

*Calanus glacialis* and  
*Calanus marshallae*  
response to an upcoming  
climate change in the  
Arctic and Bering Sea

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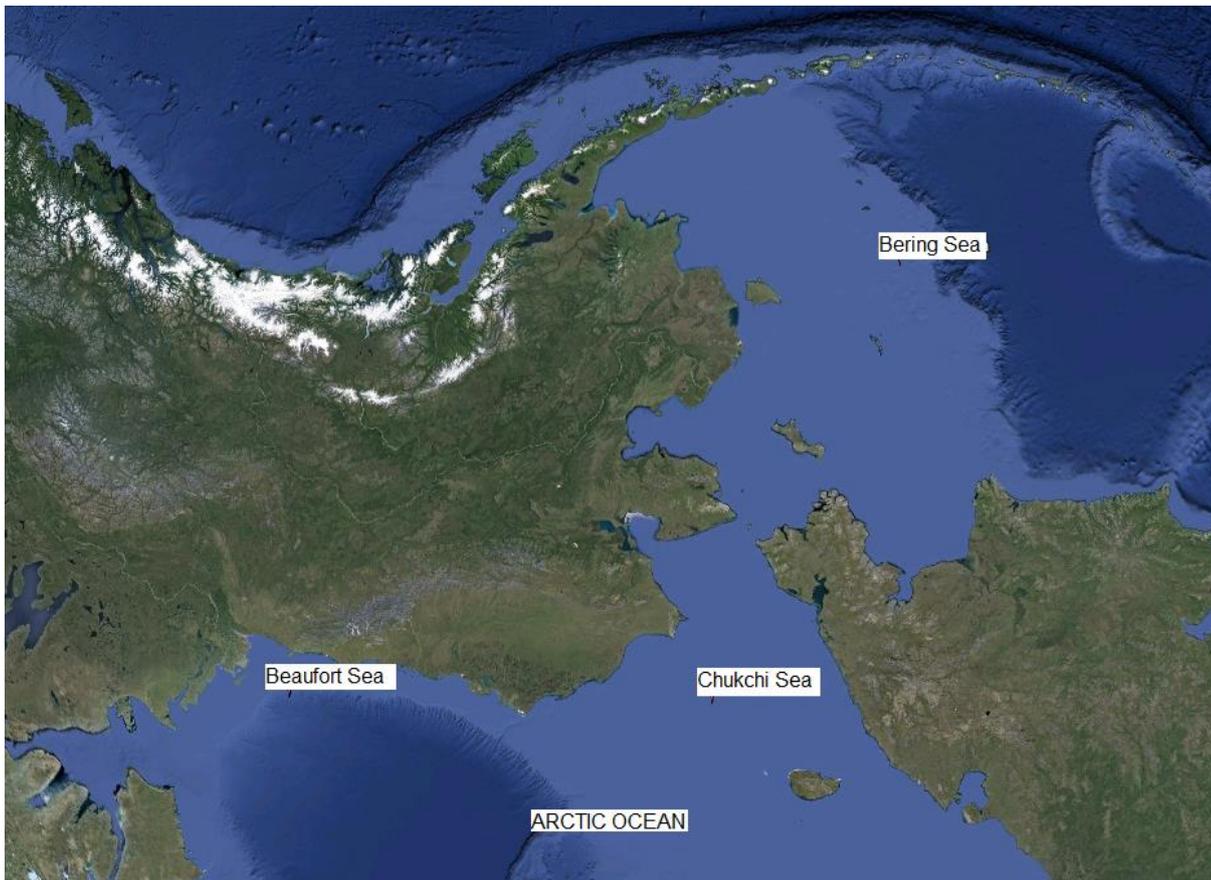
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## **Abstract**

One of the multiple consequences of global warming is the loss of sea ice cover of the Arctic and warming up of its surface waters. It is predicted that in 35 years the Arctic will be ice free in summer. It has to be considered that these changes in the environment will have irreversible consequences for marine ecosystems. Some of the consequences that are being most considered are the increase in primary productivity and the potential mismatch between the primary and secondary production. In this review I have studied the phenology and life cycle of two species of common Arctic copepods of the genus *Calanus* (*C. gracialis* and *C. marshallae*) along the Bering, Chukchi and Beaufort seas in the context of the above mentioned aspects of climate. I concluded that the most likely scenario is that primary productivity will increase and, with the exception of the Bering Sea, secondary productivity will increase as well. In addition, the successful colonization of *C. marshallae* in the Arctic Ocean likely results from the increase in primary productivity, temperature and longer growing season.

### **1. introduction**

The sea ice extent of the Arctic Ocean has declined notably during all months from 1970 to the early part of the 21<sup>st</sup> century (Serreze, Holland, & Stroeve, 2007). Ensembling 11 models used in the International Panel on Climate Change Fourth Assessment Report, Overland and Wang (2007) predicted a 40% reduction of the total sea ice extent by the year 2050. However, this prediction was made before the unexpected summer ice minimum of 2007. That year the summer sea ice extent was 23% below the previous minimum observed in September 2005 and 39% below the 1979–2000 September mean (National Snow and Ice Data Center, 2007). Taking that acceleration into account Wang and Overland (2012) predicted an ice free Arctic summer for the year 2030, which make research on the ecological consequences of the warming Arctic even more urgent than it was before. These predictions are also supported by many other studies (Markus, Stroeve, & Miller, 2009; Stroeve et al., 2008; M. Y. Wang & Overland, 2009).



**Fig. 1. Area of study.**

Sea ice plays a dual role for primary production: in the first place it provides a habitat for ice algae and regulates the light for primary production. Usually, ice algal blooms occur in March (Hegseth, 1998), while phytoplankton blooms occur after the ice break-up. An earlier and bigger ice retreat provides more productive surface area and a longer growing season, which both result in a higher annual productivity rate (Arrigo, van Dijken, & Pabi, 2008; Brown & Arrigo, 2012, 2013; E. C. Carmack, Macdonald, & Jasper, 2004; Dalpadado et al., 2014; Hirawake, Shinmyo, Fujiwara, & Saitoh, 2012; Mundy et al., 2014). This combination of effects resulted in 2007 in an estimated increase 35 Tg C (Arrigo and Pabi 2008). The increase in productivity is expected to continue in the future as new areas are available for primary producers and the growth season is longer. The extrapolation of the Arctic most conservative 10-years trend suggest that annual primary production in the Arctic could increase with 160 Tg C (reaching 700 Tg C/yr) by 2030, when the ice pack is completely melted in summer (Arrigo et al., 2008; M. Wang & Overland, 2012).

This increase in productivity will change the transfer of energy to the higher trophic levels. In the first place, an increase in productivity could mean a greater carbon flux to benthic ecosystems. However, an earlier ice retreat, although more productive, could also change the timing of the pelagic bloom, and cause a potential mismatch with the life cycle of highly adapted zooplankton (Hunt et al., 2002, 2011). It is therefore important; to assess the possible effects on zooplankton populations so that the possible changes in the higher trophic levels can be foreseen.

Copepods of the genus *Calanus* are key species in the Arctic and sub-Arctic seas, since they usually dominate the biomass of the mesozooplankton (Ashjian, Campbell, Welch, & Butler, 2003;

Conover, 1988; Falk-petersen, Mayzaud, Kattner, & Sargent, 2009). Their extremely high lipid content (50%-70% lipids of dry mass) makes them an indispensable food item for higher trophic levels ((Coyle et al., 2011; Hunt et al., 2002, 2011); ) Since some important fishes for the fishing industry feed on *Calanus* spp. alterations in the trophic chain could have both economical and ecological effects(Coyle et al., 2011; Coyle, Pinchuk, Eisner, & Napp, 2008).

In general, the life cycle of *Calanus* spp. consists of six nauplii and six copepodite stages. It is important to note that depending on their environment and specie, *Calanus* will need from 1 to 3 years to fully develop as a sexually mature individual (Daase et al., 2013; Ji et al., 2012). Typically, *Calanus* develops through these stages during summer, and if the conditions are good enough and they manage to develop until the adult stages, another spawning season will take place. By autumn they have stored enough lipids for overwintering at deep waters. Overwintering copepodites individuals develop into females and ascent in spring to reproduce and feed (K. N. Kosobokova, 1999).

In the present essay I am going to investigate if and how two species of the genus *Calanus* can change their phenology and life cycle to adapt to the forecasted changes in their environment. These species are: *Calanus glacialis* and *Calanus marshallae*. *C. glacialis* dominates in the Arctic shelves and accounts for up to 80% of the biomass there(Blachowiak-samolyk, Søreide, Kwasniewski, & Sundfjord, 2008; Søreide et al., 2008). Their regionality is limited by the low temperatures and short growth season in the northernmost areas of the Arctic Ocean. *C. marshallae*, on the other hand, is the major large copepod species on the southeastern Bering Sea (Baier & Napp, 2003; Coyle et al., 2008). At least during the 1990' they reached a biomass high enough that attracted whales to the regions where this copepod habitated (Tynan, DeMaster, & Peterson, 2001; Tynan, 2004). However, it has been found a negative correlation among *C. marshallae* and temperatures (Baier & Napp, 2003; Campbell, Wagner, Teegarden, Boudreau, & Durbin, 2001; Coyle et al., 2011, 2008; Hunt et al., 2011). *C. marshallae* regionality is limited on the north of the Bering sea due to the low temperatures and the shorter growth season (Ji et al., 2012). The limitations of both species could change due to an upcoming increase in temperatures and decrease of ice cover. As a result, both the regionality and productivity of this species could be affected, altering also the upper trophic levels.

The potential changes in the Arctic have been deeply studied. So it is possible to reconstruct the potential environment that *Calanus* spp. will have to deal with. The objective of this essay is to study those possible mismatches with phytoplankton blooms and the adaptations and plasticity of these copepod species to those changes (changes in regionality, life cycle, etc.).

This study will be focused on the Bering Sea in the Pacific Ocean and the Chukchi and Beaufort seas in the Arctic Ocean (Fig. 1). These seas are strongly interconnected and changes in one of them could sooner or later affect the rest. Besides, the connection of the Arctic Ocean and Bering Sea is the only one in the Canadian-Siberian region, and a very important nutrient supplier (Woodgate, Aagaard, & Weingartner, 2005), so any changes in this connection could cause a great disturbance in both productivity and ecosystem structures. Finally, as we can see on the Fig 2 and 4, these seas also differ in the climatology and ice cover. Bering Sea is warmer and has a longer ice free season than Beaufort and Chukchi Seas. This, as stated before, has a great impact in the *Calanus* life cycle, affecting to their regionality.

## 2. Current phenology and timing of phytoplankton bloom and *Calanus* spp. development in the Arctic Ocean and Bering Sea

### 2.1 Arctic ocean

*C. glacialis* shows many different life cycles depending on the environment (Daase et al., 2013). Here two possible scenarios on a pan-Arctic scale are presented which can also be applied to some regions of this study (Beaufort Sea and Chukchi Sea):

- (I) Regions with a long lasting ice cover, primarily Arctic water and two major microalgal (phytoplankton and ice algae) bloom events that occur with some time lag in between.
- (II) Open shelf systems with a high variability in timing of ice formation and breakup, inflow of warmer water (Pacific or Atlantic), and two bloom events that may overlap;

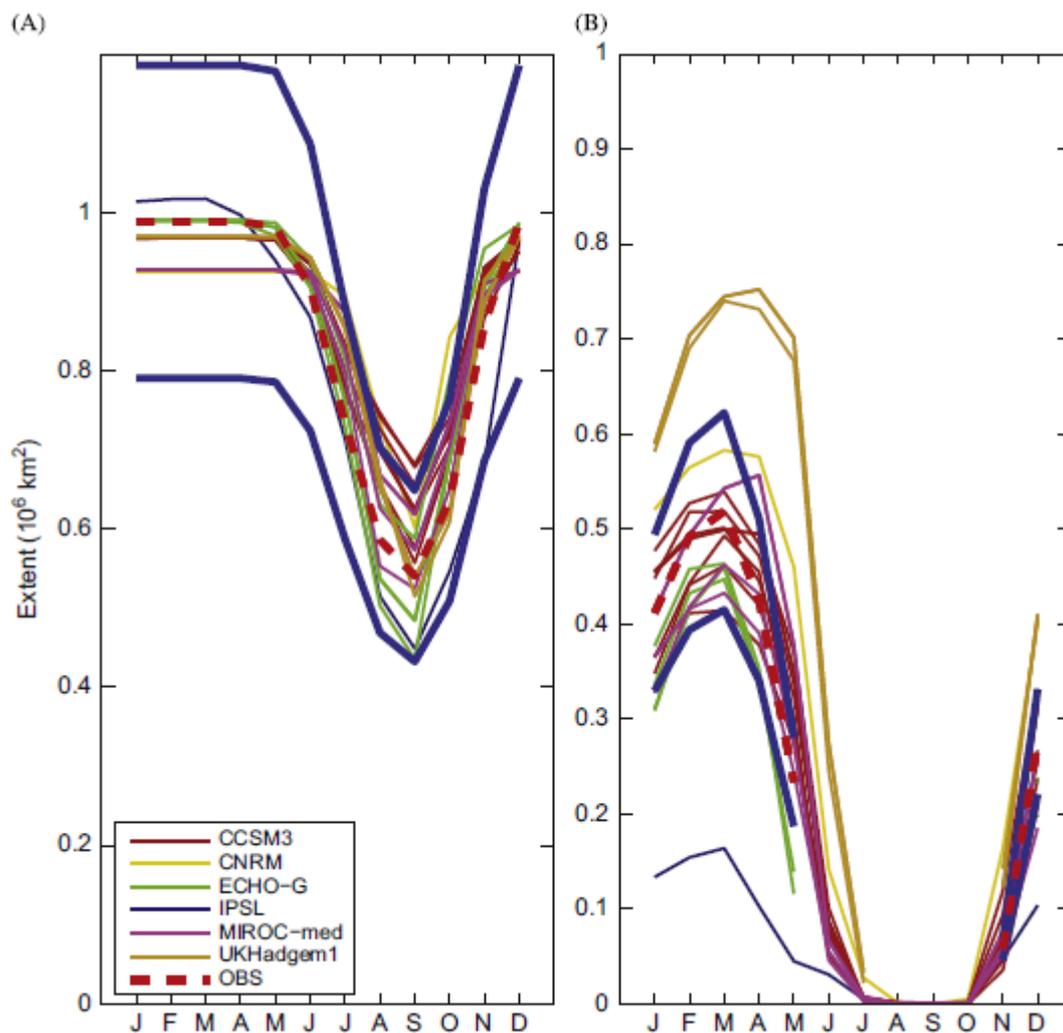
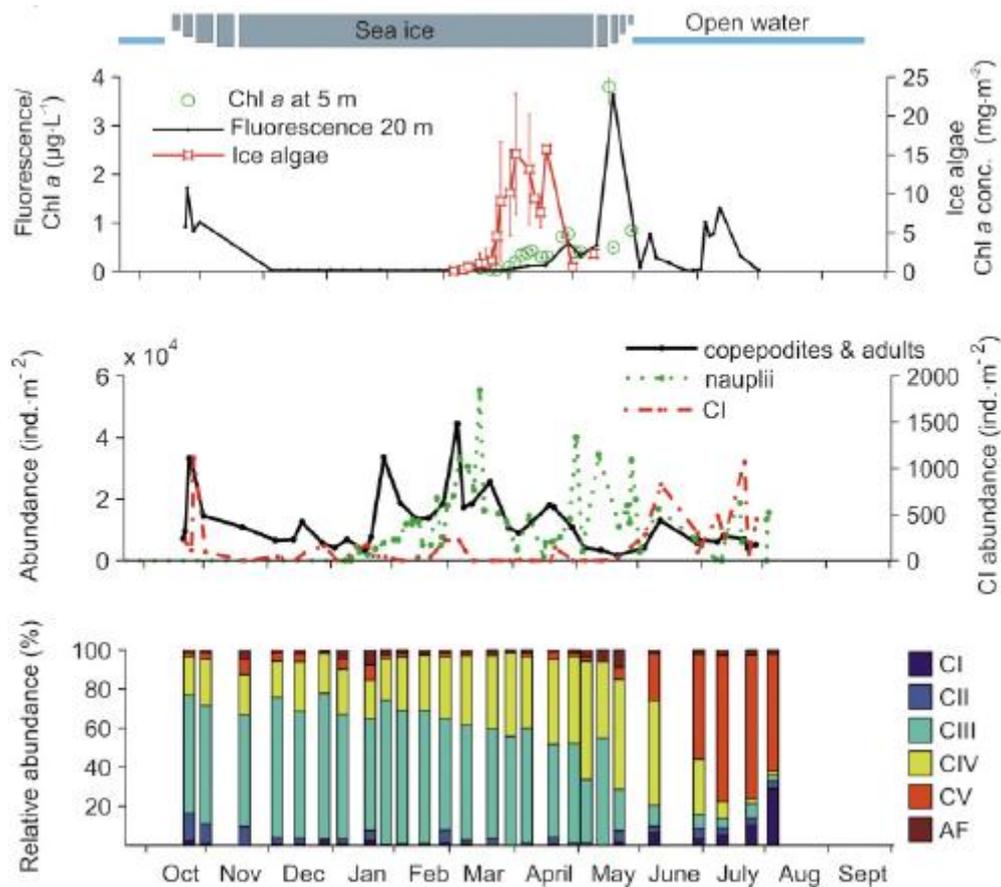


Fig. 2. Climatology of sea ice extent for the Chukchi Sea (A) and eastern Bering sea (B). The thick red dashed curve is based on the observation, and the thick blues curves mark the uncertainty around the observed value. The remaining lines represent different models. (Wang et al. 2012)

In the first case scenario, *C. glacialis* profits on ice algal bloom in April-May to fuel egg production and spawning. The new generation peak coincides with the peak of the phytoplankton bloom, ensuring good feeding conditions for the first nauplii stages of *C. glacialis*. One of the main advantages of this life cycle is that the stages in which feeding is not required (from the egg to nauplii



**Fig. 3. (based on data from 2007–2008) Seasonal development of phytoplankton Chl a concentration (based on Chl a concentration measured at 5 m and fluorescence measurements at 20 m) and ice algae Chl a concentration, total abundance of *C. glacialis* (copepodites and adults), abundance of *C. glacialis* CI and *Calanus* nauplii (middle panel), and stage composition of *C. glacialis* in Amundsen Gulf, 2007–2008 (lower panel). Timing of ice formation and ice breakup is indicated on top of each subplot. AF, adult females.. (Daase, 2013)**

stage III) occur in the lag between the ice algal and phytoplankton bloom (Daase et al., 2013; Peterson, 2001). This situation can be found in Franklin Bay, Barrow Strait, the Canadian Arctic archipelago and subarctic (Bay, Tourangeau, & Runge, 1991; Daase et al., 2013; Forest et al., 2008; Ringuette, Fortier, Fortier, & Runge, 2002; Therriault, Legendre, & Ingram, 1991). I can speculate that this would be the life cycle in the Chukchi Sea, since the timing of the ice algae and the lag with the spring bloom is very similar to the ones shown by most of the models of ice retreat.

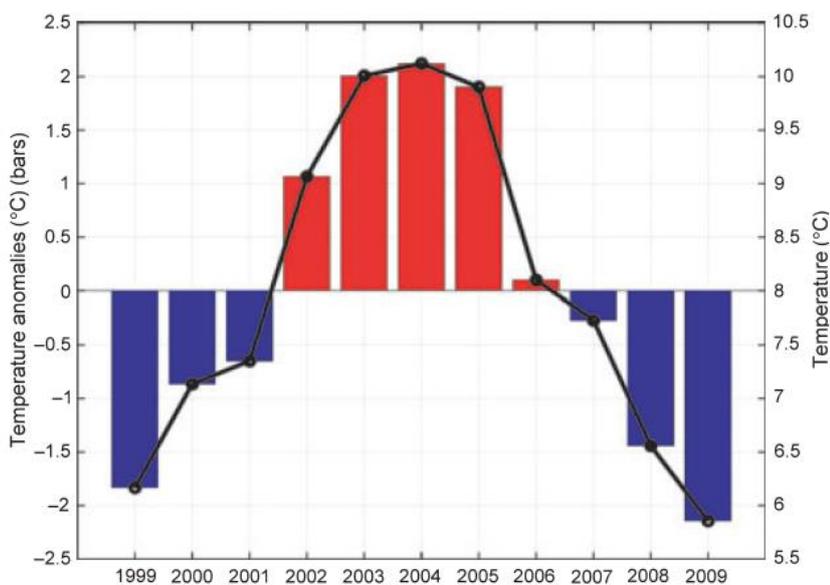
The Amundsen Gulf (Beaufort Sea) represents an example of the second case scenario (Fig. 3). The duration of the seasonal ice cover is highly variable and the ice algal and phytoplankton bloom appear very closely in time or even overlap in the spring months. For this reason, both blooms could be considered as one major bloom event. Following an income breeding strategy, the

population coinciding with the algal bloom is mainly formed by CIII-CIV individuals from the overwintering population. After being fully developed and fueled by the phytoplankton bloom, the spawning season occur (the highest egg production rate in 2007-2008 was in early May, coinciding with the highest proportion of adult females)(Daase et al., 2013). If the conditions of late summer are favourable, it is possible for *C. glacialis* to have a second spawning season. This can be exemplified in Fig. 3, where the higher proportion of early stages of copepodites at the end of July can be the consequence of a second spawning season. The development from CIII and CIV to females can be very rapid under favourable conditions, so these females would be able to spawn late in the season if food is available(Tremblay et al., 2011; Wold et al., 2011).

## 2.2 Southeastern Bering Sea and OCH

As previously stated, *C. marshallae* is restricted to the Bering Sea. In this Southeastern region production is ruled by the oscillating control hypothesis (Hunt et al., 2002, 2011).

The OCH is based in the variations on the productivity rates and timing of phytoplankton bloom and zooplankton phenology, as a consequence of the timing of ice retreat due to the temperatures in a certain year (Hunt et al., 2002, 2011). This theory states that when sea ice retreats



**Fig. 4. Summer (15 June–15 September) temperature anomalies (bars) and mean summer temperature (-, line) from the surface to 70 m depth, 1999–2009 from mooring data at M2 on the southeastern Bering Sea shelf (Coyle et al. 2011).**

early (before mid-March) the insufficient light does not allow to the ice associated spring bloom to happen. Only in May or June, when there is enough light and thermal stratification to stabilize the water column, bloom will be possible (Eslinger & Iverson, 2001; P J Stabeno, Bond, Kachel, & Salo, 2001). These blooms will therefore develop in relatively warm open waters (3-5C) (Hunt et al., 2002, 2011).

In contrast, if the ice retreats after mid-March, when there is enough light and the latest severe winter storms are over, the water column rapidly stabilizes with a very thin halocline (1-2m) resulting from the input of

meltwater. These blooms will occur as the ice is retreating and will be highly ice-edge associated; thus, ice edge blooms will typically develop in cold water (-1.7C) (Alexander, 1981; Hunt et al., 2011).

It is important to note that in late ice retreat years ice algal and pelagic blooms do not have a time lag between them, or even they overlap, functioning like a major bloom event (Brown & Arrigo, 2013). In this sense, cold years conditions in the Southeastern part of Bering Sea would be very similar to the conditions presented in the second case scenario in the Arctic Ocean(Daase et al., 2013).

As phytoplankton growth is very sensitive to temperature (Eppley, 1972), open water blooms in warm waters are expected to be more productive, and thus, early ice retreat years lead to a greater productivity (Hunt et al., 2002; Walsh, 1986).

However, these changes in temperature could also cause a shift in the phytoplankton community composition towards nanophytoplankton cells as has been observed in many studies (Noiri et al. 2005; Hare et al. 2007; Fujiwara et al. 2011; Stauffer et al. 2014). This change has been hypothesized to arise from different nutrient requirements by nano- versus microplankton (Hare et al., 2007). In cold waters there is not nutrient limitation for mikrophytoplankton. However, in warm waters nutrients are represented at much lower concentrations, leading to a nutrient limitation for mikrophytoplankton (Lomas et al., 2012). On the other hand, nanophytoplankton are better adapted to low nutrient concentration (higher surface:volume ratio), resulting in the dominance of this group over the mikrophytoplankton (Stauffer et al., 2014).

This effect could be emphasized during the post-bloom period. Even if there are nutrients below the pycnocline, if the water-column stability is high (due to the high temperatures) and the winds are not strong enough to produce mixing of nutrients into the euphotic zone (Coyle et al., 2008) low nutrients levels will be maintained.

As climatological conditions in the Bering sea are highly variable from year to year (Fig.4), very fluctuating year-to-year, the timing and temperature of the blooms varies a lot, creating great alterations among years in the transfer of energy to upper trophic levels (Brown & Arrigo, 2013).

### 2.2.1 OCH effect on zooplankton

*C. marshallae* normally produces his eggs from February to May. The egg production season is very long, and starts well before the ice algae onset. Even though at the last part of the egg production season could be fueled by ice algae, at the beginning of this season another strategy is needed. An estimation made by Baier and Napp (2003) makes income breeding possible. Although the capital breeding (use of the stored energy for the reproductive attempts) would also be a possibility, it is less likely, since this is considered an adaptation to the lack of ice algae (Daase et al., 2013)

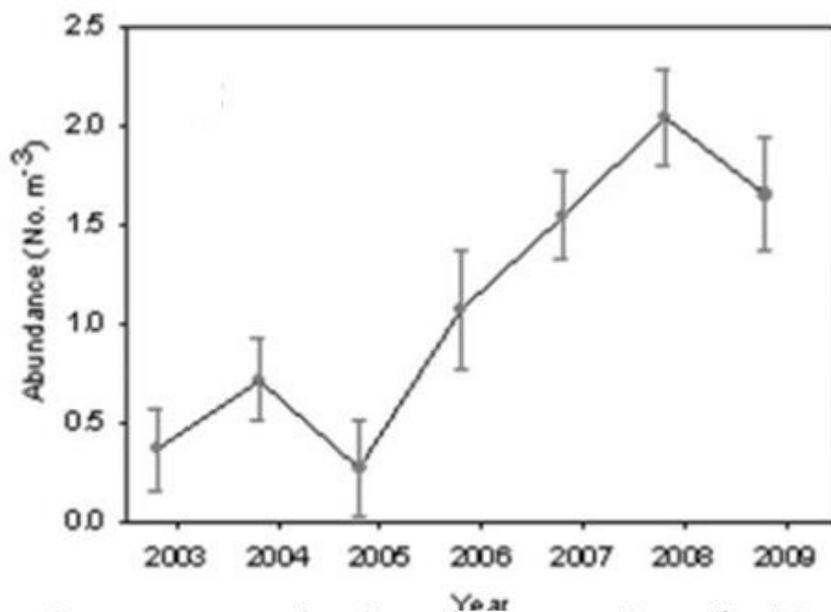


Fig. 5. Mean abundance (power transformed) of *C. marshallae* in the Bering Sea; August–September 2003–2009. (Hunt et al. 2011)

This long and early spawning season makes *C. marshallae* phenology very different from the one observed in *C. glacialis*. There are several reasons that have been proposed to explain this phenology. One of the best studied hypotheses is that in the spring bloom the diatom genera *Chaetoceros* and *Thalassiosira* are very abundant, and their ingestion inhibits copepod egg viability, so an earlier spawning could avoid this risk. Besides, copepodites recruitment coincides with the spring bloom, so the development to adult stages is favoured (Baier & Napp, 2003; Howell-kubler, Lessard, & Napp, 1996; Paffenhöfer, 2002). However the real influence of diatoms is still debated, and the reason to this phenology still to clarify (Baier & Napp, 2003).

On cold years, the timing of phytoplankton and *C. marshallae* fits perfectly the copepodites are able to accumulate enough lipid reserves for the diapause (Baier & Napp, 2003). During warm years, however, the changes on bloom timing and shorter growth season of large phytoplankton has a huge impact on the large zooplankton community, reducing their productivity. In the case of *C. marshallae*, a significant decrease of this species has been observed in warm years (fig.4 y 5).

Campbell et al. (2001) stated that for large *Calanus* species Q10 is higher for development than for growth. This implies that animals would mature earlier and at a smaller size under warm conditions, making it even more difficult to reach an already delayed spring bloom. Moreover, the shift in the phytoplankton community composition during the spring bloom, due to the higher temperatures could reduce the relative amount of diatoms, which are a much better food source compared with nanophytoplankton. This could lead to reduced lipid reserves (Stauffer et al., 2014). Thus these animals would enter in diapause sooner and with a smaller amount of lipid reserves.

The length of the diapause is based on the amount of lipid reserves and the rate of their consumption (Saumweber & Durbin, 2006). In other words, survival time during diapause would decline as temperatures increase since the copepods would increase their respiration rates at the same time that their lipid storage is smaller (Coyle et al., 2011; Ingvarsdottir, Dominic, Heath, & Hay, 1999). The spring bloom in the Bering Sea in warm years occurs later (Hunt et al., 2002, 2011) so when they are forced to leave the diapause sooner due to the consumption of their lipid reserves they would find an unfavorable foraging environment.

Finally, even if they would survive until the spring bloom, the strong stratification due to the high temperatures could block the supply of nutrients, reducing large phytoplankton production and enhancing the shift towards nanophytoplankton. As a consequence, *C. marshallae* would not be able to accumulate enough lipids to overwinter (Coyle et al., 2008; Stauffer et al., 2014).

### 2.2.2 Regional limitations of the OCH

The application of the OCH is only possible in the southeastern Bering Sea. Further to the south, beyond the shelf-break and the reach of the annual sea ice pack, ice edged blooms develop invariably in relatively warm (5-6C) open waters. Further to the north the timing of the ice retreat is restricted to a very narrow window (Fig. 2), so blooms are invariably ice related and occurring in cold waters. Thus, the OHC is constrained to the region with more a fluctuating extent of ice and do not function poleward of 60N at this time, nor are they likely to be applicable to the Arctic Ocean, where ice-edge blooms are also proposed to be ubiquitous (Perrette, Yool, Quartly, & Popova, 2011).

### 3. Discussion

#### 3.1 Current zonation of *Calanus* spp. and criteria followed to define it

The life cycles and phenology of the two Investigated *Calanus* species are very important to understand their current distribution and thus their probable future distribution. To assess the current distribution I followed the assumption that only the regions in which these species are able to

complete the life cycle with the diapause would be considered as part of their distribution.

If we comply with this assumption, *C. glacialis* only reaches diapause successfully along the edges and marginal seas, except for the Chukchi sea and western Greenland seas, where *C. glacialis* is advected out of the region due to the high levels of advection presented in those seas (Ji et al., 2012). *C. glacialis* mostly dominated the shelves and slopes, and is not very common in deep waters (Conover, 1988; Falk-petersen et al., 2009; K Kosobokova & Hirche, 2000; Ksenia Kosobokova & Hirche, 2009; Lane, Llinás, Smith, & Pilz, 2008; Wassmann et al., 2006). The central Arctic is not a suitable region for any of the existing

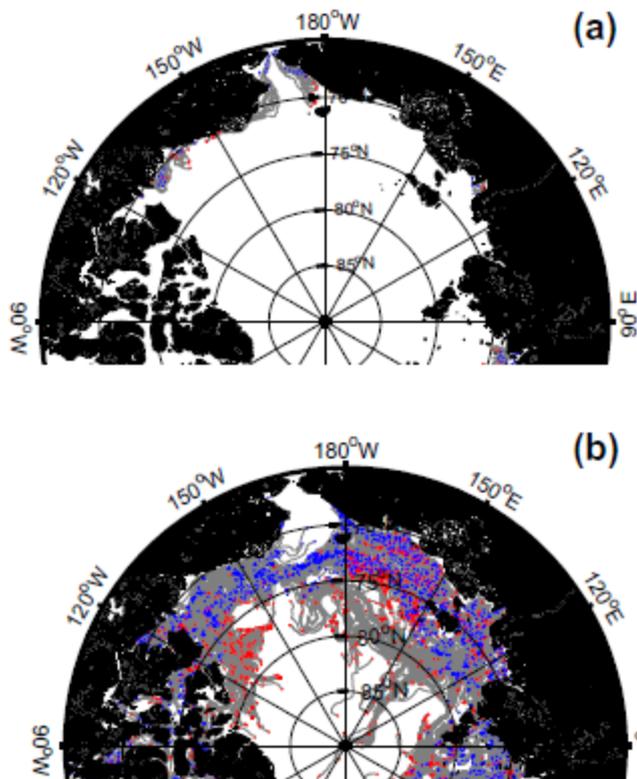


Fig. 6. Locations where *C. marshallae* (a) and *C. glacialis* (b) successfully reached diapause. Blue dots: release locations; Red dots: end locations at the end of growth season. (Ji et al. 2011)

*Calanus* species (Fig 6)(Ji et al., 2012).

*C. marshallae* is restricted to the sub-Arctic part of the Bering Sea and could only enter the Arctic through the

Bering strait (Frost, 1974; Hopcroft & Kosobokova, 2010; Plourde, Campbell, Ashjian, & Stockwell, 2005; Springer & Mcroy, 1989). However, they are adapted to longer growth seasons and higher temperatures compared with the species inhabiting the Arctic, so currently they are not present in the Arctic (6) (Ji et al., 2012).

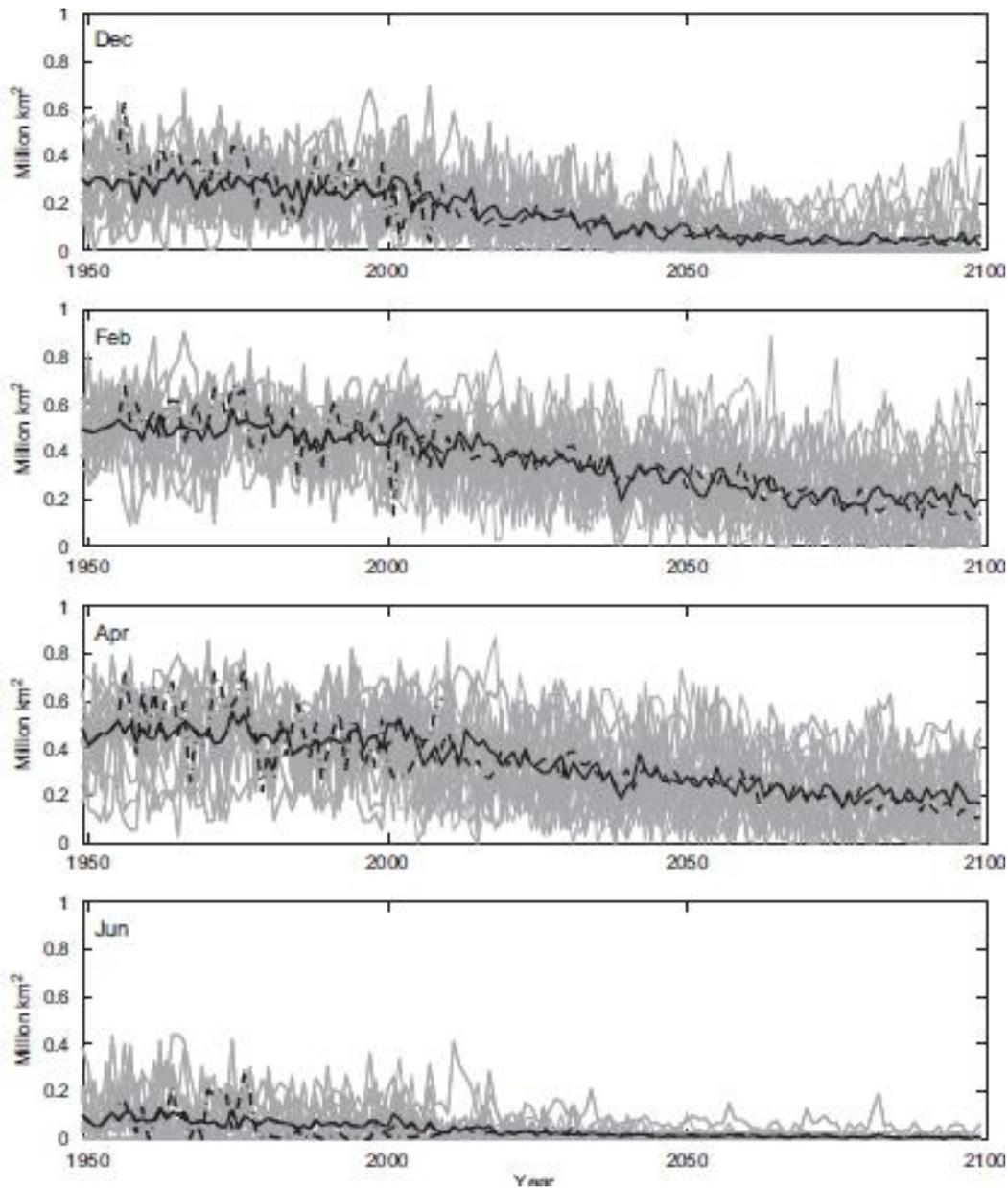
#### 3.2 Relationship between phytoplankton productivity and the climate change

Brown and Arrigo (2013) predicted an increase in NPP on the future warmer and ice free environments. This statement is based on the following assumptions:

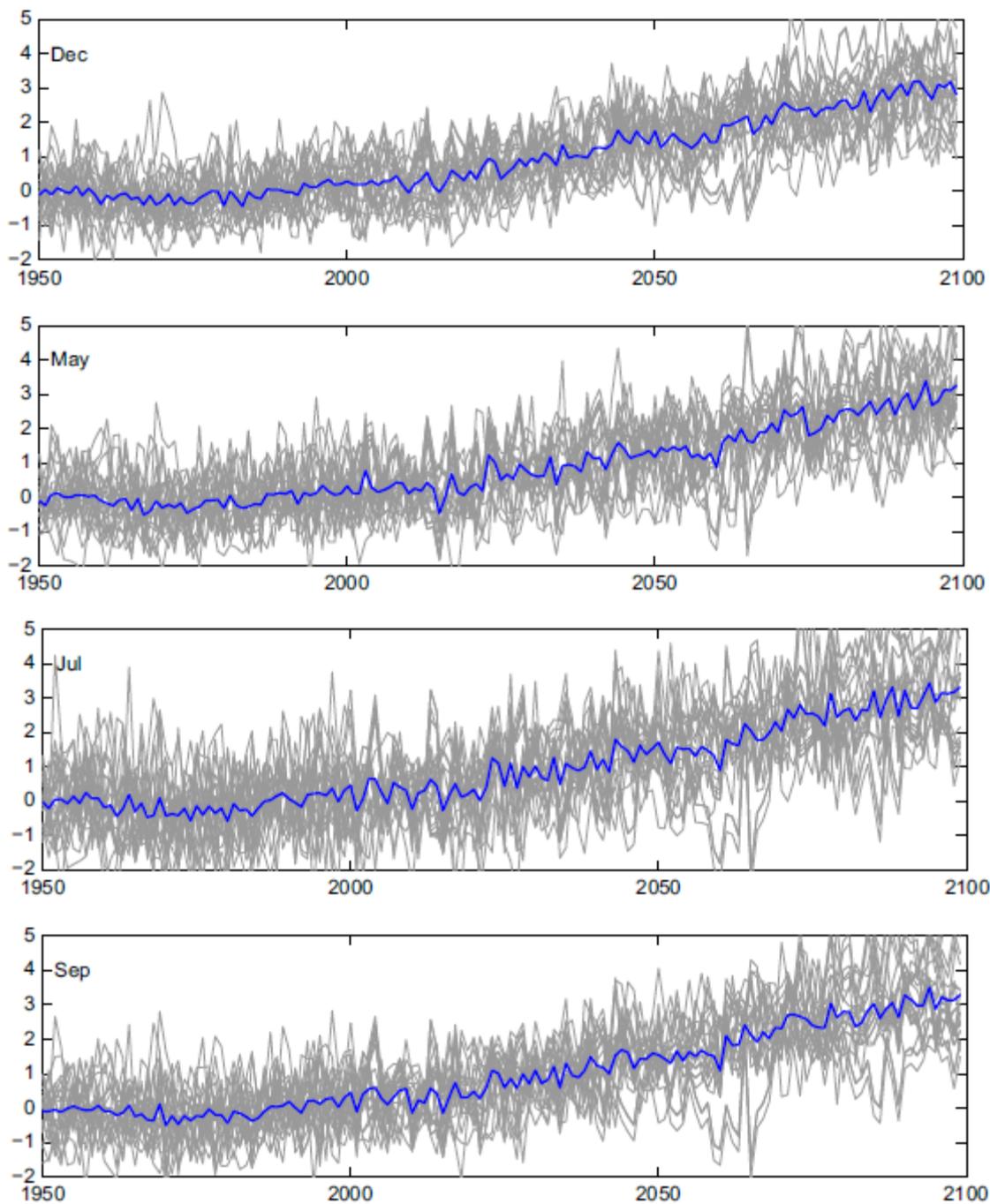
1. Phytoplankton growth is very sensitive to temperature (Eppley R. W., 1972). As open water blooms in the Bering sea are ~3 °C warmer than ice edge blooms, following the algorithm of (Brown, van Dijken, & Arrigo, 2011) they will be 26% more productive (meter aquí el aumento por SST en el ártico también).

2. If the ice retreat interrupt the ice algae bloom, there would be more nutrients available for the phytoplankton bloom (Brown & Arrigo, 2013).
3. A longer growth season
4. More habitats available due to multiyear ice loss.

All of this statements can be applied to both the Bering Sea and the Arctic Ocean, but the relevance among them, especially in the points 3 and 4, change with zonation and environment.



**Fig. 7. Model simulated sea ice extent over the eastern Bering Sea for the months December, February, April and June. The thick black curve is the result of four different models. Each gray curve represents one realization by one of these models (Wang et al. 2012).**



**Fig. 8. Sea surface temperature (SST) anomalies relative to its climatology for the 1980-1999 period for the selected month store present each season based on six models for the Bering Sea. Each grey curve represents one realization from one of these six models (13runs in all); the thick blue curve shows the ensemble mean under the A1B emissions scenario (Wang et al. 2012).**

### 3.3 Bering sea

#### 3.3.1 Ice cover and SST predictions

Currently the Bering Sea is basically ice free from June to November (fig. 2)(M. Wang, Overland, & Stabeno, 2012). Following the trend of (M. Wang et al., 2012) there will be sea ice loss of 2.1103 km<sup>2</sup>/ year for December; 3.0103 km<sup>2</sup>/year for February; and 2.7103 km<sup>2</sup>/year for April. This means that by 2050, December will show a sea ice extent average of 28% of the present value (1980-1999 mean), meanwhile in spring time (March to May) only 58% of the present sea ice extent will remain (Fig. 7)(Phyllis J Stabeno et al., 2012; M. Wang et al., 2012) (. Despite this decrease, spring will not be ice free by 2050, so the large interannual variations for which the Bering Sea is known will continue at least for the next 35 years(Phyllis J Stabeno et al., 2012).

SST has increased during summer in the Bering Sea (Fig. 8), but this increase does not correlate with the ice loss that should result from this decrease (Brown et al., 2011). Open-water extent in the Bering Sea appears uncoupled from that of seas to the north, but is instead highly correlated with wind direction: ice forms in the northern Bering Sea and is pushed southwards by the northerly winds. The contact of the ice with warmer waters causes melting and cools the water column facilitating further sea advance(Brown & Arrigo, 2012)

As can be seen in the figure 8, SST is expected to further increase, reaching temperatures

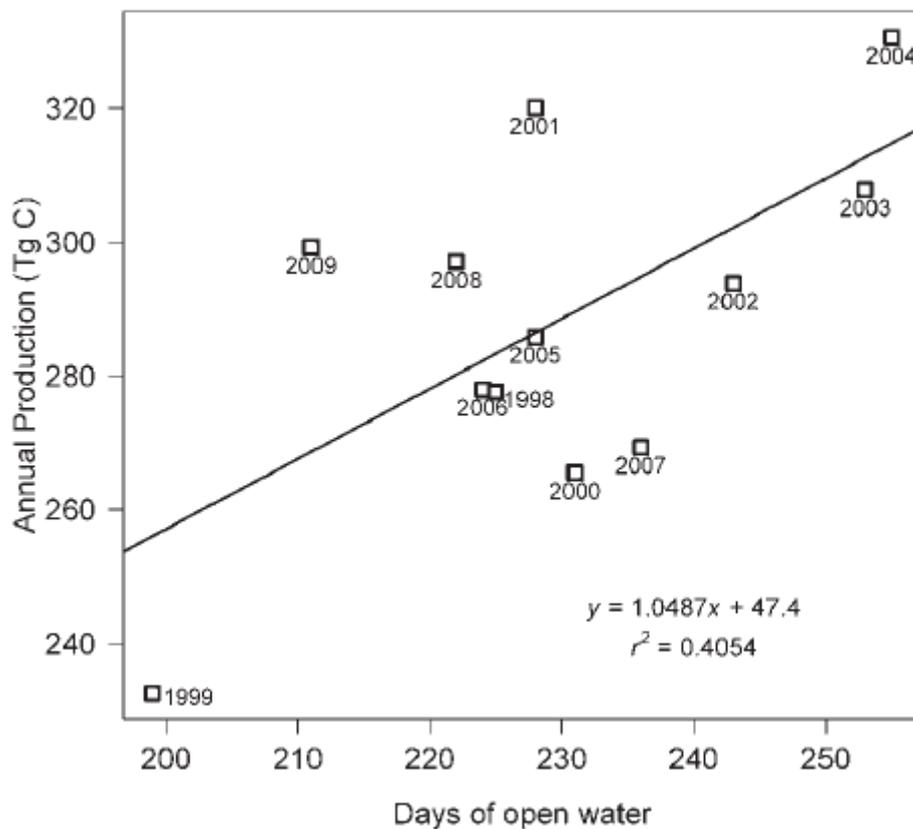


Fig. 9. Annual NPP vs. the length of the open-water season in the Bering Sea over the satellite ocean colour record, 1998–2009 (Brown & Arrigo, 2012)

close to 2C warmer than current SST in the spring months of 2050(Phyllis J Stabeno et al., 2012; M. Wang et al., 2012).

### *3.3.2 Phytoplankton productivity predictions*

As the interannual variations of ice retreat timing will continue at least for the next 35 years, the OCH will still be applicable. However, the progressive loss of ice and warming of the SST could mean that warm years will become more frequent and extreme. As a consequence of the enlargement of the growth season, the productivity will be increased (Fig. 9). However the delay of the spring blooms due to an earlier retreat will be more usual and the stronger stratification and higher temperature of the SST will make the shift in the community composition towards nanophytoplankton more extreme.

It is likely though that the increase in productivity will not be as extreme as in other Arctic regions. The possible area is already subject to high primary production at least a portion of the year. Thus, future sea-ice loss cannot provide new areas, but only enlarge the growth season (Brown & Arrigo, 2012). Despite this limitation, the increase in productivity only due to the longer growth season is already high (fig. 9).

### *3.3.3 Zooplankton productivity expectations*

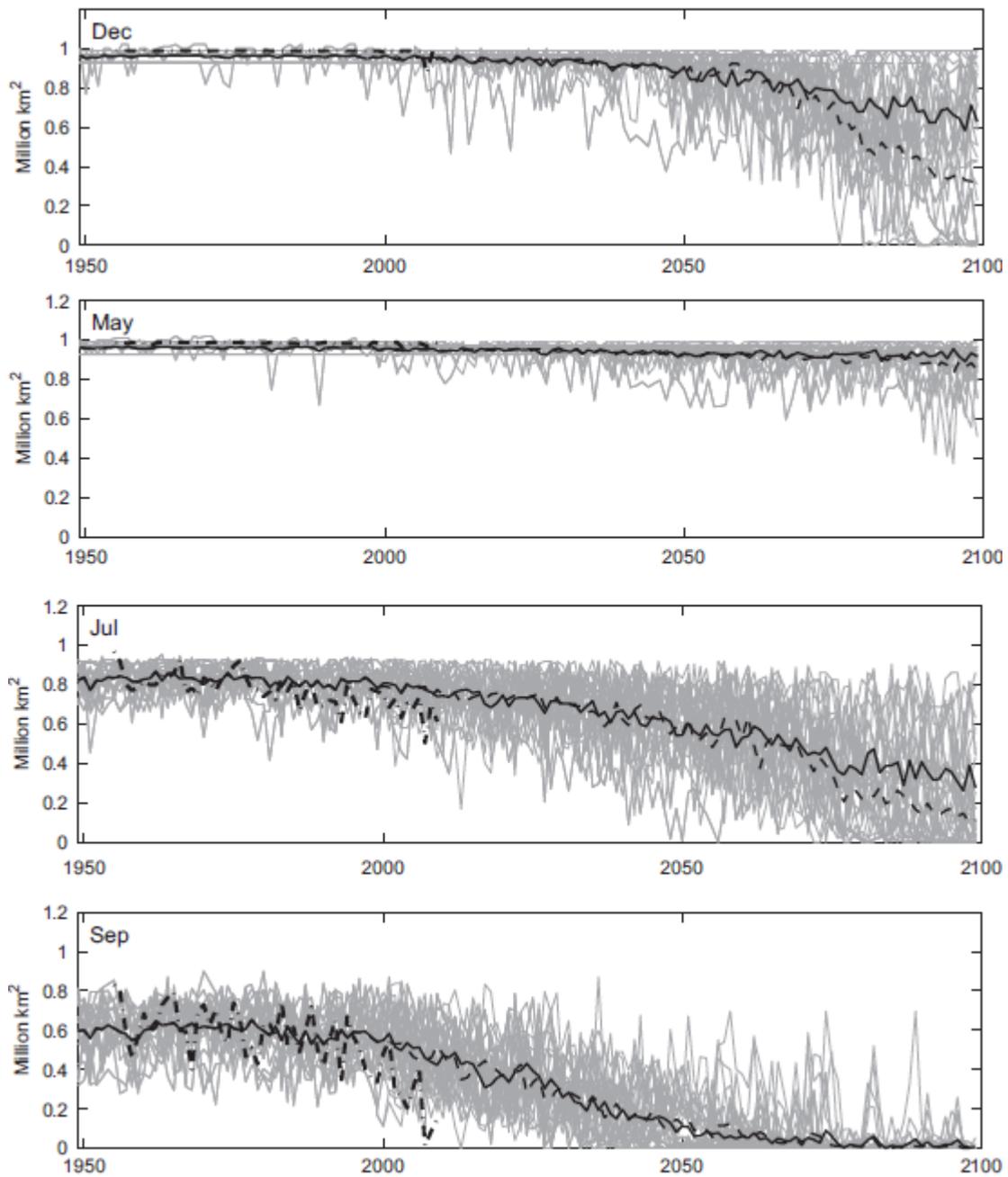
The more frequent delay of the spring bloom could have as a consequence more frequent low recruitment years of *C. marshallae*. Besides, the more extreme temperatures and shift in the phytoplankton community will exacerbate the low recruitment rates of this copepod due to an acceleration of the metabolism, an increase of the mismatch and the reduction of the proportion of phytoplankton that *C. marshallae* can feed on. Thus, it is very likely that *C. marshallae* populations will decrease. Probably the lesser increase in winter SST and the high variability foreseen among years will soften this decrease in the population, since cold late retreat years will still occur up to 2050.

## **3.4 Chukchi Sea**

### *3.4.1 Ice cover and SST predictions*

The Chukchi Sea is currently the most productive area in the Arctic Ocean (from 400 g C m<sup>-2</sup> yr<sup>-1</sup> to 100 g C m<sup>-2</sup> yr<sup>-1</sup> depending on the model) (Popova et al., 2012). Nutrient rich and low salinity water penetrates from the Bering Sea and resides in the upper mixing layer (E. Carmack & Wassmann, 2006). Analysis of the OCCAM model dynamics reveals that it takes 10 to 20 years for this rich nutrient waters to penetrate into the Arctic Ocean through the Beaufort Gyre up to the Lomonosov ridge (Popova et al., 2012).

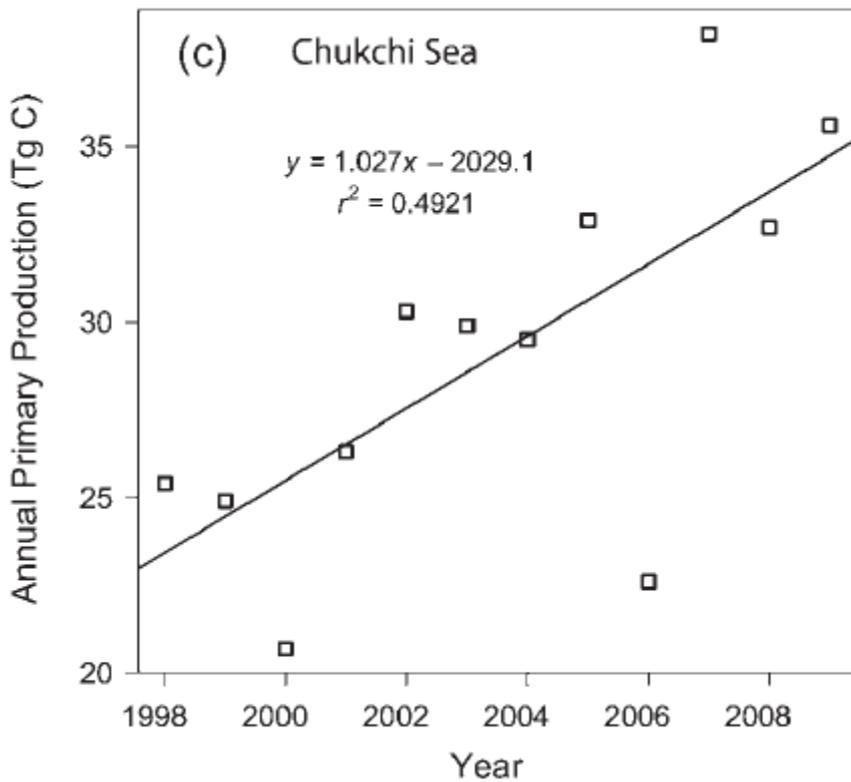
There is no ice reduction projected for winter through early spring until 2050. On the other hand, the ice decrease in summer is already obvious, but with a uncompensated reduction of ice cover: For 2050 a reduction of 25% in July and 83% in September is expected (Fig. 10). This implies that the growth season will be longer, but mostly due to a later formation of sea ice, than due to an earlier ice retreat(M. Wang et al., 2012). Taking into account the relationship between days of growth season and productivity current trend in the last years (Fig. 11), an increase in productivity without any substantial change in the spring bloom timing is very likely.



**Fig. 10. Model simulated sea ice extent over the Chukchi Sea for the months of December, February, April and June. The thick black curve is the result of four different models. Each grey curve represents one realization by one of these models (Wang et al. 2012).**

### 3.4.2 Effect on zooplankton

The increase of productivity, elongation of the growth season and increase of temperatures (Fig. 12) could create a more favourable environment for *C. marshallae*. These changes could result in an introduction of *C. marshallae* in the Arctic Ocean through the Chukchi Sea, since the low temperatures and the narrow growing window were its major distribution limits. Yet; given the high level of advection most populations would remain located in the outer part of Chukchi sea (Brown &



Arrigo, 2013; Ji et al., 2012). The major obstacle would be that the lack of retreat in early spring wouldn't change the timing of the pelagic bloom much, which is from the end of June to July (Ji, Jin, & Varpe, 2013). This timing is very similar to the one that can be found in the Bering Sea on warm years; nonetheless there are some differences that could contribute to a successful introduction of this copepod.

Fig. 11. Secular trends in annual NPP in the Chukchi Sea. (Brown and Arrigo 2012).

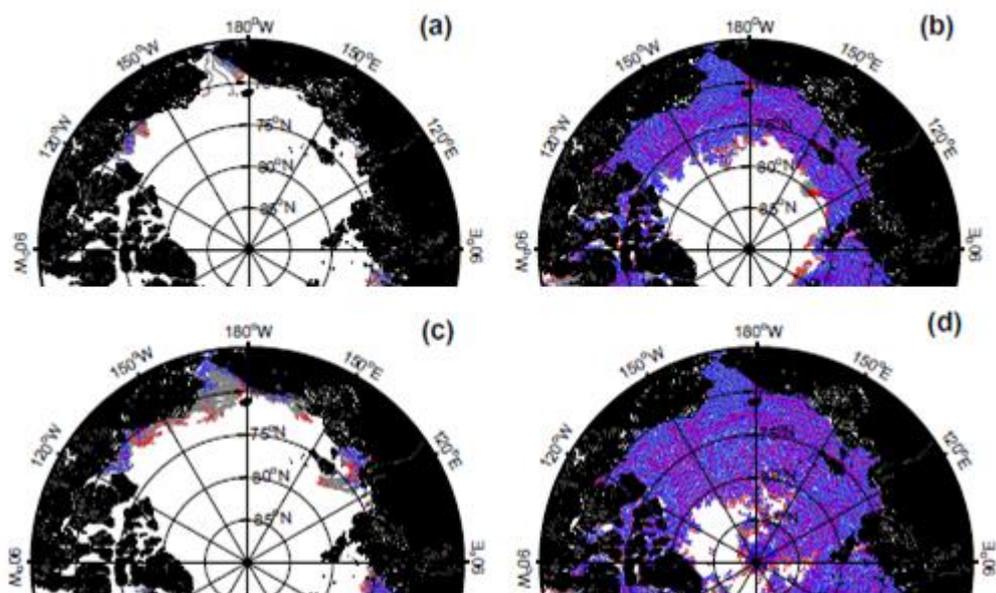


Fig. 12. Locations where individuals reached diapause at the surface with the growth season starting 2 weeks earlier (A) *C. marshallae* (B) *C. glacialis*. Locations where individuals reached diapause at the surface under temperatures 2 C warmer than the climatology (C) *C. marshallae* (D) *C. glacialis* (Ji et al. 2012)

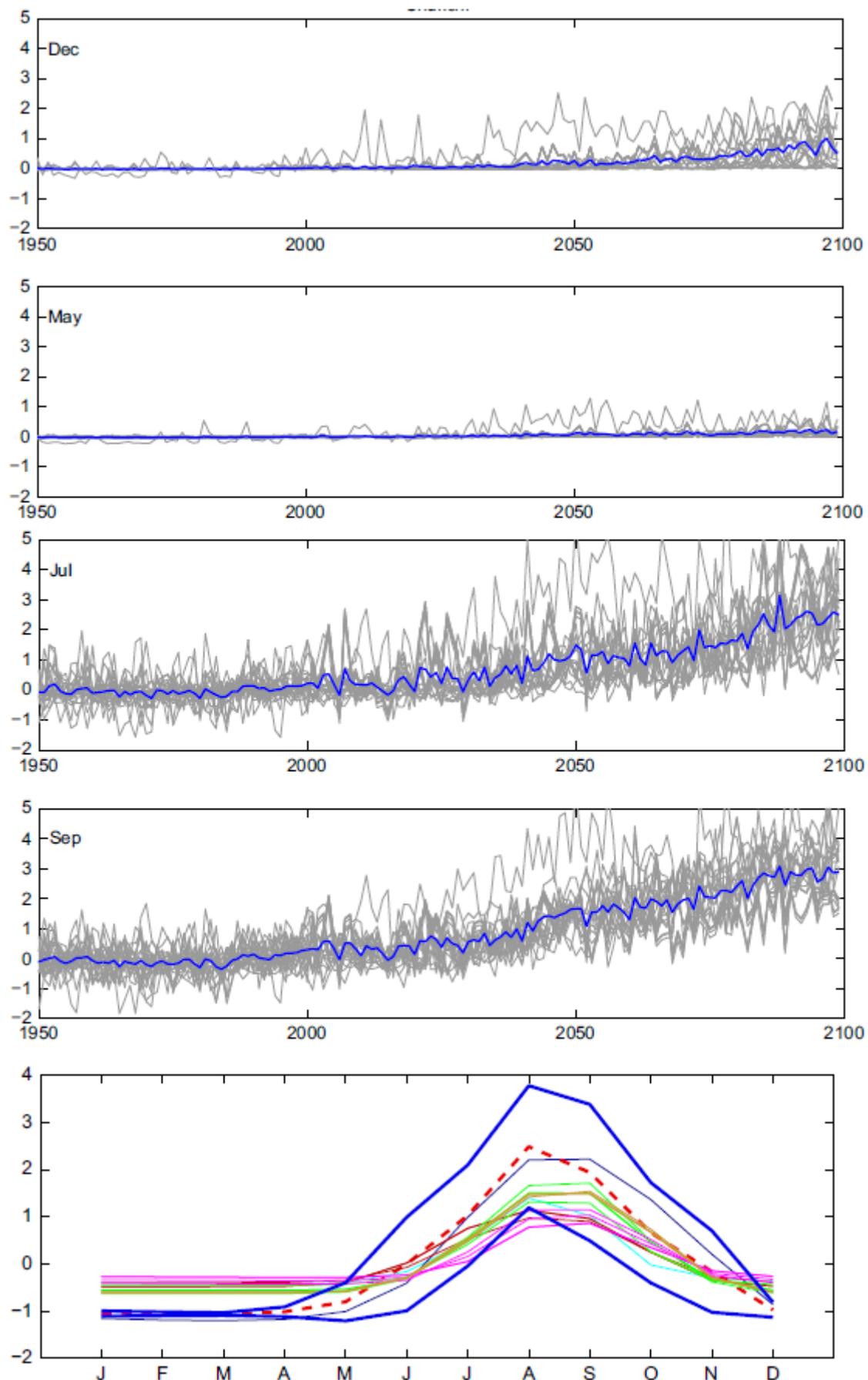


Fig. 13. Sea surface temperature (SST) anomalies relative to its climatology for the 1980-1999 period for the selected month store present each season based on six models for the Chukchi Sea. Each gray curve represents one realization from one of these six models (13runs in all), and the thick blue curve shows the ensemble mean under the A1B emissions scenario. On the bottom of the image there is the SST of the Chukchi sea from 1982 to 1999 (Wang et al. 2012).

1. The ice cover allows ice algae to grow, peaking between March and May (Ji et al., 2012), and *C. marshallae* could feed on it.
2. The temperatures present in warm years in the Bering Sea (Fig 13) are higher than the ones expected in the Chukchi sea (the highest temperature expected for 2050 in summer is 5°C); so the metabolism will not be as accelerated as in the Bering sea
3. There has been reported under ice blooms in the Chukchi sea, so *C. marshallae* could feed on them (Arrigo et al., 2012; Lowry, van Dijken, & Arrigo, 2014).

*C. glacialis* would also increase its productivity due to the increase in phytoplankton productivity. Zonation is also expected to increase because of the increase of temperature of 2 degrees: as it can be seen in figure 12, *C. glacialis* is very sensitive to the temperature. It is important to take into account though that the increase is only expected for summer months, while the model of the figure 12 is based on year round data. This implies that, the increase in zonation will probably not be that extensive. As the timing of the bloom is not predicted to change a lot, no changes in the life cycle and phenology can be expected. It is important to note that due to the high advection levels present in the Chukchi Sea, the populations will concentrate in the outer part of the sea, not in the inner (Daase et al., 2013).

### **3.5 Beaufort Sea**

#### *3.5.1 Ice cover and SST predictions*

Productivity in the Beaufort sea approach oligotrophic levels ( $IPP < 50 \text{ g C m}^2 \text{ yr}^{-1}$ ) (Sorokin and Sorokin, 1996; Carmack et al., 2004). The productivity is limited by the initial nutrient load, determined by fall and winter convection (E. C. Carmack et al., 2004) and discharge from rivers (E. Carmack & Wassmann, 2006). However, an earlier ice retreat and wind-induced upwelling (E. Carmack & McLaughlin, 2011; Pickart et al., 2009) has observed to increase productivity, since it replenishes the surface with nutrients (E. C. Carmack et al., 2004). These physical events are projected to increase in frequency as ice retreats beyond the shelf break, but would only affect to the shelf, since the strong winds are not able to erode the freshwater-induced stratification further offshore (Hill et al., 2013; Tremblay et al., 2011). The earlier ice retreat would also change the timing of the bloom. As a result, we could expect earlier spring blooms or even under-ice blooms if the ice cover is thin enough (Arrigo et al., 2012; Pickart et al., 2013) and reduce even more the lag between ice algae peak and the pelagic bloom. In any case, the frequency of overlap in Amundsen Gulf would increase.

Nonetheless, upwelling events would not be restricted to the beginning of the growth season, but distributed all along it (Pickart et al., 2013). Thanks to this upwelling, primary production can be fueled during late summer and early fall (Tremblay et al., 2011; Hill et al. 2013). This is later than the normal open water bloom, and has the potential to result in as much carbon uptake as taking place earlier in the season (Pickart et al., 2013).

#### *3.5.2 Effect on zooplankton*

This earlier ice retreat and shorter time lag between ice algal and pelagic blooms (even overlapping) won't change the life cycle described in the second case scenario for *C. glacialis*. The increase in productivity would possibly affect *C. glacialis* populations in a very positive way. The

enlargement of the growth season and the upwelling events predicted for late summer could make the second spawning event more frequent and more productive.

Although the increase in the temperature and longer growing season seems to affect the zonation of *C. glacialis* beyond offshore areas (fig. 12), my predictions are not that optimistic, since the upwelling events do not seem to affect offshore waters (Hill et al., 2013).

As can be seen in Fig. 12, *C. marshallae* could also establish in the Beaufort Sea under a warmer and longer growth season. Given the increase in productivity expected in this sea, there is no reason to believe that *C. marshallae* will not be successful there. This colonization would have to face the same obstacles as in the Chukchi Sea.

#### **4. Concluding Remarks**

The increase in temperature and retreat of the ice cover is expected to produce an increase in the primary productivity rates of the whole Arctic and sub-Arctic regions subjected to study. However, the response of zooplankton is different. If the ice retreat occurs earlier than mid-March, a delay in phytoplankton productivity is expected, producing a mismatch that results in a decrease of the general population (OCH). This would be restricted to the Bering Sea and thus for *C. marshallae*.

On a pan-Arctic scale, however, an ice retreat earlier than mid-March is not expected, so the OCH will not affect this region. Despite the timing in the pelagic bloom is very similar to the one of the OCH in warm years, there are more feeding opportunities and lower temperatures; so survival there is more likely. Besides, a longer growth season and higher temperatures facilitates the life cycle of both *Calanus* species. For these reasons it is expected a colonization of the Chukchi and Beaufort seas by *C. marshallae* and an increase of the populations of *C. glacialis*, overall in the inshore regions.

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