



## Emergence of the Arctic *Themisto libellula* (Amphipoda: Hyperiididae) on the southeastern Bering Sea shelf as a result of the recent cooling, and its potential impact on the pelagic food web

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The eastern Bering Sea shelf experienced a sequence of warm years after a regime shift in the late 1970s. Following a series of unusually warm years in the early 2000s, the climate shifted again in 2007 to a series of extremely cold years that were marked by intense ice coverage and late ice retreat. Spatial and temporal variability in zooplankton communities during the recent cold period was investigated as part of the collaborative BEST-BSIERP program. An increasing presence of the Arctic hyperiid *Themisto libellula*, which had not been reported from the southeastern Bering Sea since the 1970s, was observed in the Middle Shelf Domain, indicating a developing structural shift in the zooplankton community in response to continuous cold conditions. Simultaneously, *T. libellula* became an increasingly dominant prey in the diets of zooplanktivorous fish and seabirds, demonstrating the important role for *T. libellula* in the pelagic food web. Our analysis suggests that *T. libellula* is capable of controlling copepod populations, thus it may become a potential contributor to top-down regulation of *Calanus* spp. in the eastern Bering Sea.

**Keywords:** *Themisto libellula*, Bering Sea, climate change.

### Introduction

The Bering Sea provides habitat for both Subarctic (boreal) Pacific and Arctic fauna. Their co-existence is facilitated by warm currents from the south and by the presence of cold water, a remnant of the winter cooling, on the eastern Bering Sea shelf. The cold water is retained on the shelf in a bottom layer within the Middle Domain, a two-layered system, with an upper mixed layer separated from the deeper layer by a seasonal pycnocline at 15–40 m depth. The Middle Domain extends approximately between the 100-m and 50-m isobaths. In summer, it is bounded by the Middle and Inner Fronts on the offshore and inshore sides respectively. The shallower Inner Domain is unstratified due to wind and tidal mixing, while the Outer Domain, from 100 to 200 m depth, consists of a wind-mixed surface layer and a tidally mixed bottom layer, separated by a transition zone. The spatial coverage and temperature of the cold pool depends on the intensity of the sea ice

formation. The southward extent of the cold pool in summer is dependent on the areal extent and duration of the sea ice cover during spring. Thus, the amount of ice-melt and its distribution affects water column temperatures over the shelf for the remainder of the year (Stabeno *et al.*, 2001). Since many Subarctic species are intolerant of low temperatures associated with ice cover, the extent of ice therefore forms an effective boundary between Arctic and Subarctic demersal communities (Grebmeier *et al.*, 2006).

While even in the warmest years, sea ice is still formed in winter and, as result, a cold bottom layer with sub-zero temperatures is present on the northern shelf (~60°N to the Bering Strait), temperatures below the thermocline on the southern shelf can increase to 4–6°C or more during summer (Pinchuk and Coyle, 2008; Stabeno *et al.*, 2012a). Therefore, changes in the marine biota in response to interannual temperature fluctuations are more likely to occur in the south rather than the north.

Several periods of alternating warm and cold years, which have contributed to substantial differences in timing and persistence of ice cover, have been recorded in the Bering Sea since the mid 20th century. The longest sequence of cold years continued through the 1960s and early 1970s but abruptly ended in 1977 resulting in a regime shift (Hare and Mantua, 2000). As the warm phase continued into the early 2000s, the southern edge of the cold pool retreated ~230 km northward, resulting in community-wide northward distributional shifts in demersal and benthic fauna (Grebmeier *et al.*, 2006; Mueter and Litzow, 2008).

Since 2006, the eastern Bering Sea shelf has been experiencing a sequence of cold years marked by intense ice coverage and late ice retreat (Stabeno *et al.*, 2012b), which has resulted in extensive development of the cold pool (Coyle *et al.*, 2011; Danielson *et al.*, 2011). The rapid cooling provided a natural experiment on the response of the eastern Bering Sea ecosystem to a dramatic change in sea temperature. During the preceding warm period, euphausiid and *Calanus* spp. populations declined, diets of juvenile fish were dominated by exclusively small copepods and age-0 walleye pollock (*Theragra chalcogramma*) (Coyle *et al.*, 2011). During the cool period, large zooplankton abundance increased and juvenile fish consumed greater proportions of *Calanus* spp., euphausiids, and other large zooplankton taxa (Coyle *et al.*, 2011). Consequently, fish condition significantly increased during the cool period due to a threefold increase in lipid content provided by the higher quality prey items consumed (R. Heintz, personal communication). In addition, fish condition was positively correlated with fish survival, highlighting the importance of prey quality and quantity for fish recruitment.

*Themisto libellula* (Lichtenstein, 1822) are large (up to 60 mm in total length) hyperiid amphipods, which are widely distributed and abundant in the ice-covered central Arctic Ocean, and in most of the adjacent European and North American Arctic seas (Dunbar, 1957; Dalpadado *et al.*, 2001; Auel and Werner, 2003). Thus, *T. libellula* is recognized as a typical high boreal Arctic circumpolar species that can be regarded as a good indicator of the presence of Arctic waters in different Subarctic regions (Dunbar, 1957; Dalpadado *et al.*, 2001; Vassilenko and Petryashov, 2009). These predatory pelagic amphipods play a key role in the Arctic ecosystem linking herbivorous mesozooplankton to higher trophic level zooplanktivorous predators such as fishes, seabirds and seals (Dalpadado *et al.*, 2001; Haug *et al.*, 2004; Karnovsky *et al.*, 2008). The high nutritional value of *T. libellula* is facilitated by their high lipid content, which sub-adult and adult individuals accumulate during the summer season to survive through the winter and, subsequently, fuel reproduction in the following spring (Percy and Fife, 1981; Dale *et al.*, 2006; Noyon *et al.*, 2011). It has been noted that recent warming during the last decade in the Barents Sea led to substantial decreases in *T. libellula* abundance, indicating the importance of the thermal regime to the species survival (Dalpadado *et al.*, 2012).

In the Bering Sea, *T. libellula* belong to the northern (co-Arctic) zooplankton faunistic group and primarily occur on the shelf north of St Lawrence Island (Coyle *et al.*, 1996). Until the late 1970s, *T. libellula* were consistently reported from the entire eastern Bering Sea shelf (Bowman, 1960; Motoda and Minoda, 1974; Cooney, 1981; Hamanaka and Ogi, 1984), where they were an important constituent of the marine food web as a major prey for pelagic and semi-pelagic fishes (Yoshida, 1984), seabirds (Bedard, 1969; Ogi *et al.*, 1980; Hunt *et al.*, 1981; Ogi and Hamanaka, 1982), seals (Harry and Hartley, 1981) and whales

(Frost and Lowry, 1981). However, later surveys conducted during summer in the eastern Bering Sea in the 1990s and early 2000s found *T. libellula* only north of 57°N (Sugisaki *et al.*, 1998), and they were no longer found on the southeastern shelf (Stockwell *et al.*, 2001; Coyle *et al.*, 2008, 2011) or in the diets of seabirds at the Pribilof Islands in the 1980s (Decker *et al.*, 1995).

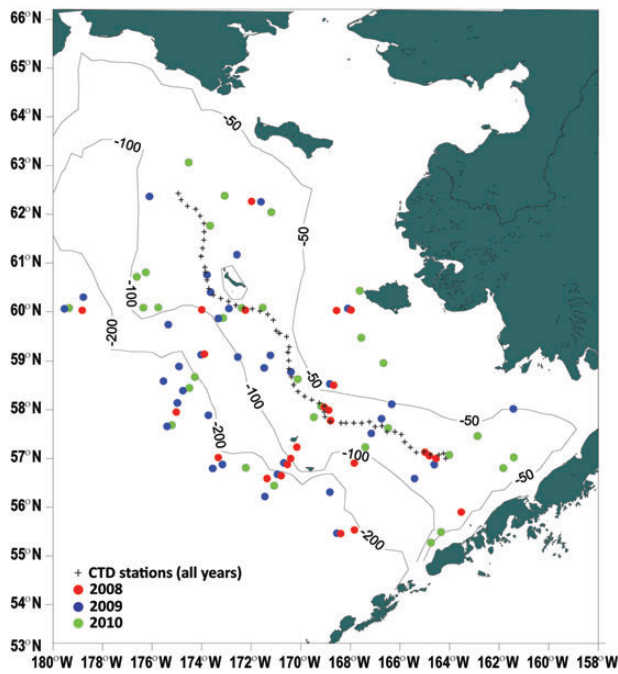
In this paper, we examine the hypothesis that, during cool periods on the southeastern Bering Sea (SEBS) shelf, Arctic *T. libellula* can establish its presence in the Subarctic community of the Middle Domain, exert top-down pressure on *Calanus* spp., and displace them in the diets of zooplanktivorous pelagic fishes and birds. To address this hypothesis, we first examine the spatial and temporal distribution of *T. libellula* among the eastern Bering Sea shelf domains during the ongoing cold phase based on zooplankton surveys conducted as a part of the collaborative Bering Sea Ecosystem Study (BEST) and the Bering Sea Integrated Ecosystem Research Project (BSIERP). Next, we examine *T. libellula* population structure to evaluate its potential impact on the copepods, *Calanus* spp., which constitute an important part of zooplankton community and provide the high quality prey for pelagic fishes in the Middle Domain. Finally, we use historic data on zooplanktivorous seabirds, least auklets (*Aethia pusilla*), and pelagic fish taxa such as Pacific herring (*Clupea pallasii*), Pacific cod (*Gadus macrocephalus*), and juvenile stages of chum salmon (*Oncorhynchus keta*), pink salmon (*O. gorbuscha*), and sockeye salmon (*O. nerka*) to show the importance of *T. libellula* as prey for these upper trophic level predators, and to link *T. libellula* emergence in the SEBS to climate variability.

## Methods

### Physical Oceanography and Zooplankton

Zooplankton samples, conductivity–temperature–depth (CTD), and fluorescence profiles were taken in the eastern Bering Sea during BEST-BSIERP summer cruises from 2008–2010 (Figure 1, Table 1). CTD profiles were taken with a Seabird model 911 Plus with dual conductivity and temperature sensors at all zooplankton stations and along the 70-m isobath (Figure 1). The time series of winter (January–March) sea surface temperature anomalies near the Pribilof Islands available from the PMEL Data Archive (<http://www.beringclimate.noaa.gov/data/>) was used as a proxy for the bottom layer temperatures to define cold and warm phases on the SEBS shelf during the past five decades. Hyperiiids and larger copepods (e.g. *Calanus* spp.) were collected using a 1-m<sup>2</sup> Multiple Opening Closing Net and Environmental Sensing System (MOCNESS) fitted with 500 µm mesh black nets and equipped with a flowmeter, conductivity and temperature probes. The MOCNESS was fished in open water at night and oblique samples were collected in 20-m increments either from 100-m depth, or from near the bottom in shallower locations, to the surface. Typically 100–150 m<sup>3</sup> of water were fished in each layer. The samples were preserved in a 10% formalin seawater solution for later analysis.

The samples were split with a Folsom splitter and the subsamples were examined to identify, count and determine the mass of hyperiidids as well as copepods. The zooplankton identification was done to the lowest taxonomic level possible. The two sibling species *C. marshallae* Frost 1974 and *C. glacialis* Jaschnov 1955 co-occurring in the Bering Sea (Nelson *et al.*, 2009; R. Campbell, personal communication) were referred to as *Calanus* spp. due to similar morphology. In practice, only small (<5 mm total body



**Figure 1.** Map of the night-time MOCNESS stations and CTD survey along the  $-70\text{-m}$  isobath during the BEST-BSIERP study in 2008–2010. The  $-50\text{-m}$ ,  $-100\text{-m}$  and  $-200\text{-m}$  isobaths delineate the Inner ( $<50\text{ m}$ ), Middle ( $50\text{--}100\text{ m}$ ) and Outer ( $100\text{--}200\text{ m}$ ) shelf domains.

**Table 1.** Summary of BEST-BSIERP summer cruises in the eastern Bering Sea.

Year	Cruise ID	Dates
2008	HLY0803	3 July–31 July 2008
2009	KNORR175-11	13 June–12 July 2009
2010	TN250	16 June–14 July 2010

length) juvenile hyperiids were enumerated from subsample counts, while the entire sample was examined to count larger specimens. Blotted preserved wet weights were measured on a Cahn Electrobalance or Mettler top-loading balance, depending on the size of the hyperiids. Similarly, wet mass measurements of each *Calanus* spp. stage were taken on each sample initially, and the coefficient of variation in average wet weight was computed. If, as subsequent samples were analysed, the coefficient of variation for any given stage changed by  $<5\%$ , the individual wet mass was no longer measured and the mean wet mass was applied to specimen counts to obtain wet biomass estimates. The data were uploaded to a Microsoft Access database, and analyses were performed using STATISTICA 6 software.

Total body length (TL, mm) of *T. libellula* individuals collected in 2010 was measured from the anterior part of the head to the tip of the uropods. All length measurements were made digitally to  $\pm 1\ \mu\text{m}$  with an accuracy of  $\pm 5\ \mu\text{m}$  (Roff and Hopcroft, 1986). Length-frequency histograms were resolved into normally distributed components (cohorts), and the Separation Index between each pair of successive cohorts was calculated using NORMSEP analysis, as implemented in FiSAT II (Gayaniolo et al., 1996). Dry weight (DW, mg) of *T. libellula* was estimated using the following allometric relationship between DW and TL derived from

measurements conducted on the Konigsfjord (Svalbard) population (Table 1 in Noyon et al., 2009):

$$DW = 0.0045 * TL^{2.7071} (r^2 = 0.97).$$

The calculated coefficients are similar to those reported on *T. libellula* from Frobisher Bay in the Labrador Sea (Percy, 1993a).

Stage-specific dry weight of *Calanus* spp. was estimated as 25% of the corresponding wet weight as has been demonstrated for other closely-related Arctic and Subarctic *Calanus* species (Scott et al., 2000).

We analysed a total of 305 MOCNESS samples. MOCNESS samples from the same tow are autocorrelated and cannot be treated as independent when running statistical analyses. Therefore an integrated estimate of abundance or biomass for each station was computed as follows. The abundance and biomass of each taxon was computed for each net as numbers  $\text{m}^{-3}$  or  $\text{g m}^{-3}$ . The data were integrated through the depth interval for each net to estimate abundance or biomass  $\text{m}^{-2}$  for each net sample, and these values were summed to estimate values  $\text{m}^{-2}$  for the whole water column. If net depths overlapped, the mean of the overlapping portion for each net was computed for each depth interval before summing. Since nets were fished in an oblique manner from 100 m or from near the bottom to the surface, little overlap was observed. The value  $\text{m}^{-3}$  for each station was determined by dividing the numbers  $\text{m}^{-2}$  by the total depth interval (m) sampled by the tow. Due to the uneven spatial distribution, the abundance and biomass data were log-transformed to stabilize the variance. The stations were grouped by domain (Outer, Middle and Inner) and subdivided into the northern and southern groups with the boundary at  $60^\circ\text{N}$  latitude. Analysis of variance (ANOVA) was used to test for significant effects of location and year on physical and biological variables, and the distribution of residuals was analysed. When the residuals satisfied the normality assumption (in practice always after log-transformation of the raw data) and ANOVA results indicated significant effects, a Tukey *post hoc* test was applied to identify significant differences ( $p < 0.05$ ) between the means.

A Pearson correlation index was calculated between *T. libellula* biomass and *Calanus* spp. biomass sampled simultaneously to test for potential predation in 2010. Potential daily predation impact ( $PI_c$ , % of *Calanus* spp. biomass  $\text{d}^{-1}$ ) of *T. libellula* (excluding the recently hatched recruits) on *Calanus* spp. was calculated as

$$PI_c = \frac{DIR_c * \sum B_{Ti}}{\sum B_{Cj}}$$

where  $B_{Ti}$  is the biomass of *T. libellula* cohort  $i$ ,  $B_{Cj}$  is the biomass of *Calanus* spp. developmental stage  $j$ , and  $DIR_c$  is the *T. libellula* daily ingestion rate of *Calanus* spp. copepodites (% of body dry weight  $\text{d}^{-1}$ ) among other prey. We assumed that *T. libellula* feeding pattern in the Bering Sea is similar to that observed in the Arctic and North Atlantic, where *Calanus* spp. copepodites were the most abundant prey items comprising up to 75% of total prey (Marion et al., 2008). *T. libellula* of TL 10–24 mm were assumed to consume *Calanus* spp. copepodite Stages III and IV (Noyon et al., 2009), and individuals  $> 24\text{ mm}$  TL to feed on copepodite Stage V (Marion et al., 2008), since few adult copepods occurred in the samples. The daily ingestion rate of *T. libellula* on *Calanus* spp. was assumed to be 3.4–4.02% of



**Table 2.** Number of fish stomachs used for diet analysis in 2003–2010.

Species	2003	2004	2005	2006	2007	2008	2009	2010
<i>Clupea pallasii</i>	38	15	11	20	25	25	10	6
<i>Gadus macrocephalus</i>	8	23	23	40	17	10	1	37
<i>Oncorhynchus gorbuscha</i>	12	27	41	1	25	5	22	16
<i>Oncorhynchus keta</i>	31	87	84	53	116	8	22	24
<i>Oncorhynchus nerka</i>	48	58	73	17	46	12	14	23

*T. libellula* body dry weight  $d^{-1}$ , as estimated from stomach contents from two different locations in the Gulf of St Lawrence (Marion *et al.*, 2008).

### Fish and Seabird diets

Fish samples were collected in the SEBS from mid-August to early October 2003–2010, as part of the North Pacific Anadromous Fish Commission's Bering Aleutian Salmon International Survey program (BASIS). Fish were collected during the day with a rope trawl (Farley and Moss, 2009) and the catches were subsampled for diet analysis; processing of fish for diet analysis was done on the ship using standard methodology as described by Moss *et al.* (2009). A total of 1229 stomachs were used for the diet analysis (Table 2).

Least auklet diets were assessed by collecting chick meals on St Paul and St George Islands (Pribilof Archipelago). Samples in the 1970s were collected by G. Hunt (Hunt *et al.*, 1981). Since 1980 seabird diets have been collected by monitoring crews for the U.S. Fish and Wildlife Service as part of an ongoing monitoring program by the Alaska Maritime National Wildlife Refuge (Byrd, 2007). Since adults carry food for the chick in a throat pouch, the food, regurgitated when captured in a noose carpet or mist net (e.g. Jones *et al.*, 2007), was collected throughout the chick-rearing period (late June–early August) from 1975–1978 and from 1996–2010. Prey samples were preserved in 70% ethanol for later analysis. Samples were split with a Folsom splitter and the subsamples were examined to identify and count each prey species.

## Results

### Physical/biological oceanographic conditions

In all three years (2008–2010), a two-layered water column structure marked by a thermocline located at ~20 m was observed along the 70-m isobath with the cold pool extending south of 56°N (Figure 2). During the 2008 cruise, which occurred later in the summer (Table 1), the coldest (<0°C) water was located north of 59°N, while in 2009 and 2010 it extended over the entire domain, leading to significantly colder conditions in the south (Figure 2, Table 3). The cross-shelf distributions of the water properties were consistent during all cruises; the cold pool was bounded by the Inner Front near the 50-m isobath and the Middle Front along the 100-m isobath. Examination of the time series of sea surface temperature anomalies in winter reveals that two sequences of cold years occurred after the regime shift in the late 1970s during 1989–1993 and 1999–2000 (Figure 3).

### Spatial distribution and interannual variability

There were significant differences in *T. libellula* cross-shelf distribution. Most *T. libellula* occurred in the Middle Domain during all three years, with only a few specimens observed in the Outer and the Inner Domains (Figure 4a and c). An ANOVA revealed significant interannual differences in *T. libellula* abundance and

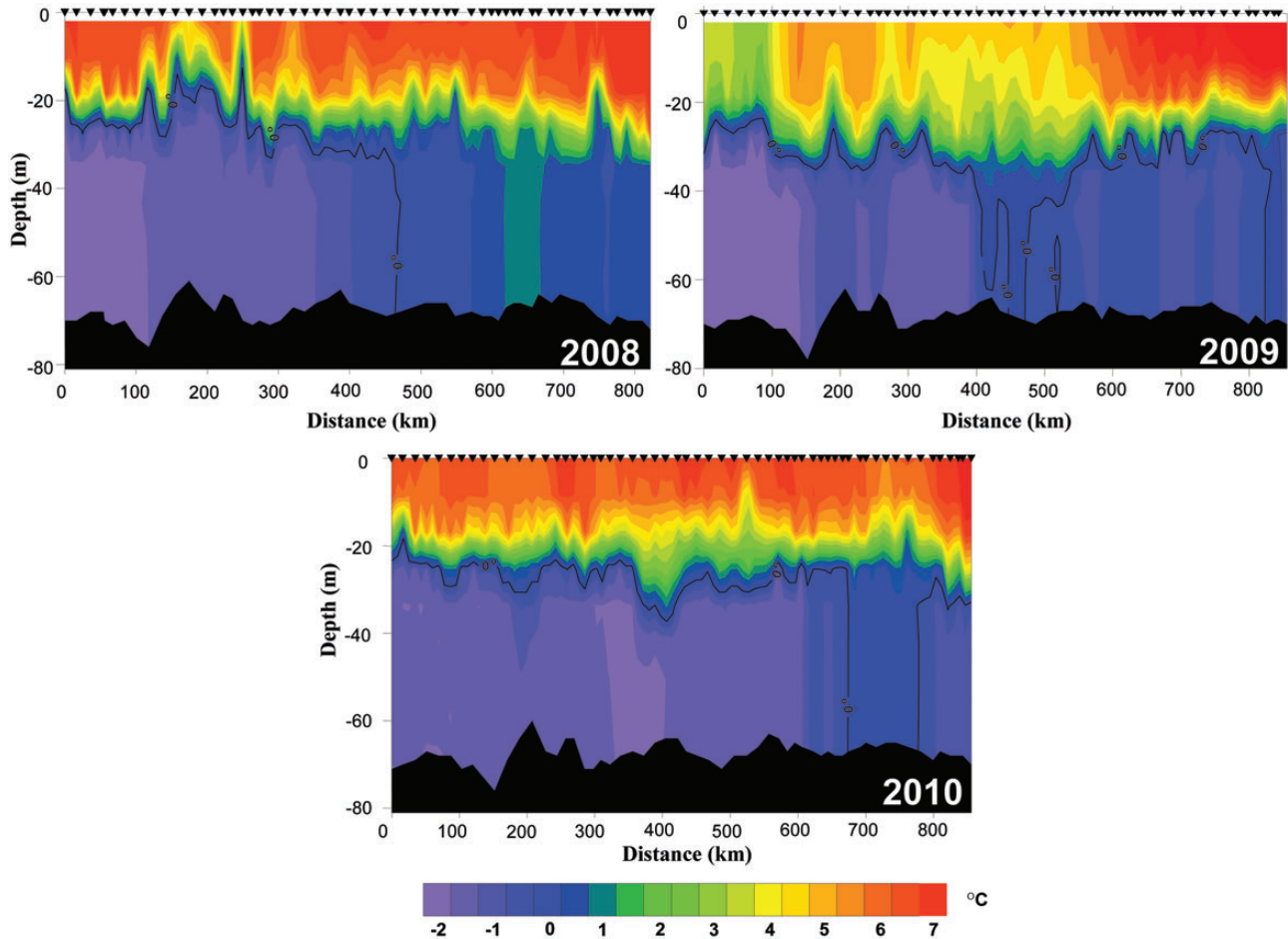
biomass in the Middle Domain ( $F = 7.82$ ,  $p = 0.001$ , and  $F = 6.5$ ,  $p = 0.003$ , respectively). There was a significant increase in abundance in 2009, while biomass significantly increased in 2010 (Tukey tests on log-transformed data). While the mean abundance was no different in 2009 and 2010, the maximum range value was 2.5 times higher (391 individuals  $100\text{ m}^{-3}$  in 2009, versus 989 individuals  $100\text{ m}^{-3}$  in 2010), indicating the presence of denser aggregations of *T. libellula* on the shelf in 2010. There was no significant interannual difference in *T. libellula* abundance or biomass in the northern Middle Domain. In contrast, in the southern Middle Domain *T. libellula* showed a significant increase in both abundance and biomass from 2008 to 2010 ( $F = 6.12$ ,  $p = 0.006$ , and  $F = 5.28$ ,  $p = 0.013$ , respectively) (Figure 4b and d).

### Population structure

The length-frequency distribution of *T. libellula* in 2010 was resolved into three distinct cohorts (Figure 5). The total length of *T. libellula* varied from 2–40.6 mm, however amphipods > 30 mm were excluded from the statistical analysis due to underrepresentation in the samples. Statistical splitting of length-frequency distributions gave 3 modes with mean lengths of 3.66 mm, 6.18 mm and 17.04 mm. The low value of the Separation Index for the first two modes (1.94) suggests that they belong to the same 0+ year class and probably resulted from an extended spawning event during the preceding spring. In contrast, the third mode (Separation Index = 2.77) presumably represents the 1+ year class, and the larger specimens appear to be even older.

### Predation impact on *Calanus* spp. population

A significant negative correlation ( $r = -0.5277$ ,  $p < 0.001$ ) was observed between *T. libellula* and *Calanus* spp. biomass, which may be due to predation (Figure 6). The correlation explains about 30% of the variance with the rest attributed to other causes. Inspections of *T. libellula* stomach contents revealed the presence of *Calanus* spp. remains. The mean daily predation impact of *T. libellula* on the *Calanus* spp. population in the Middle Domain in the early summer of 2010 was estimated at < 1% of *Calanus* spp. standing stock based on mean species distributions (Table 4). However, at the individual stations, where both *Calanus* spp. and 1+ and older *T. libellula* co-occurred (~50% of all stations in the Middle Domain), the daily predation impact during the period of observations was much higher, averaging 35.8%. No information is available about *T. libellula* feeding in other seasons. While, in addition to the predominant prey *Calanus* spp., *T. libellula* diet may include other zooplankton such as copepods (e.g. *Pseudocalanus* spp.), euphausiids, chaetognats etc. (Marion *et al.*, 2008; Noyon *et al.*, 2009); no attempt was made to estimate *T. libellula* impact on those taxa.



**Figure 2.** Temperature profiles ( $^{\circ}\text{C}$ ) from the north to the south along the 70-m isobath in the Middle Domain of the Eastern Bering Sea shelf. The inverted triangles indicate CTD locations.

**Table 3.** Temperature ( $^{\circ}\text{C}$ ) above and below the thermocline, and thermocline depth (Mean  $\pm$  95% CI) in the SEBS Middle Domain in early summer 2008–2010.

Variable	2008		2009		2010	
	North	South	North	South	North	South
Upper Layer, $^{\circ}\text{C}$	$6.18 \pm 0.4$	$6.47 \pm 0.27$	$3.79 \pm 0.41$	$4.98 \pm 0.26$	$5.84 \pm 0.41$	$5.60 \pm 0.26$
Lower Layer, $^{\circ}\text{C}$	$-1.24 \pm 0.26$	$0.25 \pm 0.17$	$-1.16 \pm 0.27$	$-0.43 \pm 0.17$	$-1.05 \pm 0.27$	$-0.60 \pm 0.17$
Water Column, $^{\circ}\text{C}$	$0.39 \pm 0.28$	$2.21 \pm 0.18$	$0.52 \pm 0.29$	$1.45 \pm 0.18$	$0.98 \pm 0.29$	$1.36 \pm 0.18$
Thermocline Depth, m	$16.9 \pm 2.1$	$23.2 \pm 1.4$	$25.2 \pm 2.2$	$26.1 \pm 1.4$	$19.8 \pm 2.2$	$21.2 \pm 1.4$

### Fish and seabird diets

The contribution of *T. libellula* to the diets of Pacific herring, Pacific cod, and juvenile pink, chum and sockeye salmon dramatically increased after the onset of the recent cold phase in 2006 (Figure 7). While *T. libellula* were completely absent from the stomachs before 2007, they comprised approximately 25–55% of the total of fish diets by weight by 2010. The first appearance of *T. libellula* in the diets lagged by one year after the onset of the cooling in 2006, implying that an interval of one year was required before *T. libellula* populations increased sufficiently to impact the fish diets.

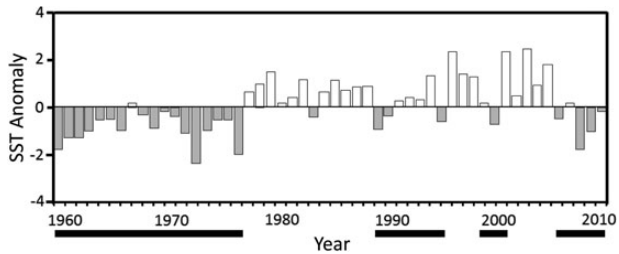
Long-term observations on the planktivorous least auklets from the Pribilof Islands indicated that *T. libellula* availability as a prey coincided only with cold conditions on the shelf

(Figure 8). The species occurred in the diets during the cold phases in the late 1970s, in 2000–2001 and during the ongoing cooling initiated in 2006. Similar to the fish dietary patterns, the first appearance of *T. libellula* in the diet of the least auklets also lagged by one to two years after the onset of the cooling phases in 1999 and 2007.

### Discussion

Zooplankton surveys conducted in 2008–2010 indicated an increasing *T. libellula* population in the Middle Domain of the SEBS shelf not seen since the 1970s. This emergence of *T. libellula* was associated with cold conditions in the SEBS. Survey data were corroborated by planktivorous seabird and fish diets. Both physical and biological factors may have contributed to the observed

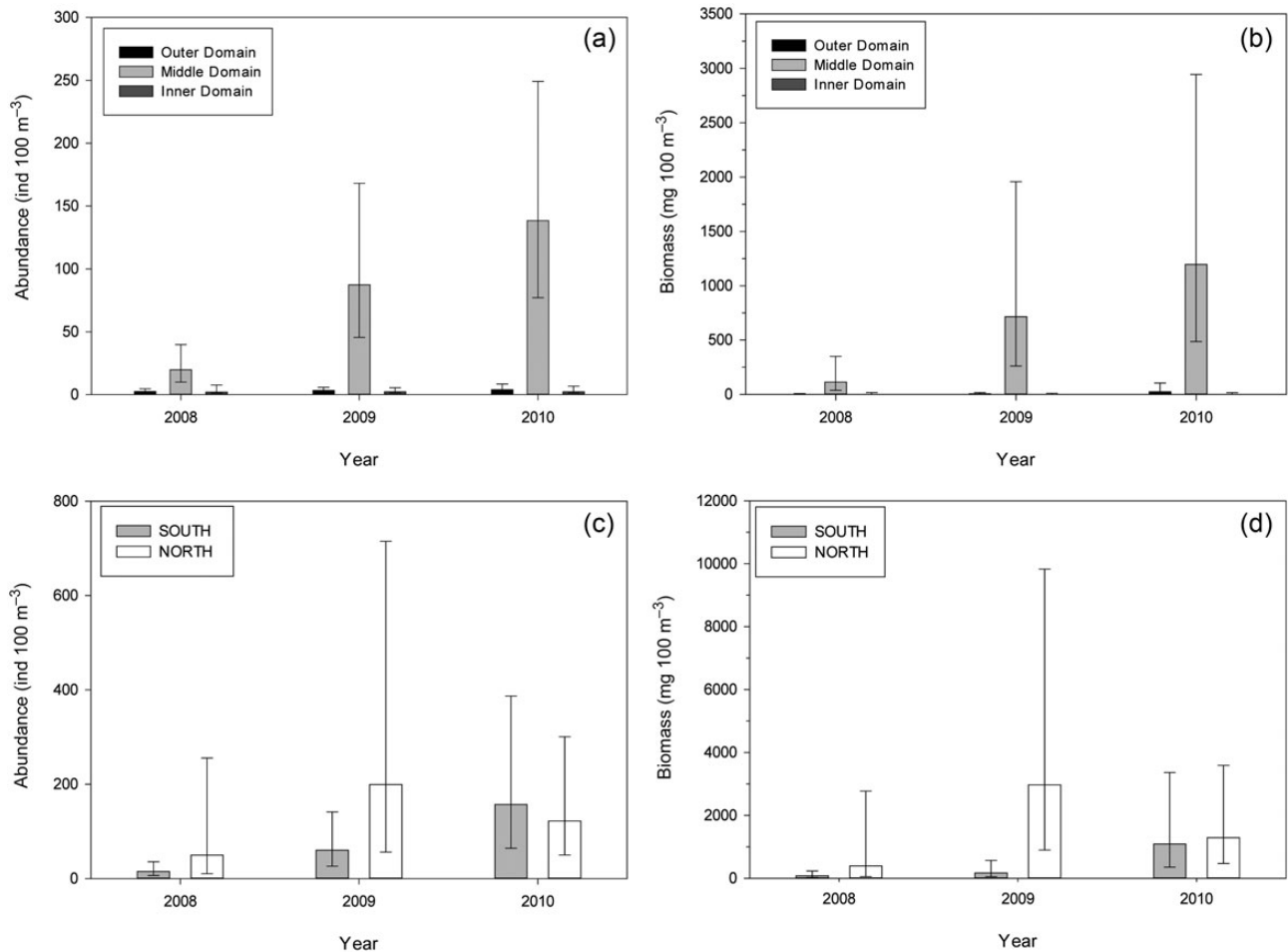
reintroduction of the *T. libellula* population to the SEBS shelf during the recent cold phases. The cold-water *T. libellula* has a High Boreal Arctic zoogeographic distribution: in addition to the Arctic Ocean and its marginal seas, it occurs in the northern Bering and Okhotsk seas, as well as in the North Atlantic south to the Gulf of St Lawrence, and in the southeast Alaskan glacial fjords and Prince William Sound (Coyle and Pinchuk, 2005; Harvey *et al.*, 2009). Outside of the Arctic Ocean, *T. libellula* typically inhabit areas where cold-water ( $<3^{\circ}\text{C}$ ) layers are present



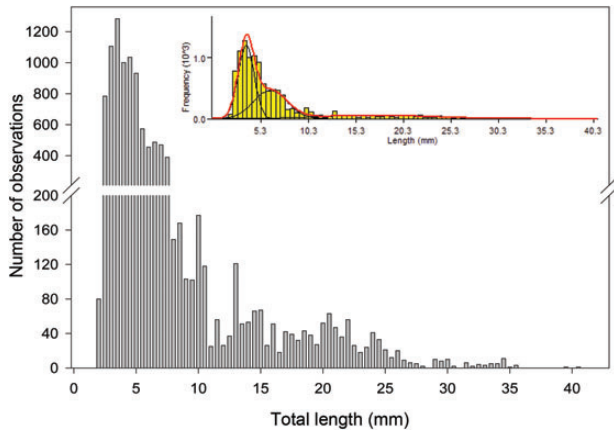
**Figure 3.** Winter (January–March) sea surface temperature (SST) anomalies in the vicinity of the Pribilof Islands, SEBS. PMEL Data Archive <http://www.beringclimate.noaa.gov/data/> (cold phases are underlined).

throughout the summer. Both the northern Okhotsk Sea and the Gulf of St Lawrence have a three-layered water column structure with intermediate cold layers between  $\sim 25$  m and 200 m depth, which, like the Bering Sea shelf bottom water, are the remnants of the near-freezing winter surface waters, initially formed by winter cooling (Luchin, 1996; Gilbert and Pettigrew, 1997). In the Gulf of St Lawrence, *T. libellula* typically has occurred within the intermediate cold layer (Harvey *et al.*, 2009), while in the northern Okhotsk Sea it also has been observed in the adjacent surface layer (Lubny-Gertzky, 1959).

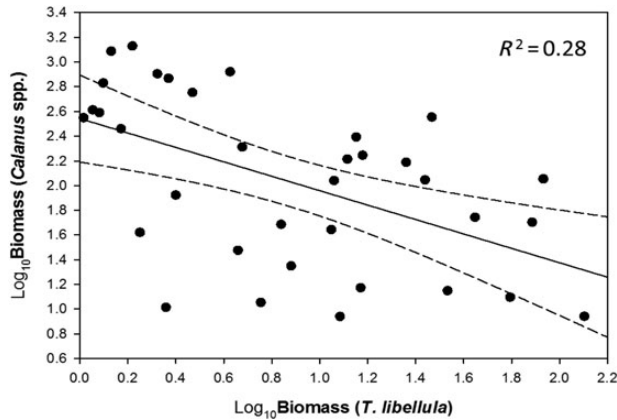
Interestingly, the Prince William Sound and the Inner Passes of south-central and southeastern Alaska appear to be exceptions, since no extensive cold layers are formed within their boundaries, and the water temperature below the thermocline is typically about  $5.5\text{--}7.5^{\circ}\text{C}$  on average throughout the year (Coyle and Pinchuk, 2005). The southeast Alaska population markedly differs in its response to thermal conditions by shifting both their sensitivity and the upper lethal temperature limit to  $4\text{--}5^{\circ}\text{C}$  higher than those of the Arctic *T. libellula*, which indicates a physiological adaptation to a warmer environment (Wing, 1976; Percy, 1993a). Paleoclimatological reconstructions suggest that cold temperature and freezing conditions existed in the Gulf of Alaska during the last glacial period, providing a suitable environment



**Figure 4.** Distribution of *T. libellula* by domain (Inner, Middle and Outer) and by region (North and South) on the eastern Bering Sea shelf. (a) Mean abundance by domain; (b) mean abundance by region; (c) mean biomass by domain; (d) mean biomass by region. Error bars are 95% confidence intervals.



**Figure 5.** Size frequency distribution of the *T. libellula* population in the SEBS in 2010 (insert shows fitted curves from NORMSEP analysis).



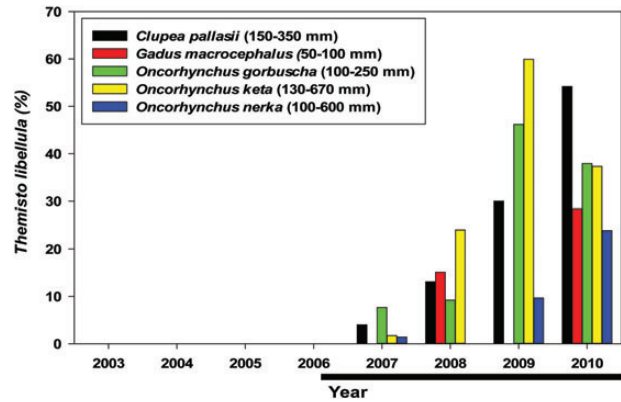
**Figure 6.** Relationship between *T. libellula* and *Calanus* spp. log-transformed biomass ( $\text{mg m}^{-3}$ ) (solid line is linear regression, dotted lines are 95% confidence limits).

**Table 4.** Abundance (individuals  $\text{m}^{-3}$ ) and Dry Biomass ( $\text{mg m}^{-3}$ ) of *T. libellula* and *Calanus* spp. in the Middle Domain of the SEBS in 2010.

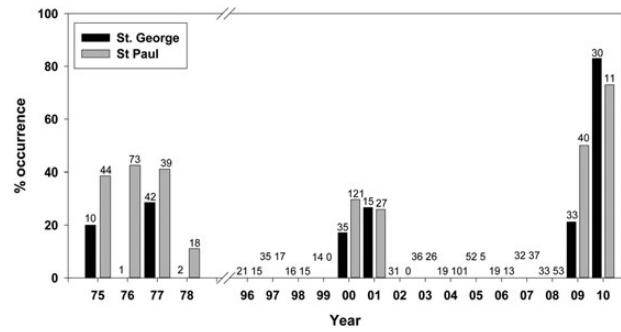
	Mean Abundance (Range)	Mean Dry Biomass (Range)
<i>Calanus</i> spp. CIII	66.9 (4.1–331)	4.4 (0.27–21.6)
CIV	80.6 (1.8–290)	18.1 (0.41–65.1)
CV	32.1 (0–139)	15.9 (0–69.3)
Total	178.9 (7.2–760)	38.4 (1–156)
<i>Themisto libellula</i>		
10–25 mm	0.356 (0–2.19)	5.29 (0–47.58)
25–40 mm	0.029 (0–0.211)	1.76 (0–12.58)
Total	0.385 (0–2.361)	7.05 (0–57.26)
<b>Daily Predation Impact</b>		
$\text{DIR}_C = 4.02$		0.74
$\text{DIR}_C = 3.40$		0.62

Daily Predation Impact (% of *Calanus* spp. biomass  $\text{d}^{-1}$ ) was calculated for two Daily Ingestion Rates ( $\text{DIR}_C$ , % of body dry weight  $\text{d}^{-1}$ ) adopted from Marion *et al.*, 2008.

for cold-water biota (e.g. sea ice-related diatoms) (de Vernal and Pedersen, 1997; Barron *et al.*, 2009). Tidewater glaciers in Alaskan fjords may have provided a cold refuge to relict *T. libellula* populations after the last ice age.



**Figure 7.** Percentage of *T. libellula* by wet weight in the diet of pelagic fish collected in the Middle Domain, SEBS (cold phases are underlined).



**Figure 8.** Percent frequency of occurrence (i.e. number of samples containing at least one individual) of *T. libellula* in the diet of least auklet (*Aethia pusilla*) from the Pribilof Islands, SEBS. Numbers above the bars indicate sample size (cold phases are underlined).

Cold layers appear to be essential for *T. libellula* survival in Subarctic seas, where they may provide both a retreat from warmer temperatures during summer, and a better overwintering environment. Summer temperature in the upper 20-m layer of the eastern Bering Sea shelf is approximately 9°C during the coldest years, but may reach 14°C during the warmest years (Stabeno *et al.*, 2012a). In contrast, the upper lethal temperature limit for Arctic *T. libellula* was found to be 9.4°C (Percy, 1993a), which makes it prohibitive for *T. libellula* to spend much time foraging above the thermocline in summer in the SEBS.

Like other Arctic zooplankton, *T. libellula* accumulates lipid in summer when prey is abundant (e.g. Noyon *et al.*, 2011), and its lipid content may increase from 18% to as much as 35% of dry body mass by the end of summer (Percy and Fife, 1981). Colder winter conditions would slow metabolic rates and lower lipid consumption, leading to higher survival and higher reproductive success by *T. libellula* in winter and early spring (Dunbar, 1957; Wing, 1976; Percy, 1993b). Oxygen consumption by *T. libellula* of 8.7–26.9 mm TL is not substantially affected by temperature changes below 3°C, but rapidly increases at warmer temperatures, nearly tripling the initial respiration rate at 10°C (Percy, 1993a), indicating that interannual temperature fluctuations in the SEBS (e.g. Stabeno *et al.*, 2012a) may substantially impact *T. libellula* metabolism. The potential impact of warmer bottom temperatures can be estimated by converting weight-specific respiration rates to



carbon-specific rates (e.g. Ikeda *et al.*, 2000) using a respiratory quotient of 0.97 (Gneiger, 1983) and a carbon content of 35% of DW (Percy, 1993a). During the recent warm phase in 2001–2005, the near-bottom temperature in the southern Middle Domain exceeded 2°C for most of the year, while during the cold 2008–2010 phase the near-bottom temperature remained close to 0°C (Stabeno *et al.*, 2012b). The resulting carbon-specific rates are 0.016 d<sup>-1</sup> at 0°C and 0.018 d<sup>-1</sup> at 3°C. Applying these rates to the winter thermal regime, conservatively estimated to be 7 months long, the difference in weight-specific energy expenditure of *T. libellula* is 0.42, which means that an individual animal may spend an extra 42% of its body weight on metabolic activity during warmer relative to colder winters.

Our regression analysis suggests a potential impact of *T. libellula* predation on *Calanus* spp. populations in the SEBS. An alternative explanation for the observed negative correlation may invoke a concurrent biogeographical shift in *Calanus* spp. distribution away from the expanding *T. libellula* population. The dominant circulation patterns in the SEBS Middle Domain suggest only two possible vectors: northward along the shelf following the Alaska Coastal and Bering Slope currents, and westward across the shelf during occasional advective events (Danielson *et al.*, 2012). The consistent low abundance of *Calanus* spp. in the zooplankton assemblages occupying the Outer Domain during last decade (Eisner *et al.*, in review) indicates the improbability of such shift. While *T. libellula* can ingest a variety of prey, they prefer lipid-rich *Calanus* spp. over other copepods in the Arctic and Gulf of St Lawrence (Auel *et al.*, 2002; Dalpadado *et al.*, 2008; Marion *et al.*, 2008; Noyon *et al.*, 2009). Older *Calanus* spp. copepodites have high lipid contents by the end of the production season, which presumably fuels their maturation and subsequent reproduction in the following winter and spring. *Calanus* spp. populations were low during the warmer years of 2001–2005 but increased after 2005, when sea ice cover during spring was heavy (Baier and Napp, 2003; Coyle *et al.*, 2011). The causes of these fluctuations in *Calanus* spp. populations probably involve the timing and magnitude of the spring bloom when *Calanus* spp. reproduction occurs, and the extent and intensity of summer stratification, which limits post-bloom production in summer and fall, which is required for *Calanus* spp. growth and lipid accumulation (e.g. Coyle *et al.*, 2011; Hunt *et al.*, 2011). Both weak stratification and cold temperatures should favor *Calanus* spp. population growth during years of heavy ice cover. At the same time, since the success of seasonal lipid accumulation by *T. libellula* depends on food availability as well as on temperature, colder temperatures and weaker stratification should also support elevated *T. libellula* populations during years when the cold pool is developed on the SEBS shelf. A similar effect has been reported from Kongsfjorden (Svalbard), when *T. libellula* failed to accumulate lipids during an intrusion of warm Atlantic water populated with lower quality prey (Noyon *et al.*, 2011).

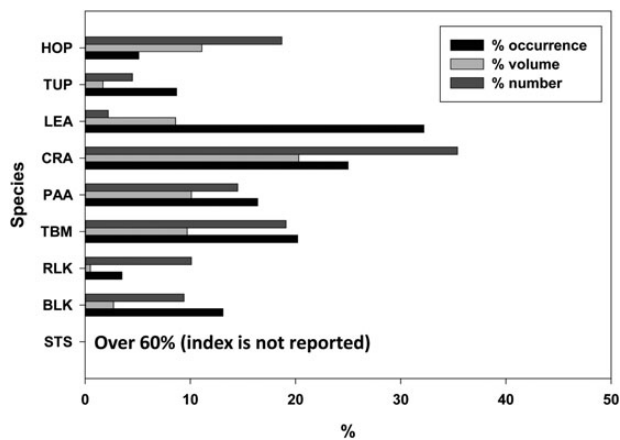
Our estimates indicate that *T. libellula* predation may substantially lower *Calanus* spp. populations in areas of *T. libellula* aggregations. While plausible, these estimates, based on the rates measured from other areas, must be taken as a rough approximation of potential impact, rather than as an accurate evaluation, and they would benefit from a more detailed investigation of *T. libellula* feeding patterns in the Bering Sea. As *Calanus* spp. abundance declines relative to *T. libellula* biomass, the diet of *T. libellula* will probably include greater proportions of alternate prey and *Calanus* spp. losses to *T. libellula* predation will likely decline. Thus, we

assume that  $PI_C$  represents saturated predation on *Calanus* spp. by *T. libellula* relative to *T. libellula* biomass. If the cold phase persists, at some point *T. libellula* may reduce *Calanus* spp. populations despite favorable conditions for *Calanus* spp. growth and reproduction. Since *Calanus* spp. are the principal food for many larval fish, such as walley pollock, *Themisto libellula* becomes an effective competitor, capable of limiting their larval survival and, therefore, the adult recruitment. On the other hand, *T. libellula* also experience growing predation by many pelagic fishes and seabirds. The contribution of *T. libellula* to the diet of Pacific herring, juvenile Pacific cod, and pink, chum and sockeye salmon increased from zero before the recent cold phase to 20–60% in 2010, indicating a major shift in fish feeding preferences from piscivory to planktivory (Coyle *et al.*, 2011). Similarly, our data indicate a growing importance of *T. libellula* in the diet of least auklets and, potentially, that of other seabirds. Thus, data presented here are suggestive of a trophic cascade, where predation by apex predators influences populations down through the trophic chain.

The two sub-peaks in the first size cohort of the *T. libellula* population indicate a prolonged reproduction event in 2010. In the Arctic, newly released juveniles from the brood pouches have a length of 2–4 mm and the peak release of juveniles occurs in March–May (Percy, 1993b; Dalpadado, 2002; Dale *et al.*, 2006). This reproduction timing matches our observations of newly released juveniles of *T. libellula* co-occurring with large (25–30 mm TL) females in the Bering Sea in April 2008–2009. Applying the growth model developed for the Kongsfjorden (Svalbard) population (Noyon *et al.*, 2011) for the time period of 45 days since the earliest release (presumably in mid-April) yields a TL of 10.6 mm—the length limit of the 0+ cohort observed in June 2010. At the same time, the presence of *T. libellula* specimens < 5 mm TL in our samples indicates that the release was still ongoing at our time of sampling in June. Data from gut content analysis and fatty acid trophic markers indicated that early juveniles fed on both phytoplankton and small zooplankton (Noyon *et al.*, 2009). Therefore, an early and prolonged phytoplankton bloom in the SEBS, which is characteristic of cold years, is beneficial to the new recruits. Young *T. libellula* have limited starvation capacity due to a relatively low lipid content, since most of their energy is invested in somatic growth, rather than in building up lipid storage (Noyon *et al.*, 2011). Therefore, a delayed bloom during warm years may lead to a mismatch between the new recruits and their food supply, and substantially affect survival of young *T. libellula*, which in turn will influence *T. libellula* population dynamics by determining the recruitment of mature individuals in a particular year. The annual recruitment success of the young individuals can eventually affect the size of the spawning population and rate of population growth.

The broad *T. libellula* size range observed in this study indicates a multi-year life span in the Bering Sea. Using the above growth model, we project that by the end of the production season (90 days after our observations) the animals from the 0+ cohort will reach their overwintering size of ~15–19 mm TL, which corresponds well to the 1+ cohort sizes from our observations. According to the model, those individuals would reach 22–25 mm TL by the end of the next production season, assuming no growth in winter, thus representing a 2+ cohort, which we were not able to resolve statistically (presumably due to the limited number of observations and possible escape from the





**Figure 9.** Contribution of *T. libellula* to the diets of seabirds from the Pribilof Islands, SEBS in 1975–1978 (after Hunt *et al.*, 1981): percent frequency of occurrence is the percentage of samples containing at least one individual; percent volume is the sum of the *T. libellula* volumes from all samples divided by the total volume of all samples combined; percent number is the total number of *T. libellula* divided by the number of all prey individuals; HOP = Horned Puffin (*Fratercula corniculata*), TUF = Tufted Puffin (*F. cirrhata*), LEA = Least Auklet (*Aethia pusilla*), CRA = Crested Auklet (*A. cristatella*), PAA = Parakeet Auklet (*A. psittacula*), TBM = Thick-billed Murre (*Uria lomvia*), RLK = Red Legged Kittiwake (*Rissa brevirostris*), BLK = Black-Legged Kittiwake (*R. tridactyla*), STS = Short-Tailed Shearwater (*Puffinus tenuirostris*).

nets). The small number of animals > 30 mm TL indicates the possibility of an even longer life-span of up to 3 years, similar to that suggested for European Arctic waters (Koszteyn *et al.*, 1995). While analysing the particular reproductive state of mature animals was beyond the scope of this study, we suggest that the first spawning will occur during the second year of life when they reach 20–25 mm TL, similar to the population from the Frobisher Bay (Percy, 1993b). Previous studies indicate a second reproduction in the following year when the animals are > 30 mm TL (Dunbar, 1946; Percy, 1993b). Considering the *T. libellula* multi-year life-span, the combined effects of successful spawning, early survival and strong recruitment of mature individuals in the following year may be cumulative, decreasing or increasing population abundance depending on the nature and extent of the climatic phase. The progressive increase in abundance of *T. libellula* by the end of production season during the recent cold phase (Coyle *et al.*, 2011) supports this suggestion.

The mechanism of southward expansion is probably related to occasional wind-induced transport during winter (Danielson *et al.*, 2012), so the new area is seeded by relatively small numbers of ovigerous females prior to the next summer, before the wind pattern changes to predominantly southeasterly. Therefore, one to two years are required for the new cohort to reach maturity and reproduce. The least auklet diet data show a consistent lag of one to two years after the beginning of each cold phase before *T. libellula* occur in diet samples, further supporting the suggestion of a slow start of re-colonization. However, once the first cohort matures, the population size would dramatically increase as long as the favourable conditions of the cold phase continue. An alternative explanation employs the possibility that reproduction occurred elsewhere and newly hatched individuals were advected onto the SEBS shelf. The only

potential source of new recruits outside of the SEBS is *T. libellula* populations in the Prince William Sound and Southeast Alaska (Wing, 1976, Coyle and Pinchuk, 2005). However, such an advection would undoubtedly result in high numbers of *T. libellula* in the coastal Gulf of Alaska, a projection that is not supported by ongoing oceanographic surveys (K. Coyle, personal communication).

The Bering Sea had been very cold for decades before the climate shift occurred in the late 1970s. Therefore, it is instructive to revisit old data to obtain insights into the role of *T. libellula* in well-established Arctic-like conditions in the Bering Sea. While occasional publications do acknowledge the generic presence of *T. libellula* over the SEBS shelf in the past (e.g. Motoda and Minoda, 1974, Wing, 1976), quantitative estimates are rare due to a lack of consistent zooplankton surveys that employed larger nets suitable for quantitative sampling of micronekton. According to Cooney (1981), *T. libellula* exhibited a similar cross-shelf distribution in the early summer of 1975, as was observed in this study; however, the reported abundances are not strictly comparable with our estimates due to different sampling techniques. Nevertheless, seabird diets near the Pribilof Islands in the 1970s show the importance of *T. libellula* as a prey for a wide range of species, thus indicating the presence of large *T. libellula* concentrations (Figure 9; Hunt *et al.*, 1981). It is worth noting that piscivorous puffins and kittiwakes, accustomed to larger prey sizes than planktivorous auklets, were also foraging on *T. libellula* in the late 1970s, suggesting that individuals of larger sizes were present in the area. Thus, similar to the Arctic, *T. libellula* appears to have been a key component of the SEBS shelf ecosystem in the past and, if the ongoing cooling marks the beginning of a long-term cold phase, as some models predict (D'Aleo and Easterbrook, 2010), the *T. libellula* population will continue to thrive and may substantially change trophic pathways in the SEBS.

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