


Fig. 1. Location of CPR samples and years when each transect was sampled (see Table 1 for data availability in each year). The midpoint of each 18.5 km CPR sample used in this study is shown as a dot. Note the consistency of the Cook Inlet transect; there are over 50 separate monthly transects but they overlap almost entirely. Two other data sources used in the study are shown; Seward Line sampling stations are shown as "+" and the GAK1 station as a star.

60°N (Fig. 1). Start and end of sampling was always at the discretion of the vessel's Captain. The second transect was remarkably consistent with almost identical transect positions each month, particularly at the northern end with which this study is concerned. Frequency of sampling was at approximately monthly intervals in most years (occasionally two transects occurred in one calendar month), commencing in about April and ending in about September, but occasionally sampling March and October (Table 1). Mechanical failures, human error and marine debris mean that in any one year, one or two months may have reduced, or no, data available. In summary, while the available data have gaps, they represent a sufficiently lengthy and spatially expansive time series of seasonal data with which to examine lower trophic level variability in this region.

A summary is given here but for a full description of the CPR instrument and sampling protocols see Batten et al. (2003a) and see Richardson et al. (2006) for data analysis methods.

The CPR was towed in the wake of the ship at a depth of about 7 m. Water and plankton enter the front of the CPR through a small square aperture (sides of 1.27 cm), pass along a tunnel, and then through the silk filtering mesh (with a mesh size of 270 μm) which retains the plankton and allows the water to exit at the back of the machine. The movement of the CPR through the water turns an external propeller which, via a drive shaft and gear-box, moves the filtering mesh across the tunnel at a rate of approximately 10 cm per 18.5 km of tow. As the

Table 1
Months for which data were available in each year.

| Transect | Year | Mar | Apr | May | Jun | Jul | Aug | Sep | Oct |
|---|---|---|---|---|---|---|---|---|---|
| PWS | 2000 | X | X | | | X | X | | |
| PWS | 2001 | | X | X | X | | | X | |
| PWS | 2002 | | X | | | X | | | X |
| PWS | 2003 | | | X | | | X | | |
| Cook Inlet | 2004 | X | X | | X | X | X | | |
| Cook Inlet | 2005 | | X | X | | X | X | | |
| Cook Inlet | 2006 | X | X | | | X | X | X | X |
| Cook Inlet | 2007 | | X | | X | | X | X | |
| Cook Inlet | 2008 | | | | X | | X | | |
| Cook Inlet | 2009 | | X | X | X | | X | | |
| Cook Inlet | 2010 | | X | | | X | | X | |
| Cook Inlet | 2011 | | X | X | | X | X | X | |
| Cook Inlet | 2012 | | X | X | X | X | | X | X |
| Cook Inlet | 2013 | | X | X | X | X | X | X | |
| Cook Inlet | 2014 | X | X | X | X | X | X | | |
| Cook Inlet | 2015 | | X | | X | | X | X | |

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filtering mesh leaves the tunnel it is covered by a second band of mesh so that the plankton are sandwiched between these two layers. This mesh and plankton sandwich is then wound into a storage chamber containing buffered 40% formaldehyde preservative (which dilutes in the seawater to a concentration of about 4%, sufficient to fix and preserve the plankton). After each transect the CPR was transferred to a laboratory, where the samples were unloaded. The towed mesh was processed according to standard CPR protocols; first cut into separate samples (each representing 18.5 km of tow and about 3 m³ of seawater filtered) which were randomly apportioned amongst the analysts for plankton identification and counting. Every fourth oceanic sample was distributed for analysis with the remainder being archived, but over the Alaskan shelf consecutive samples were processed. The ship's log was used to determine the mid-point latitude and longitude of each sample (shown in Fig. 1), along with the date and time.

## 2.2. Taxonomic analysis

As with all plankton samplers the CPR has biases. The mesh size is 270 μm and so organisms with dimensions smaller than this may not be quantitatively sampled, however, the effective mesh size may be much smaller depending on the abundance and morphology of plankton that are caught (see Batten et al., 2003a for more details) and organisms such as coccolithophores with a diameter of a few tens of microns are caught and identified. The formaldehyde preservative used in the instrument does not fix naked dinoflagellates or ciliates so these groups are not at all represented in the database. The sampling method can also result in damage to the organisms so fragile groups, especially gelatinous plankton, may only be identifiable to a coarse level.

There were four steps in analysing the plankton retained in a CPR sample. The first step was the assessment of phytoplankton colour (the greenness of the sample, or Phytoplankton Colour Index, PCI), which was determined by comparison with standard colour charts. This is a semi-quantitative representation of the total phytoplankton biomass and includes the organisms that are too fragile to survive the sampling process intact but which leave a stain on the mesh (Batten et al., 2003b; Raitsos et al., 2013). Hard-shelled phytoplankton were then semi-quantitatively counted under a purpose-built microscope by viewing 20 fields of view (diameter 295 μm) across each sample under high magnification (× 450) and recording the presence of all the taxa in each field (presence in 20 fields is assumed to reflect a more abundant organism than presence in 2 fields for example). Small zooplankton were then identified and counted from a sub-sample by tracking across the filtering mesh with the microscope objective (a 2 mm diameter field of view = 2% of the sample width) whilst all zooplankton larger than about 2 mm were removed from the mesh and counted, usually without sub-sampling. Identification in all cases was carried out to the most detailed practicable taxonomic level and was a compromise between speed of analysis and scientific interest. For example, since copepods make up the majority of the zooplankton and remain mostly intact after sampling, most copepods were identified to species level whilst rarer groups, or those not preserved well by the sampling mechanism (such as chaetognaths), were identified to a lower level such as phylum. A list of taxa and their abundance in each sample was thus generated, and from this summary indices (such as estimated zooplankton biomass, total diatom abundance, etc.) were also calculated.

## 2.3. Comparison of CPR Phytoplankton indices and satellite data

To compare the in situ phytoplankton seasonal cycles (PCI and diatoms from the CPR data) with a satellite-derived ocean colour dataset, the monthly near-surface Chlorophyll-a (Chl-a) was acquired from NASA's Oceancolor website (http://oceancolor.gsfc.nasa.gov). The Moderate-resolution Imaging Spectroradiometer (MODIS on-board the Aqua platform) 4 km resolution Chl-a data were processed for the period 2003–2011 (O'Reilly et al., 2000). Standard NASA algorithms

were used for Chl-a (OC3) estimates; these are routinely processed by the Ocean Biology Processing Group at the Goddard Space Flight Centre (Feldman and McClain, 2012). Using the monthly mean datasets, we constructed the area-averaged monthly climatologies.

Remotely sensed Chl-a data have known limitations especially in coastal, optically complex, Case II waters where suspended sediments, particulate matter and/or dissolved organic matter do not covary in a predictable manner with Chl-a (IOCCG, 2000). For example, scattering by sediments in turbid waters and underwater reflectance from shallow shelf regions may result in relatively high water-leaving radiance in the near-infrared (NIR) wavelengths, which could overestimate the correction term. For this reason satellite data from CI were excluded. Even so, the Chl-a data used in the analysis may be influenced (generally resulting in an overestimation) by the factors mentioned above, especially in the most coastal waters and/or very shallow waters of the Alaskan Shelf area. However, the scope of the current study is to compare the general variability of satellite-derived Chl-a and CPR phytoplankton in the Alaskan Shelf, regardless of absolute concentrations. In addition, to gain confidence on the variability and pattern of satellite derived Chl-a, we also compared the MODIS results with those from SeaWiFS. The area-averaged monthly means, and the seasonal climatologies of the two satellite-derived Chl-a datasets were significantly correlated ($r^2$ = 0.78, p < 0.0001, and $r^2$ = 0.98, p < 0.0001 respectively).

## 2.4. Analysis of CPR plankton time series

All shelf samples were extracted from the database. These samples were south of PWS 2000–2003, and in CI and southeast of it 2004–2015 owing to the change in transect position.

### 2.4.1. Abundance and seasonal timing

The mean abundance per sampling event (monthly transects) was calculated for the entire shelf region for various taxonomic groupings (e.g., total mesozooplankton, large copepod abundance, large diatom abundance, dinoflagellates, etc). Mean seasonal cycles were calculated by averaging the monthly averages for each month of the year (restricted to March to October). Seasonal timing and annual abundance indices were calculated using a method proposed by Grieve et al. (2005) that relies on cumulative integration. In this case we integrated between day 60 and day 300 each year (assuming 0 abundance on days 60 and 300), and summed daily values to give a cumulative total for the year. All years had 5–6 samplings, spaced at least monthly, except 2003, 2008 and 2010 so these years should be treated with caution if data are shown. The day of the year when 50% of the cumulative abundance occurred was calculated (this is the mid-season, as an index of timing). An annual abundance anomaly (Log10, based on the geometric mean of all years) was calculated for each year for the cumulative integrated biomass/abundance at day 300.

### 2.4.2. Community composition

The same samples as described above were used but individual taxon abundances were extracted to examine interannual variability in the taxa present. Data were divided into spring (April, May and June) and late summer/autumn (August and September). Phytoplankton and mesozooplankton were treated separately (microzooplankton were excluded). The mean annual abundance of each taxon in each group (phyto or zooplankton, spring or autumn) was calculated and then the data were transformed (Log{x + 1}) to reduce the impact of dominant taxa. Bray Curtis dissimilarities were calculated for each pair of years, and then NMDS (in the SYSTAT software package) used to display the ordinations in 2 dimensions.

### 2.4.3. Copepod community length

Size of its members is an important zooplankton community attribute, likely governing trophic interactions. Change in size can only be

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accurately determined for the copepods captured by the CPR as they are the only important and dominant group identified mostly as species. The methodology of Richardson et al. (2006) was applied to the copepod counts. Mean copepod community size ($\overline{S}$) for each sample was calculated:

$$\overline{S} = \frac{\sum_{i=1}^{N}(L_i \cdot X_i)}{\sum_{i=1}^{N} X_i}$$

Where $L$ is the mid-range adult female total length (mm) per species (i) obtained from Chihara and Murano (1997) and when not available, from Razouls et al. (2012), and X is its abundance.

Monthly means were calculated for the five warmest (2001, 2003, 2005, 2014 and 2015) and five coldest years (2002, 2007, 2008, 2009 and 2012), based on the GAK1 dataset.

### 2.4.4. Physical data

In order to explain the patterns within the plankton data, time series of physical variables were used. Temperature observations were available from the GAK1 dataset (location shown on Fig. 1), available at http://www.ims.uaf.edu/gak1/, which was the geographically closest source to the CPR data of seasonally resolved in situ temperature. Monthly measurements have been made at GAK 1 from 1970 to present from surface to depth. For this study, a mean of the four upper-most water column measurements was calculated (0, 10, 20, and 30 m) from each month to represent water temperatures that most of the planktonic organisms would have experienced. Where a month was not sampled in a particular year, the long term mean for that month was used instead to create an unbroken time series of March to October values.

Some in situ temperature measurements were also available from a logger on the CPR itself from 2000 to 2002 and 2011–2015. For each transect where a logger was fitted, temperature was recorded every 5 min (15 min in 2000 to 2002) for the duration of the tow. Data collected between 59°N and 60°N (2000–2002) or 57.5°N to 59°N (2011 onwards) were averaged to represent temperature on the shelf at the depth of the CPR each sampled month.

The CPR transect into Cook Inlet intersects with the outermost stations of the Seward Line (Fig. 1). The mixed layer depth (MLD), an index of stratification (Potential Energy) and salinity measurements were available from the Seward Line cruises in May of each year to provide spring water column characteristics (the Seward Line is only sampled in May and September/October so May was selected as best describing the conditions which might influence the plankton through spring and summer when most of the CPR sampling occurred). A CTD was deployed at each station and the MLD computed as the depth at which the density is greater than 0.03 kg m$^{-3}$ at 5 m depth. The stratification parameter, the potential energy required to redistribute the water-column mass by complete vertical mixing (J/m$^3$), was also computed (Simpson et al., 1977). The thermocline is not necessarily fully established by the time of the May cruise leading to variability along the line. We therefore averaged the values for all stations to provide the best index of spring water column stability. Salinity data (from all depths) were also available from all stations along the Seward Line.

## 3. Results

### 3.1. The physical environment

Physical data (SST, salinity, Potential Energy and Mixed Layer Depth) are shown in Fig. 2. The early part of the time series was relatively cool and then temperatures increased from 2003 to 2005. Another cool period followed, with 2008 being the coldest year of the record, before temperatures rose in 2014 as the influence of the anomalous off-shore warming became apparent. The time series ends with warm conditions resulting from the 2014 anomaly and the 2015 El

Niño. Salinities on the Seward Line stations in May each year were freshest in 2004 and 2015 (warm years, so likely some influence of early, or increased, snow melt) and most saline in 2000 and 2013 but note that outer stations were not sampled in 2008 (the coldest year). Water column stability indices show that in the earlier warm period of 2004–05 the MLD was shallow and the energy required to mix the water column was large (high Potential Energy), indicating stronger stratification. While the colder period was missing data from 2008, 2007 showed a deeper MLD and lower Potential Energy, suggesting weaker stratification. In the more recent warm period of 2014 and 2015 the MLD was shallow in 2014 but deeper in 2015 and the Potential Energy was quite low in both years, suggesting quite weak stratification.

### 3.2. Abundance and seasonal timing

#### 3.2.1. Phytoplankton

The phytoplankton counts from the CPR are not representative of the whole phytoplankton community, with a large mesh compared to most of the cells, and a preservative unsuitable for athecate cells; however, it is an internally consistent time series and larger and more robust phytoplankton are captured well. A comparison with satellite-derived chlorophyll-$a$ data demonstrates that CPR phytoplankton data generate realistic seasonal cycles (Fig. 3). The CPR PCI values peak on average one month earlier than the satellite measurements of chlorophyll-$a$ in both the spring and autumn peaks, but the diatom abundances match the satellite-derived seasonal cycle very closely. The general pattern shows two diatom blooms; in spring and a lesser peak in late summer/autumn. This is typical of a shelf system where autumnal storms may increase mixing, bringing up nutrients and allowing a second phytoplankton bloom while light levels are sufficient. Thecate dinoflagellates are most abundant only in the summer and autumn when waters are warmer. The PCI index closely follows the diatom cycle, but increases earlier (as evident in Fig. 3 when compared with the satellite chlorophyll data). The difference between spring and autumn PCI is less than the difference between spring and autumn diatoms, perhaps because the index also incorporates a signal from the dinoflagellates.

Annual abundance anomalies of diatoms (calculated as previously described for March to October) are shown in Fig. 4. During the first 14 years of the time series it was noted that there was a moderate, positive, significant correlation between diatom abundance and temperature (r$^2$ = 0.28, p < 0.05 with either the annual mean GAK 1 temperature, or with the annual mean PDO index) with warm, PDO positive years having greater numbers of diatoms (Fig. 4). However, 2014 and 2015 did not follow this pattern and abundances were low, despite the very warm conditions. Numbers were also low in 2011 which was neither a warm nor cold year.

Thecate dinoflagellates are numerically much less dominant than diatoms in CPR samples, ranging from between one third and one sixtieth of the diatom abundance. There were no significant relationships between the dinoflagellate mean annual abundance anomalies and physical variables, however, the linear decline through time is significant (r$^2$ = 0.23, p < 0.05). This could be because of a regional difference as the region south of PWS, sampled only in 2000–2003, had consistently higher abundances of dinoflagellates than the Cook Inlet and nearby shelf region sampled from 2004 and afterwards, however, since the two regions were not sampled simultaneously we cannot be certain. From 2004 onwards the pattern shows inter-annual variability with no trend.

Although the CPR sampling resolution is not sufficient to identify the exact timing of the spring phytoplankton bloom, we focused on just the spring diatom data, integrating abundances between days 60 and 180 (as described previously for the whole season) and taking the day of the year where 75% of the spring diatom abundance was reached as an index of spring timing (years 2002, 2003, 2008 and 2010 were not

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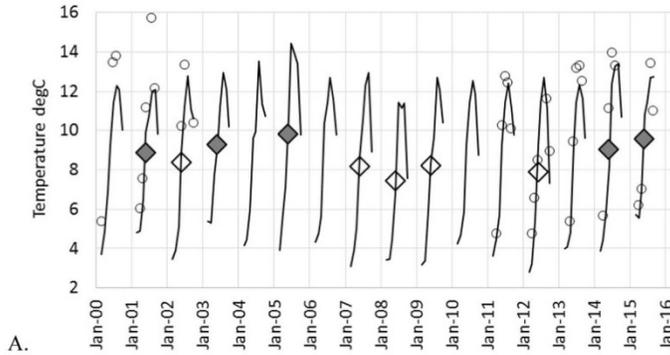
Fig. 2. Physical variables. Panel A. Mean monthly (Mar-Oct) SST from the GAK1 station (lines) and mean monthly in situ SST from loggers on the CPR (○). Filled diamonds indicate the mean annual (March-October) temperature for the 5 warmest years, unfilled diamonds indicate the mean for the 5 coldest years. Panel B. Salinity Data from May cruises on the Seward Line (error bars show st. dev.) Panel C. Water column stability shown by: solid line – mean Mixed Layer Depth, dashed line – mean Potential Energy.
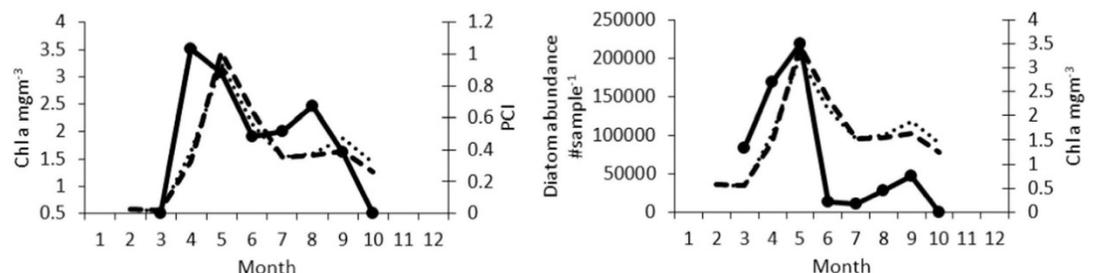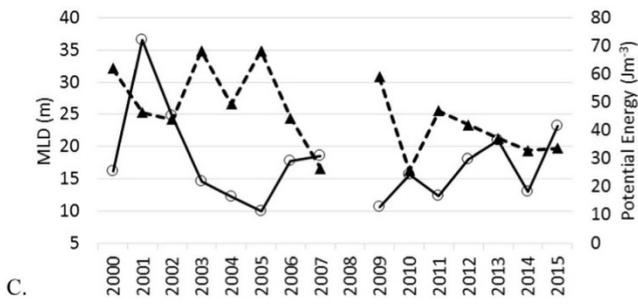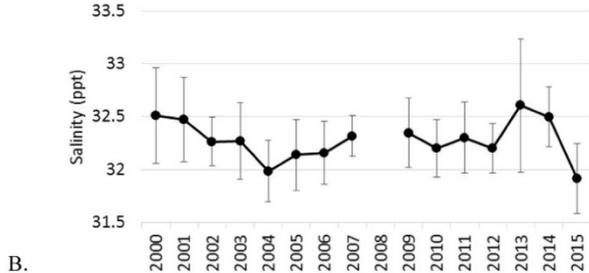


Fig. 3. Mean monthly phytoplankton indices from CPR data (solid line, Phytoplankton Colour Index at left, diatom abundance at right) and satellite-derived chlorophyll-a (from MODIS, heavy dashed line and SeaWiFS, lighter dashed line on both graphs) for the region shown in Fig. 1, excluding Cook Inlet.
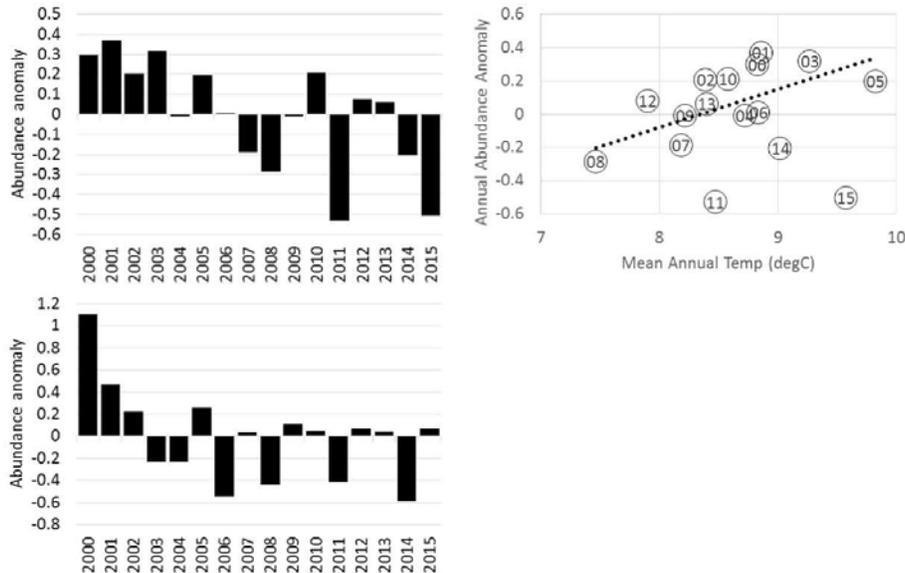
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Fig. 4. Annual abundance anomalies of diatoms (top left) and thecate dinoflagellates (bottom left). Right panel shows the relationship between diatom abundance and mean temperature (mean of March to October monthly GAK1 temperature). The dashed line indicates the relationship from 2000 to 2013 with year shown inside each data point.
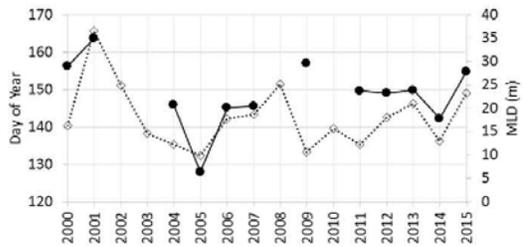


Fig. 5. Spring diatom timing (day of year when 75% of the integrated daily abundance at day 180 was reached) for years when sampling resolution was sufficient (solid line), together with the time-series of mean May MLD along the Seward Line (dashed line).

sampled sufficiently often in the spring to calculate this index). There was no significant correlation between spring timing and temperature as indexed by mean annual GAK 1 temperature or the PDO (although 2005 and 2014 did have the earliest dates and the modest relationship was negative), however, the Seward Line MLD correlated significantly with diatom timing (n = 11, $r^2$ = 0.39, p < 0.02), so that in years with a greater MLD in May the spring peak was later (Fig. 5). The correlation with potential energy of the water column was negative, but non-significant. There was also a significant correlation between diatom spring timing and the NPGO (p < 0.02) so that with a positive NPGO (stronger westerly winds are associated with positive NPGO further south and through the shelf edge currents influence MLD in this region), the diatom peak is later.

### 3.2.2. Zooplankton

Estimated mesozooplankton biomass is a summary index of the overall zooplankton community, and the anomaly time series is shown in Fig. 6, together with annual abundance anomalies of five of the dominant taxonomic groups (large copepods > 2 mm length, small copepods < 2 mm length, euphausiids, hyperiids, and pteropods). Also shown is an index of seasonal timing for each zooplankton variable, as

day of the year when 50% of the integrated daily biomass/abundance was reached. No long term trends are evident in the time series, with the exception of hyperiid abundance which has generally increased over the 15 year period. Between-year variability is large in all six cases.

There was a very strong positive correlation between the annual diatom abundance and zooplankton biomass anomalies from 2000 to 2013 ($r^2$ = 0.49, p < 0.005) so that years with a higher abundance of diatoms had a higher zooplankton biomass, suggesting a trophic link. This relationship was not present in 2014 and 2015 which had high zooplankton biomass but low diatom abundance. All of the five major zooplankton taxonomic groups had positive correlations between their abundance and diatom abundance until 2013, but none were individually significant. Similarly, there were positive correlations between most of the zooplankton groups and temperature, however, none were significant at the p < 0.05 level. Temperature does, however, have an effect on seasonal timing. The mid-point of the zooplankton biomass season is later in cold years. This is also true for small and large copepods. For small copepods this is a strong, negative relationship between seasonal timing and the PDO/temperature ($r^2$ = 0.5, p = 0.003 with the PDO), but less so for large copepods ($r^2$ = 0.2, p = 0.09) and for both groups the difference in timing between the earliest and latest years was more than two months. There were no significant relationships between euphausiids, hyperiids and pteropod seasonal timing and temperature. To summarise; years with higher diatom abundance had higher zooplankton biomass (at least until 2013), and in cold years the abundance of copepods was shifted later in the year.

### 3.3. Community composition

83 phytoplankton taxa were recorded during the time series and 89 mesozooplankton taxa (eggs and microplankton groups such as tintinnids and foraminifera were excluded). Table 2 shows the most abundant 30 taxa for phytoplankton and zooplankton in spring and in late summer. While many taxa are common to both seasons, their relative abundance does change (their position in the table) and contributes to

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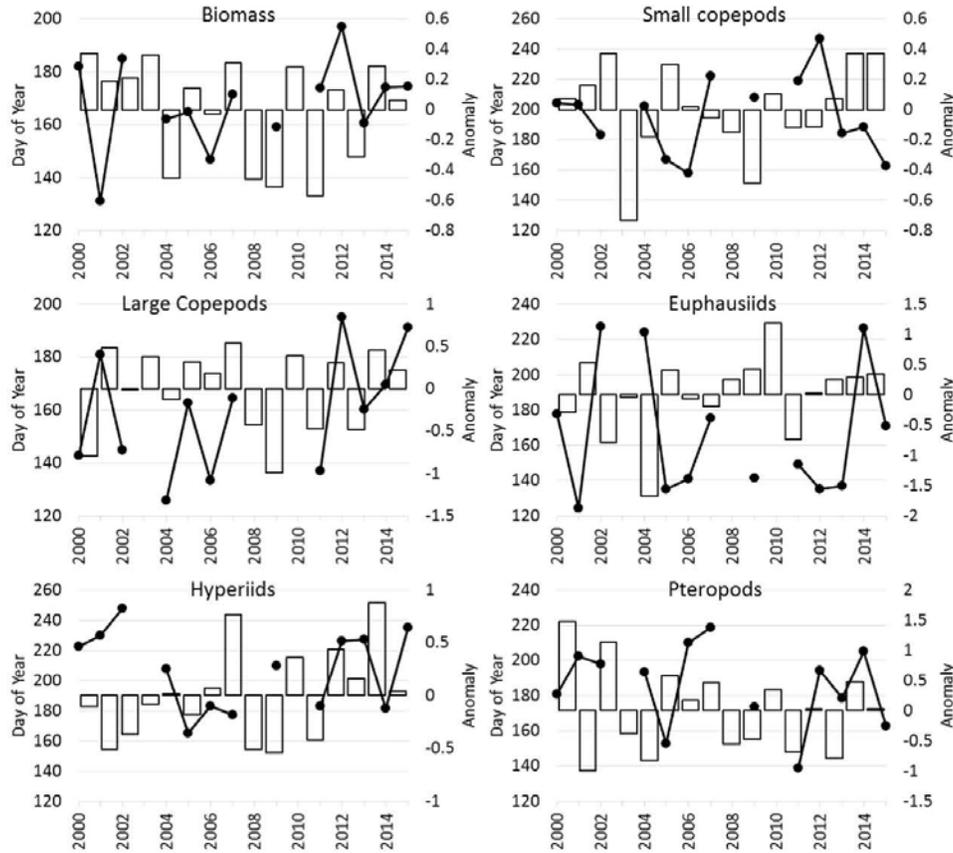
Fig. 6. Annual anomalies of zooplankton groups (bars) and seasonal timing (lines with dots). Top left panel shows total mesozooplankton biomass (estimated from taxonomic abundance data, see methods). Other five panels show abundance anomalies for groups as indicated; large copepods (length > 2 mm), small copepods (length < 2 mm), euphausiids, hyperiids, and pteropods.

the community differences seen between seasons. Some taxa are only abundant in one season; for example, dinoflagellates of the genus *Ceratium* are more common in late summer and the large *Neocalanus* copepods are typically only found in surface waters in spring. The MDS plots (Figs. 7 and 8) are 2 dimensional representations of the similarity of the spring or late summer/autumn communities between years (using all the taxa), so that years with the most similar communities in each treatment plot closest together. Stress values were moderately low, being between 0.12 and 0.17 for all analyses indicating that a two dimensional representation was appropriate.

### 3.3.1. Phytoplankton

The MDS analyses in Fig. 7 show no strong division between the two time periods of sampling, first adjacent to PWS (2000–2003) and then Cook Inlet from 2004 onwards (e.g., in the spring analysis 2002 plots closer to 2008 and 2013 than it does to 2000 or 2001 and the autumn analysis is similarly mixed). This suggests a similar phytoplankton community across the wider southern Alaska shelf (at least as the CPR sees it), likely a result of the distribution of plankton along the shelf by the Alaska Coastal Current.

In the spring analysis there is one main cluster with 3 years somewhat more distant and therefore dis-similar to other years; 2005, 2007,

and 2015. The x-axis has little variability along it and the greater variability on the y-axis is likely related to temperature, with most of the warmer years plotting negatively on this axis. The exception is 2005, however, if this year is removed the relationship between temperature and the y-axis is significantly correlated ($r^2 = 0.40$, $p < 0.01$). 2015 is quite distinct; as well as having generally low numbers of diatoms overall (Fig. 4), there were several taxa found for the first time in the region in spring 2015 (e.g. *Dactyliosolen fragilissimus* and *Guinardia striata*) and some taxa commonly found in late summer but which occurred in spring 2015 for the first time (*Bacteriastrum* spp, *Ceratium tripos*).

In the late summer/autumn analysis 2010 and 2008 plot distantly from other years and account for the variability along the x-axis. The y-axis has years with higher numbers of dinoflagellates (such as *Ceratium* spp.) plotting positively, and this axis is also positively correlated with temperature ($p = 0.07$) and potential energy ($p = 0.06$). Dinoflagellates prefer warm, well-stratified conditions.

### 3.3.2. Zooplankton

The PWS shelf samples from 2000 to 2003 do not cluster separately from the 2004–2015 Cook Inlet shelf samples in the zooplankton analyses either (Fig. 8). In the spring analysis the years 2000 and 2009

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**Table 2**
The 30 most abundant phytoplankton and zooplankton taxa occurring in each season.

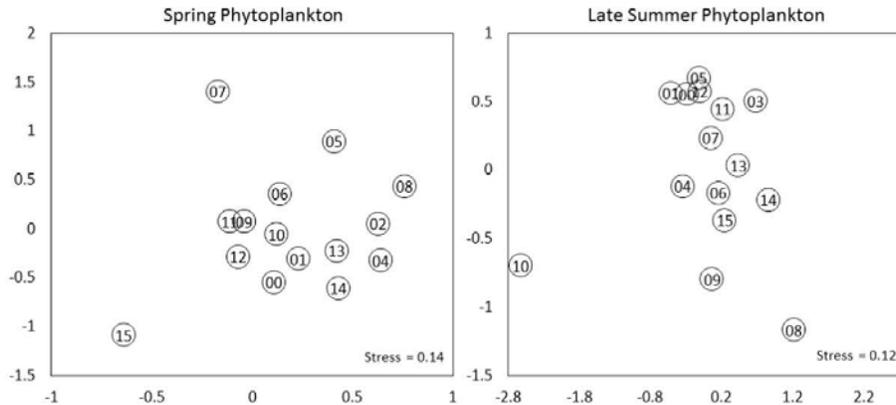| Phytoplankton, Spring | Phytoplankton, Late Summer | Zooplankton, Spring | Zooplankton, Late Summer |
|---|---|---|---|
| Thalassiosira spp. | Thalassionema nitzschioides | Pseudocalanus spp. C6 | Pseudocalanus spp. C6 |
| Chaetoceros spp. (Hyalochaetes) | Bacteriastrum spp. | Acartia longiremis | Acartia longiremis |
| Chaetoceros spp. (Phaeoceros) | Thalassiosira spp. | Calanus spp. C1-4 | Echinoderm larvae |
| Corethron hystrix | Silicoflagellatae | cirrpede larva | Calanus spp. C1-4 |
| Thalassionema nitzschioides | Chaetoceros spp. (Hyalochaetes) | Neocalanus plumchrus C5 | Oithona spp. |
| Silicoflagellatae | Chaetoceros spp. (Phaeoceros) | Echinoderm larvae | Acartia spp. |
| Neodenticula seminae | Pseudo-nitzschia seriata | Limacina helicina | Appendicularia |
| Unidentified Coscinodiscus spp. | Thalassiothrix longissima | Oithona spp. | Limacina helicina |
| Odontella aurita | Ceratium fusus | Euphausiacea calyptopis | Centropages abdominalis |
| Thalassiothrix longissima | Skeletonema costatum | Acartia spp. | Calanus pacificus C5-6 |
| Rhizosolenia hebetata semispina | Rhizosolenia hebetata semispina | Neocalanus plumchrus/flemingeri C4 | Euphausiacea calyptopis |
| Skeletonema costatum | Pseudo-nitzschia delicatissima complex | Appendicularia | Podon spp. |
| Pseudo-nitzschia delicatissima complex | Rhizosolenia setigera | Neocalanus plumchrus/flemingeri C2 | Cirripede larva |
| Coccolithaceae | Detonula confervacea | Neocalanus flemingeri C5 | Tortanus discaudatus |
| Rhizosolenia styliformis | Ceratium lineatum | Cirripede nauplii | Clausocalanus spp. |
| Hyalochaete resting spore | Ditylum brightwellii | Euphausiacea | Calanus marshallae C5-6 |
| Proboscia alata | Ceratium pentagonum | Calanus marshallae C5-6 | Cyphonautes larva |
| Dinoflagellate cysts | Ceratium longipes | Clausocalanus spp. | Acartia danae |
| Ceratium pentagonum | Ceratium tripos | Decapoda larvae | Decapoda larvae |
| Pseudo-nitzschia seriata | Coscinodiscus spp. | Chaetognatha juveniles | Paracalanus spp. C6 |
| Protoperidinium spp. | Coccolithaceae | Centropages abdominalis | Metridia pacifica C5-6 |
| Stephanopyxis spp. | Biddulphia longicruris | Metridia spp. C1-4 | Harpacticoida Total |
| Guinardia striata | Neodenticula seminae | Neocalanus cristatus C5-6 | Chaetognatha juvenile |
| Cylindrotheca closterium | Pterosperma spp. | Neocalanus plumchrus/flemingeri C3 | Euphausiacea |
| Ditylum brightwellii | Coscinodiscus concinnus | Cyphonautes larva | Neocalanus plumchrus/flemingeri C2 |
| Detonula confervacea | Proboscia alata | Lamellibranch larvae | Hyperiidea |
| Unidentified Nitzschia spp. | Hyalochaete resting spore | Eurytemora pacifica | Evadne spp. |
| Ceratium furca | Ceratium horridum | Hyperiidea | Lamellibranch larvae |
| Ceratium horridum | Cylindrotheca closterium | Metridia pacifica C5-6 | Ctenocalanus spp. |
| Paralia sulcata | Dinoflagellate cysts | Paracalanus spp. C6 | Chaetognatha Adult |



Fig. 7. Non-Metric Multidimensional Scaling analysis results of transformed spring (left, April to June) and late summer (right, August and September) phytoplankton taxonomic abundance data. The year is given in the centre of each point. Stress values for each ordination are given in the lower right.

appear to be different from other years, and different from each other. Examination of the taxa showed that several copepod taxa were absent or in low abundance in 2000 and there were high numbers of pteropods in this year (also evident from the anomaly plots in Fig. 6 where copepods were low in numbers and pteropods were high). The year 2009 contained some occurrences of rarer taxa such as *Paraeuchaeta* spp., sergestids and higher numbers of appendicularians. These taxa were present in some other years, but their combined effects influenced the overall difference in 2009 community composition. There were no strong relationships between the axes and physical variables. The y-axis of the spring plot is likely related to the PDO/temperature with PDO positive, warm years mostly positive on this axis. 2008 is, however, in the centre and not as negative as might be expected if this relationship

was a significant driver.

The late summer analysis has several years near the lower half of the plot that are dis-similar to the main cluster with 2003 standing out as particularly distinct. Many taxa were absent in this year and two copepod taxa, *Epilabidocera* spp. and *Centropages abdominalis* were relatively abundant. The y-axis of this plot relates strongly to the abundance of diatoms. Years with a positive diatom anomaly plot negatively on the y-axis while years with low numbers of diatoms are near the top ($r^2 = 0.44$, $p < 0.01$) suggesting a relationship between phytoplankton abundance and zooplankton community structure.

### 3.3.3. Copepod community size

A total of 43 copepod taxa were recorded, ranging from individual

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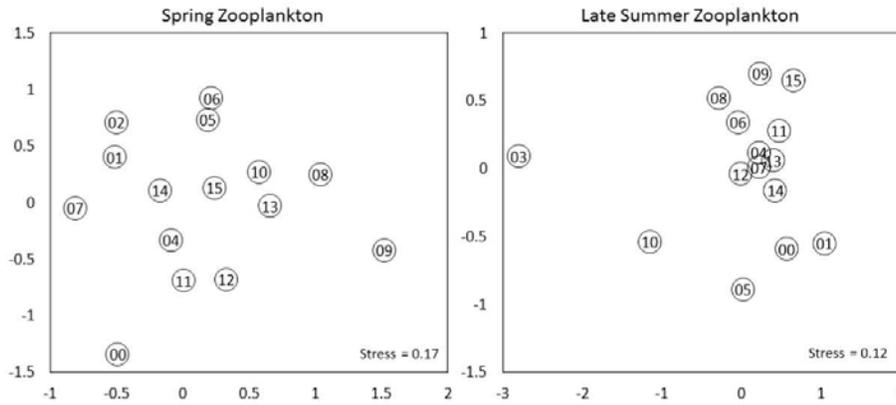Manuscript available as Open Access at http://dx.doi.org/10.1016/j.dsr2.2017.04.023

**Fig. 8.** Non-Metric Multidimensional Scaling analysis results of transformed spring (left, April to June) and late summer (right, August and September) zooplankton taxonomic abundance data. The year is given in the centre of each point. Stress values for each ordination are given in the lower right.
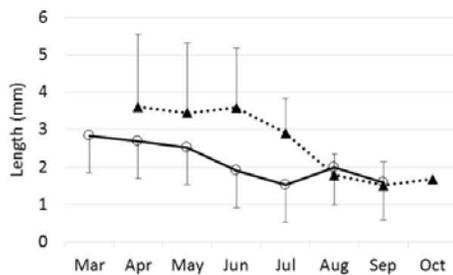


**Fig. 9.** Monthly mean copepod length (mean Copepod Community Size, see methods section for derivation) for the 5 warmest years (solid line with circles) and the 5 coldest years (dashed line with triangles). Error bars show standard deviation (in one direction only to avoid clutter).

stages in the case of the dominant species *Neocalanus plumchrus* (stages C2 to C6 were separately counted, though adults were rare) to genus level for those species more difficult to distinguish such as *Oithona* spp. The dominant taxa are shown in Table 2. The seasonal cycle of copepod community size, or the mean length of copepods in the community as represented by adult female length, (CCS) is shown in Fig. 9 and reveals the expected pattern where large copepods are more prevalent earlier in spring and, as these species descend to diapause in summer, the community becomes dominated by smaller species reducing the CCS, as reported in Coyle and Pinchuk (2003). The influence of temperature on the copepod community is clear, however, with the group of 5 warmest years having significantly smaller mean CCS in all spring and early summer months than the group of 5 coldest years ($t$-test, $p < 0.05$ for April and May, $p < 0.0001$ for June and July). Smaller species are both more numerous in warm than in cold years and have an earlier seasonal cycle, both factors contributing to a lower CCS in warm years. In August and September there was no significant difference in CCS between groups of years since even in cold years large *Neocalanus* copepods have almost all entered diapause by this time and the community is always dominated by smaller species such as *Acartia, Pseudocalanus* and *Paracalanus* spp.

## 4. Discussion

Our analyses have treated the shelf as one water body, which is an over-simplification since influences of the various current systems which run along the shelf will likely be different on the inner versus the outer shelf. The large scale resolution of CPR sampling (each sample covers 18.5 km) is some mitigation for this approach. Where whole-shelf temperature data from the CPR logger are available (Fig. 2, Section 3.1) they show the same broad inter-annual patterns as the GAK1 time series but this is only part of the story. Horizontal temperature gradients on the Gulf of Alaska shelf are weak compared to salinity gradients but there are, however, cross-shelf gradients in stratification. In spring, the inner half of the shelf stratifies primarily due to salinity and is thus affected by the magnitude and/or timing of winter and spring runoff (Janout et al., 2010). In contrast, the onset of springtime stratification over the outer half of the shelf is controlled by vertical temperature gradients. However, anomalously weak downwelling (or upwelling-favourable) winds can spread low-salinity waters over the outer shelf and thereby affect the stratification here meaning salinity variability has a strong influence on water column structure across the entire shelf (Weingartner et al., 2002). We may therefore expect climate forcing which influences the timing and intensity of freshwater run-off from the surrounding watersheds to have a large influence on the plankton. Temperature variability will also impact lower trophic levels directly in a number of ways; via basic metabolic processes with temperature-dependent rates and for at least some species the timing of life history events is related to ambient temperature (e.g. Batten et al., 2003c). We would therefore expect physical processes which create variability in either, or both, freshwater and heat content of the Alaskan Shelf waters to lead to variability in the plankton communities there.

Although the CPR was not designed as a phytoplankton sampler, and the mesh size is larger than many phytoplankton cells, there are nonetheless valuable insights into phytoplankton variability that can be gained from CPR data, because it is an internally consistent sampler and does retain a representative proportion of even quite small cells (especially if chain-forming). Fig. 3, Section 3.2.1 demonstrates that seasonal cycles derived from the CPR data closely replicate those seen from satellites for the same area, confirming that useful information can be gained. Through the first 14 years of the time series of CPR sampling on the Alaskan Shelf we have found that warm years had generally higher abundances of the larger cells retained by the CPR, particularly of diatoms (Fig. 4). The diatom anomaly time series has some similarity to a chlorophyll-*a* anomaly time series derived from satellite measurements for a wider area of the coastal Gulf of Alaska (Waite and Mueter, 2013). Their time series showed positive anomalies from 1998 to 2002, negative anomalies from 2003 to 2005, close to average for 2006–2010, and strongly negative in 2011. The CPR diatom anomalies were high in the early years also, suggesting a widespread event, and the decline in

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the middle years was probably not related to the change in time series location since the Waite and Mueter study showed a similar decline in chlorophyll-*a* at this time. The strongly negative anomaly in 2011 was common to both studies. Causes of this low productivity year are still being explored, however, the CPR zooplankton data show that the effects passed up the food chain from the phytoplankton; zooplankton biomass had the lowest anomaly of the time series to date in 2011 (Fig. 6). Interestingly, the community composition analyses did not identify 2011 as an anomalous year (Figs. 7 and 8). In terms of the type of taxa present and their relative abundance, 2011 was quite similar to several other years.

Diatom spring timing revealed an influence of water column conditions (Fig. 5). We might expect temperature to have a direct effect on diatom timing but this was not apparent, instead it was the degree of water column stability in May that provided the influence with a less stable water column (particularly a deeper MLD and to a lesser extent the lower potential energy) having a later spring peak in diatoms. There was also a significant correlation with the NPGO index, which is known to explain salinity variability further south in the California Current system (Di Lorenzo et al., 2008). The NPGO reflects both regional and basin scale variations in wind-driven circulation and advection processes. The relationships between the diatom timing and MLD and NPGO emphasises that phytoplankton processes are very much dependent on the physical oceanographic conditions.

Hard-shelled dinoflagellates are numerically much less important than the diatoms, typically having an abundance one tenth that of the diatoms in the CPR data, so the decline over time seen in Fig. 4 is not likely to have had much influence on total phytoplankton biomass. It has, however, contributed to the changing phytoplankton community composition shown in Fig. 7 by influencing the late summer composition, when dinoflagellates are typically most abundant. The NMDS analysis also showed an influence of the spring stratification strength (potential energy, shown in Fig. 2.) on summer phytoplankton composition. While stratification data from summer would be desirable to examine this further, it is feasible that the water column stability measured in late spring (May) would influence the community structure in the late summer, especially the numbers and types of dinoflagellates that prefer well-stratified waters.

Total mesozooplankton biomass was strongly positively correlated with diatom abundance for the years 2000–2013. The CPR data up to 2013 support the hypothesis that the physical environment of the Gulf of Alaska shelf (temperature and water column stability) influences the phytoplankton (diatom abundance and timing, dinoflagellate abundance), which in turn controls the quantity of mesozooplankton. However, these relationships were not apparent in the warm years of 2014 and 2015 when diatoms were unexpectedly low, in what has been termed a "marine heatwave" (DiLorenzo and Mantua, 2016) influenced first by the anomaly known as the Blob (Bond et al., 2015) and then an El Niño in 2015. These two years had the highest numbers of small copepods recorded in the time series which also were biased earlier in the year than average (Fig. 6). It is possible that the data for these two years show top-down control of the large diatoms by copepod grazing pressure, which was not seen in other warm years with high diatoms and high zooplankton abundance/biomass such as 2005. It is unlikely that the higher temperatures caused a non-linear response of lower productivity in the diatoms since these species also occur further south where such temperatures are normal. An alternative explanation is that the unusual conditions caused an unfavourable nutrient regime which reduced the productivity of large diatoms. The taxa recorded by the CPR in spring 2014 and 2015 did show a bias towards diatoms with longer, narrow cells (e.g. *Proboscia* spp., *Thalassiothrix* spp. and pennate species). Fig. 10 shows that only 2004 had a similarly high proportion of such cells and the spring community composition analyses also show 2004 and 2014 as very similar. Cells with this narrow morphology have a high surface area to volume ratio which would facilitate the take-up of nutrients; studies have shown that smaller cells which also have a
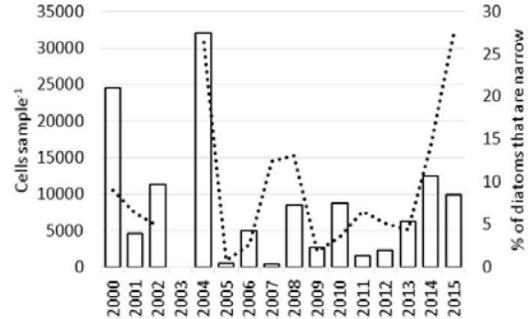


Fig. 10. Bars show the number of narrow, long diatom cells in spring of each year (April–June) while the dashed line shows the proportion of the total diatom community that they represent.

higher SA:Vol take up nutrients faster (Friebele et al., 1978; Geider et al., 1986). If nutrients were scarce they would have an advantage over the rounder cell types. However, the stratification indices shown in Fig. 2 do not suggest that 2014 and 2015 were especially stratified which might have limited the nutrients introduced by mixing. In 2015 there was an even higher proportion of these narrow cells, with low diatoms overall and high numbers of copepods still. The years 2014 and 2015 were also the only years of the time series when no coccolithophores were recorded in the samples, so other as yet unknown factors that influence phytoplankton community structure were also in play. It is also clear that the high numbers of copepods in these years must have been eating something, if not the large diatoms then some part of the plankton community not well resolved by the CPR.

Copepod seasonal timing is dependent on temperature since copepods are poikilothermic and their metabolic processes, including development rate, are faster in warm conditions (see Batten et al., 2003c; Mackas et al., 2007). The index of season mid-point calculated here ranged from day 126 to day 200 for large copepods, and day 163 to day 247 for small copepods. This is a considerable amount of variability – over 2 months in each case, and could potentially impact larger predators that time their reproduction or migration to take advantage of a peak in their prey. Zooplankton community composition was also likely influenced by temperature (Fig. 8 and Section 3.3.2). These changes were not as dramatic as a replacement of many species by others, rather a change in relative abundances with temporary occurrences of some rare species (e.g., the copepod *Acartia danae*, usually found below 40°N but found in the CPR samples from the Alaskan shelf in the warm years 2005 and 2015). CPR data from the oceanic NE Pacific have noted the northwards extension of warm water species to the GOA in the warmest years of the last decade (Batten and Walne, 2011) and Hopcroft et al. (2007) report a seasonal ingress of southern species along the Seward Line also in the warm year 2005. As well as warm water species occurring, there is also a shift towards a smaller mean size of copepod (Fig. 9 and Section 3.3.3) through increased productivity of smaller species (which have multiple generations in one year) and an earlier increase in numbers. If smaller and/or warm water species contribute a significant amount to the zooplankton populations, they could present a dietary challenge to zooplankton predators assuming their nutritional quality varies from the more typical subarctic diet.

In summary, we have documented interannual variability in concentration and composition of the plankton community of the region over a 16 year time period. At least in part and suggested by correlative relationships, this variability can be attributed to changes in the physical environment, particularly temperature and its direct effects on metabolic processes as well as indirect effects on water column stability. The study ends with two anomalous years (2014 and 2015) for which previous relationships between temperature, diatom abundance

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and small copepod abundance under warm conditions do not hold. The unusual warmth also continued into 2016 and impacts on the plankton communities from such sustained anomalous conditions remains unknown. The CPR continues to sample the Alaskan Shelf and given the rapidly changing climate the importance of regular, consistent sampling cannot be over-emphasised.

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