Neocalanus copepods as an integral component for ecological modeling in the PICES regions

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What's "Neocalanus" ?

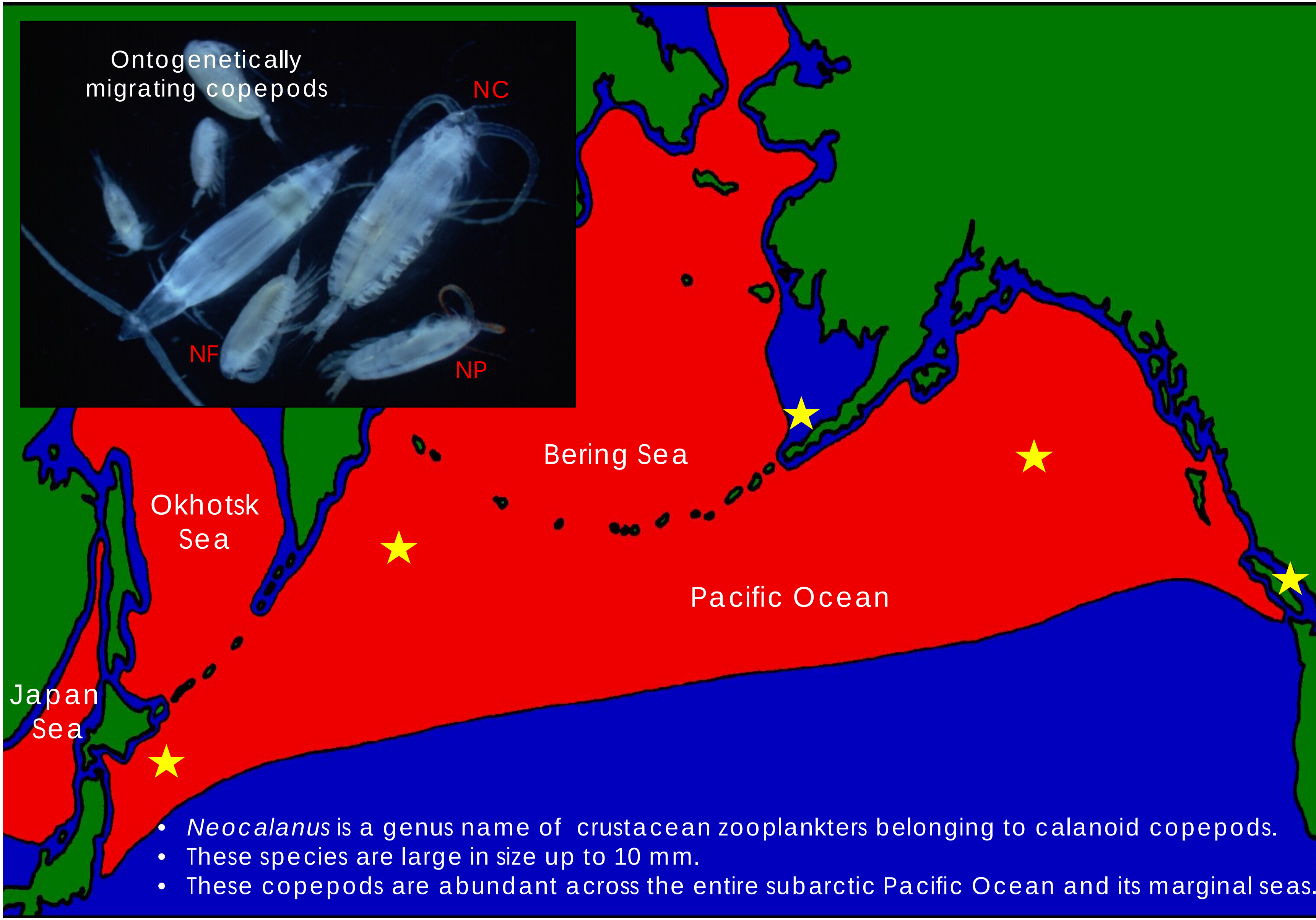


Fig. 1. Geographical distribution of the three *Neocalanus* copepods in the North Pacific Ocean and its marginal seas (after Kobari in press). Stars show study site where their life histories revealed to date.

Life cycle pattern

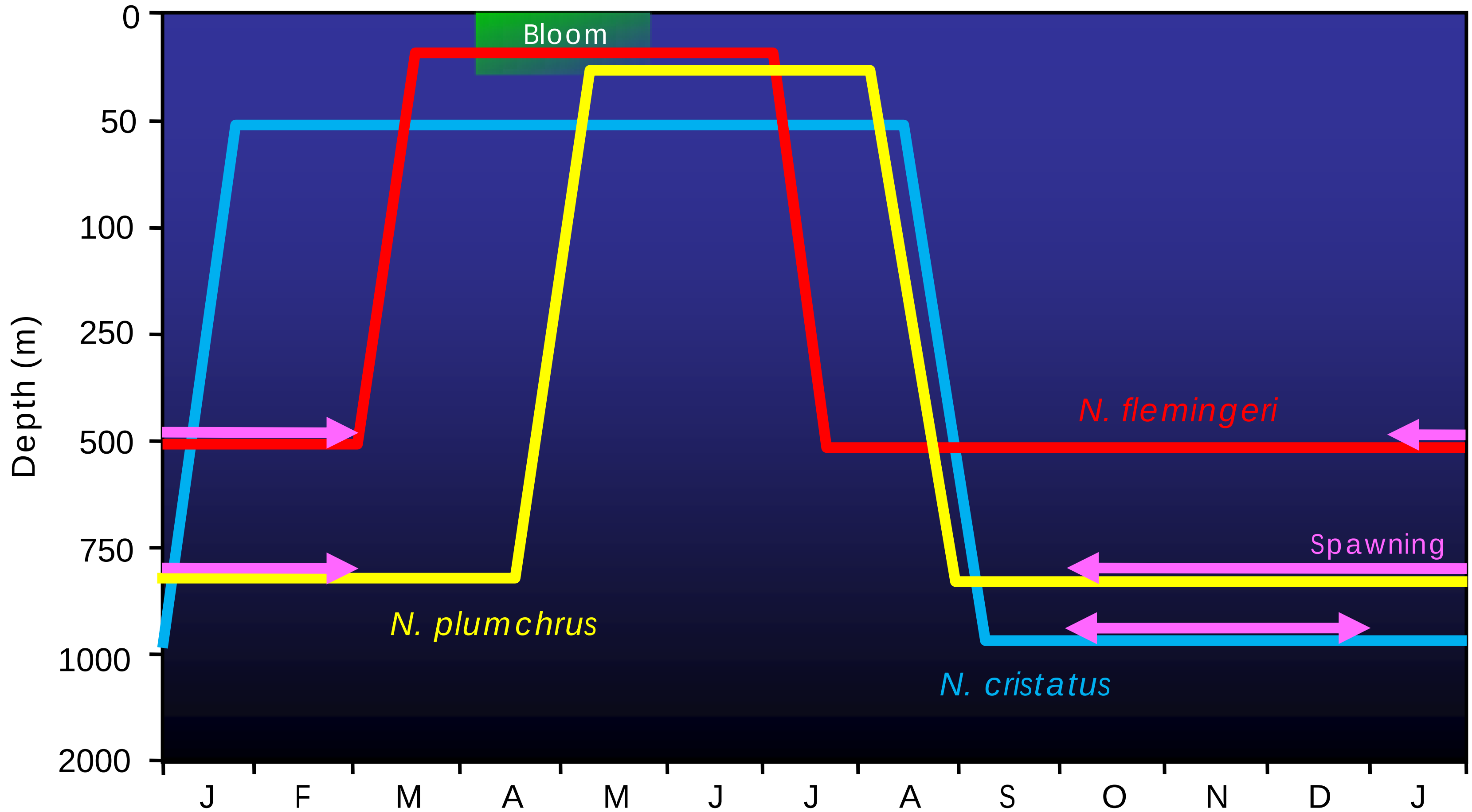


Fig. 2. Schematic diagram of life cycles for *Neocalanus* copepods in the Oyashio region (modified from Kobari 2008).

- *Neocalanus* copepods carry out an extensive ontogenetic migration in their life cycles.
- Young specimens develop from early spring to summer. *N. cristatus* reside at subsurface from January to August. The other species appear at near surface but the seasons are segregated during March to June for *N. flemingeri* and during April to August for *N. plumchrus*.
- They migrate down to mesopelagic depths in late summer, diapause for several months and then reproduce there from autumn to winter.
- Thus, their life cycles are suited to the seasonal fluctuations of food (phytoplankton) availability and thermal condition in surface layers.

Regional comparison of life cycle

Table 1. Regional comparisons of life cycles for *Neocalanus* copepods (modified from Kobari, in press).

Parameters			Oyashio region	Gulf of Alaska
Environments	Ambient water temperature		Low	High
	Food availability		High	Low
	Seasonal fluctuations		Large	Small
Life span	*Neocalanus*	*cristatus*	1 year	1 year
	N.	*flemingeri*	1-2 years	1 year
	N.	*plumchrus*	1 year	1 year
Dormant stage	*Neocalanus*	*cristatus*	C5	C5
	N.	*flemingeri*	C4/C6 Female	C6 Female
	N.	*plumchrus*	C5	C5
Surface development	*Neocalanus*	*cristatus*	Jan - Aug	Feb - Aug
	N.	*flemingeri*	Mar - Jun	Feb - Jun
	N.	*plumchrus*	May - Aug	Apr - Aug
Reproduction	*Neocalanus*	*cristatus*	Oct - Dec	Oct - Dec
	N.	*flemingeri*	Jan - Feb	Jan - Feb
	N.	*plumchrus*	Oct - Mar	Aug - Feb

- Geographical difference has been evident for oceanographic conditions.
- For example, Oyashio is characterized by cold thermal regime, high food availability and large seasonal fluctuations.
- With part of *N. flemingeri* population as an exception, *Neocalanus* copepods show comparable life histories.
- Life span is annual, development occur from spring to summer, reproductive seasons are from autumn to winter, and dormant stages are C5 or C6 female.

Biomass/Production

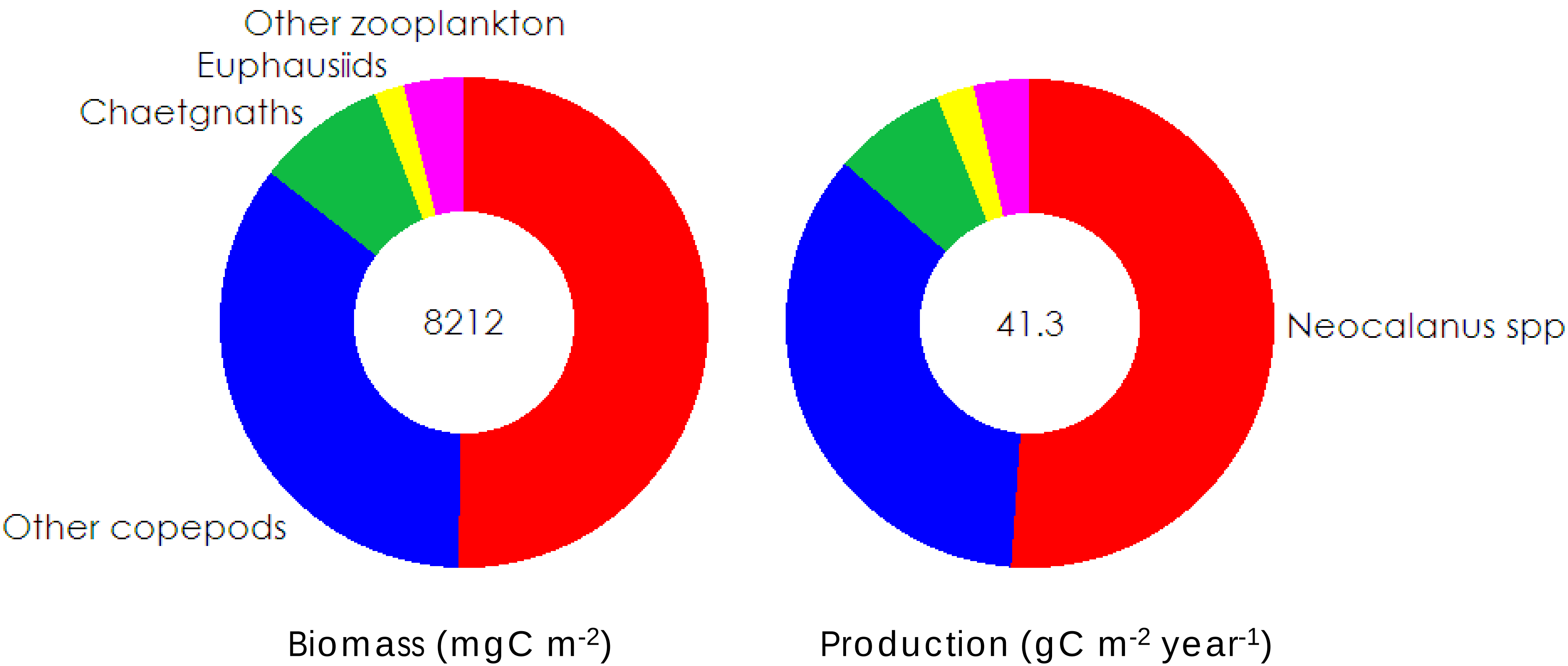


Fig. 3. Contribution of *Neocalanus* copepods to annual biomass and production of zooplankton community in 0-2000 m water column in the Oyashio region (modified from Ikeda et al. 2008).

- Annual mean biomass of zooplankton integrated over 0-2000 m is 8.2 gC m^{-2}.
- Biomass of *Neocalanus* species composed of more than half of the zooplankton biomass.
- The most predominant species are different between the regions, *N. cristatus* for the Oyashio, but *N. plumchrus* in the Gulf of Alaska.
- Zooplankton production is estimated to be 41.3 gC m^{-2} $year^{-1}$, and that of *Neocalanus* copepods contribute up to 51% of it.
- These results indicate that *Neocalanus* copepods are the most important components of zooplankton community in the Oyashio region and possibly in the other PICES regions.

Surface/Mesopelagic biomass

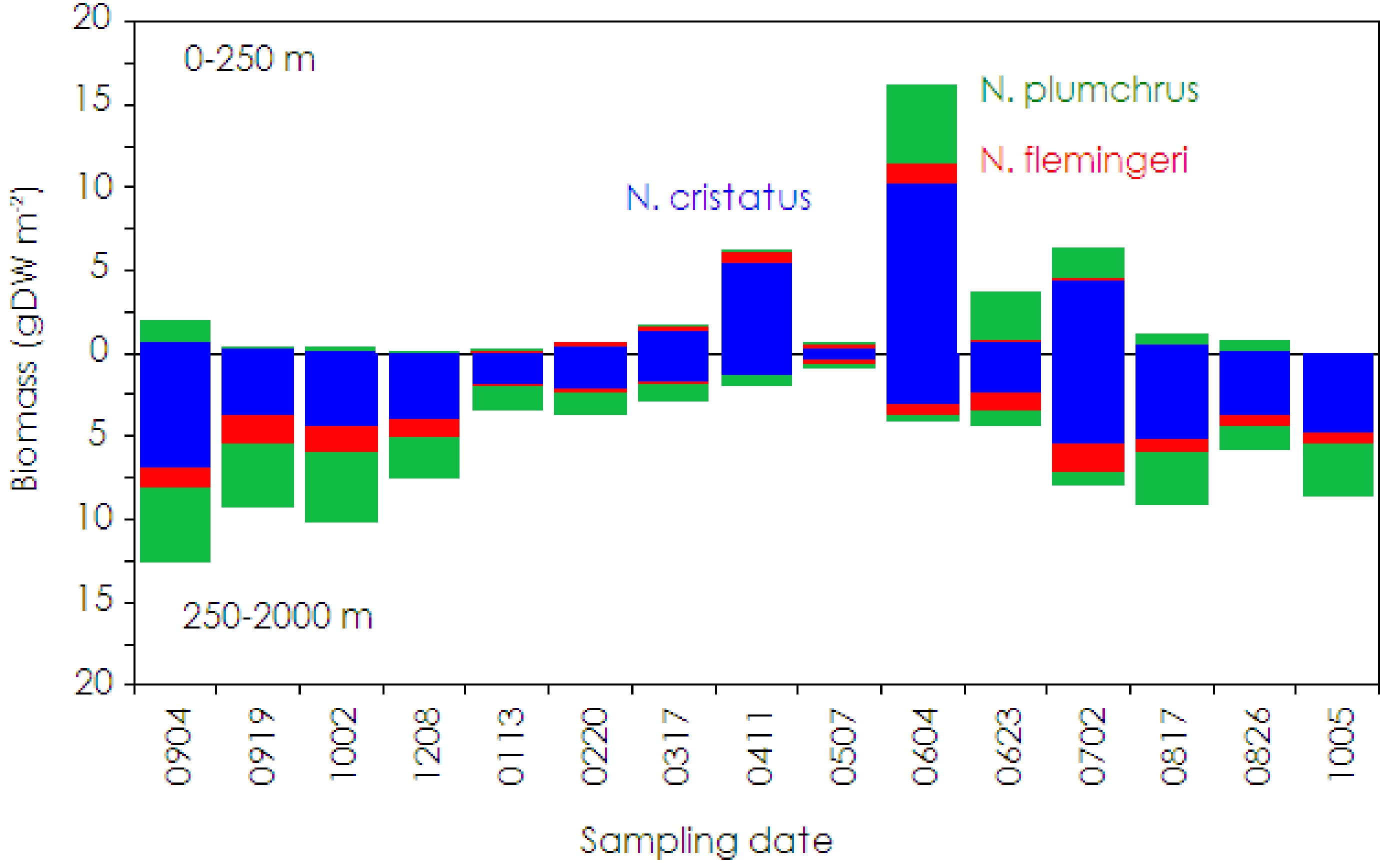


Fig. 4. Seasonal migration of biomass for *Neocalanus* copepods from surface (0-250 m) to deep layers (250-2000 m) in the Oyashio region (modified from Kobari & Ikeda 2000).

- *Neocalanus* copepods form the greatest biomasses in the surface layers within 4 months from spring to early summer and then they disappear from the surface waters.
- Most of the biomasses in the surface layers are transported to mesopelagic depths during summer by ontogenetic vertical migration.
- The mesopelagic biomass decreases gradually toward spring of the next year.
- Thus *Neocalanus* copepods form a vital link between epipelagic and mesopelagic ecosystems via their seasonal migration of biomasses.

Linkage to higher trophic levels

Table 2. Incidence of *Neocalanus* copepods in the stomachs of animals at higher trophic levels of the subarctic marine ecosystems (+: positive, -: negative).

Predators on Neocalanus	N. cristatus	N. flemingeri N. plumchrus	References
Epipelagic Fishes			
Pacific saury	+	+	Odate 1994
Sockeye salmon	+	+	Burger et al. 1991
Pink salmon	+	+	Fukataki 1967, Pearcy et al. 1988
Masu salmon	+	-	Fukataki 1969
Chum salmon	+	-	Pearcy et al. 1988
Mesopelagic fishes			
Bathylagus ochotensis	+	+	Beamish et al. 1999
Diaphus theta	+	+	Moku et al. 1999
Leuroglossus schmidti	+	+	Beamish et al. 1999
Stenobrachius leucopsarus	+	+	Beamish et al. 1999; Moku et al. 1999
Stenobrachius nannochir	+	+	Beamish et al. 1999; Moku et al. 1999
Demarsal fishes			
Walleye Pollack	+	+	Yamamura et al. 2002
Sea birds			
Auklets	+	+	Hunt et al. 1993
Whales			
Fin/Sei/Bryde's whales	+	+	Kawamura 1982

- As mentioned above, *Neocalanus* copepods have often been found in the stomachs of mesopelagic fishes.
- *Neocalanus* are major food items for saury, salmon, walleye pollack, sea birds and whales.
- These results indicate strongly that *Neocalanus* are playing a integral role in the trophodynamics of the subarctic marine ecosystems.

Size selective feeding

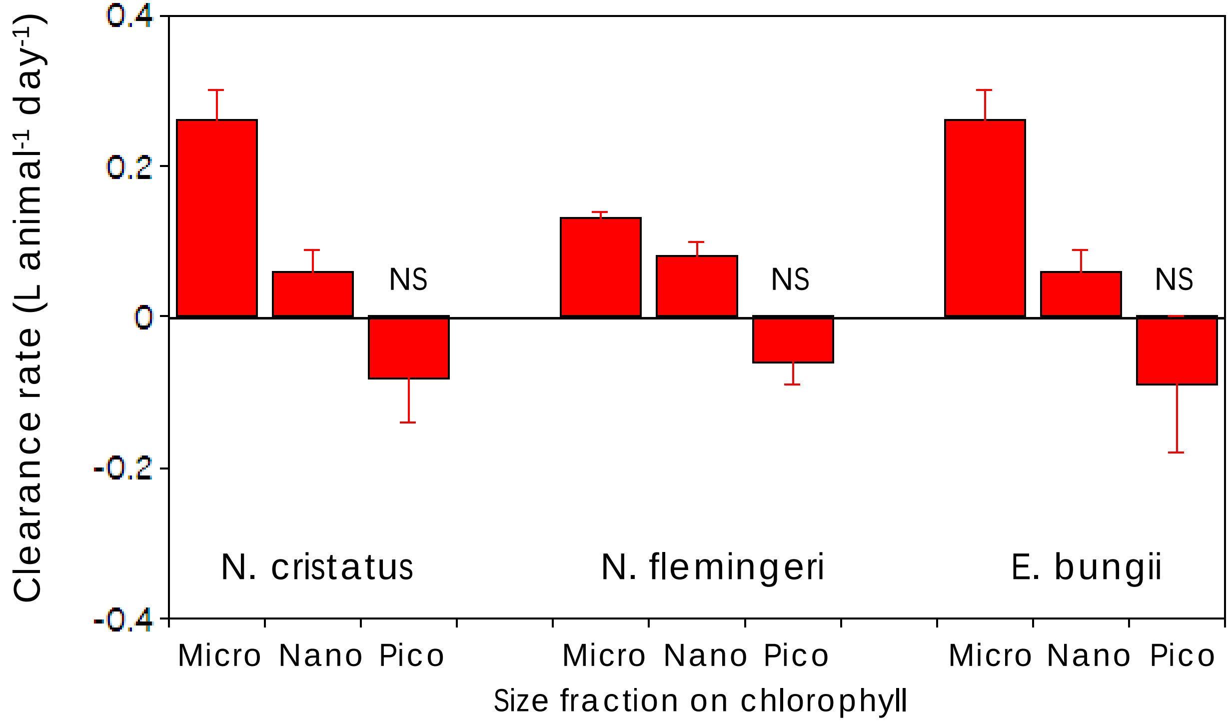


Fig. 5. Clearance rate on size-fractionated chlorophyll a for *Neocalanus* and *Eucalanus* copepods during the spring phytoplankton bloom in the Oyashio region (Kobari et al. in prep). Positive values mean significant selective feeding on the particles. Bars show SE. NS: No selective feeding (p>0.05, t-test).

- Feeding experiments show that *Neocalanus* species prefer larger particles as food resources.
- Negative clearance rates for the smallest phytoplankton suggest that these small phytoplankton cells increased during the process of copepod feeding.
- "Increase" not "decrease" of small phytoplankton during *Neocalanus* feeding has been observed by other workers, and is explained by the trophic cascading effects.
- *Neocalanus* species have impacts on microbial food webs via feeding.

Food items

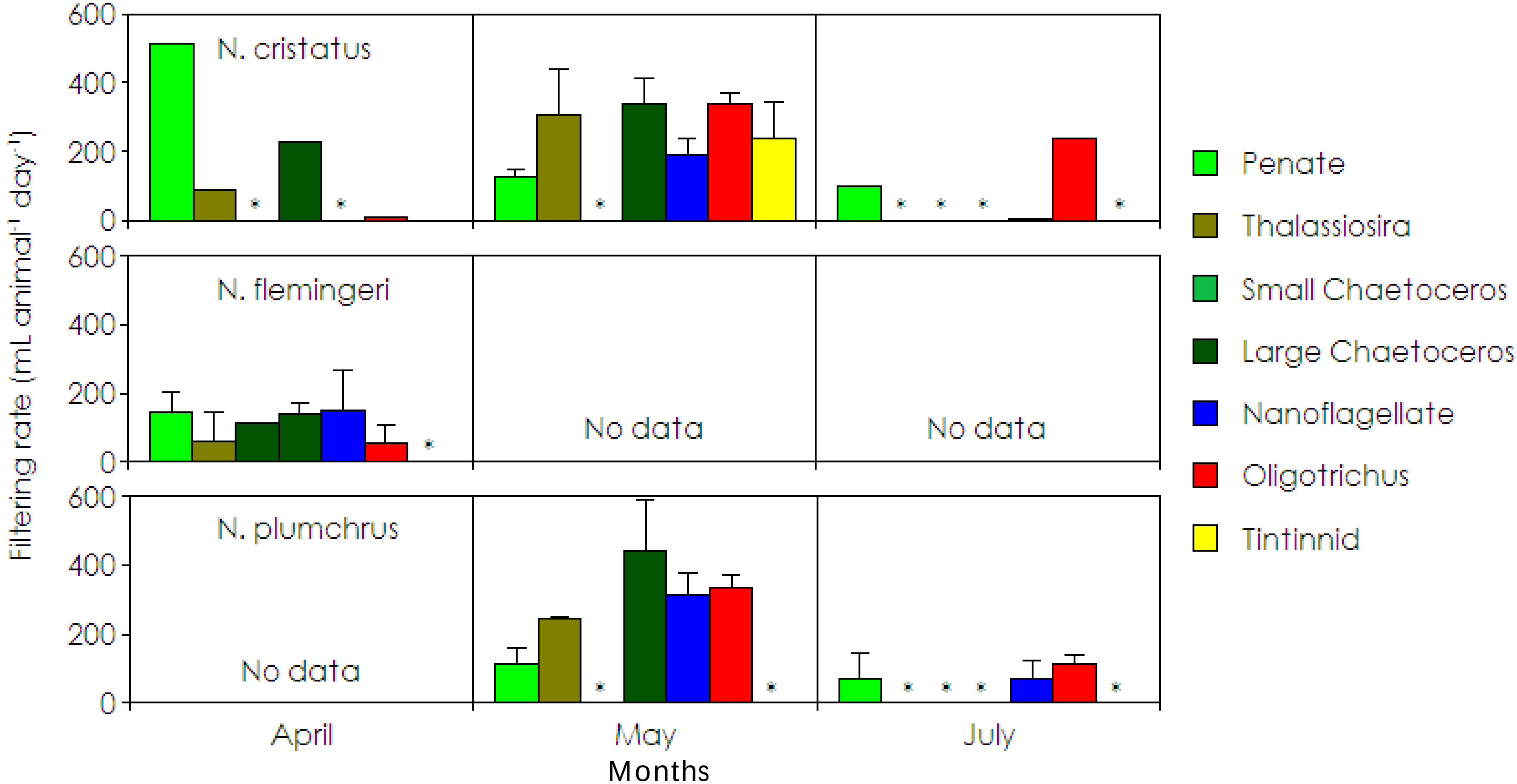


Fig. 6. Monthly changes in filtering rate of *Neocalanus* copepods on microbial assemblages in the Oyashio region (modified from Kobari et al. 2003). Bars show SD. Asterisks are zero.

- During spring phytoplankton bloom, *Neocalanus* copepods feed on centric and penate diatoms which are the most predominant components of the bloom.
- Ciliates and nano-flagellates become the important food resources during the post bloom where the diatoms no longer predominate.
- In the Gulf of Alaska, *N. flemingeri* and *N. plumchrus* have reported to feed protozoans at near surface layer while *N. cristatus* feeds on sinking particles at subsurface layer.
- Thus, *Neocalanus* copepods are better termed as omnivores, of which major food items change with season and region.

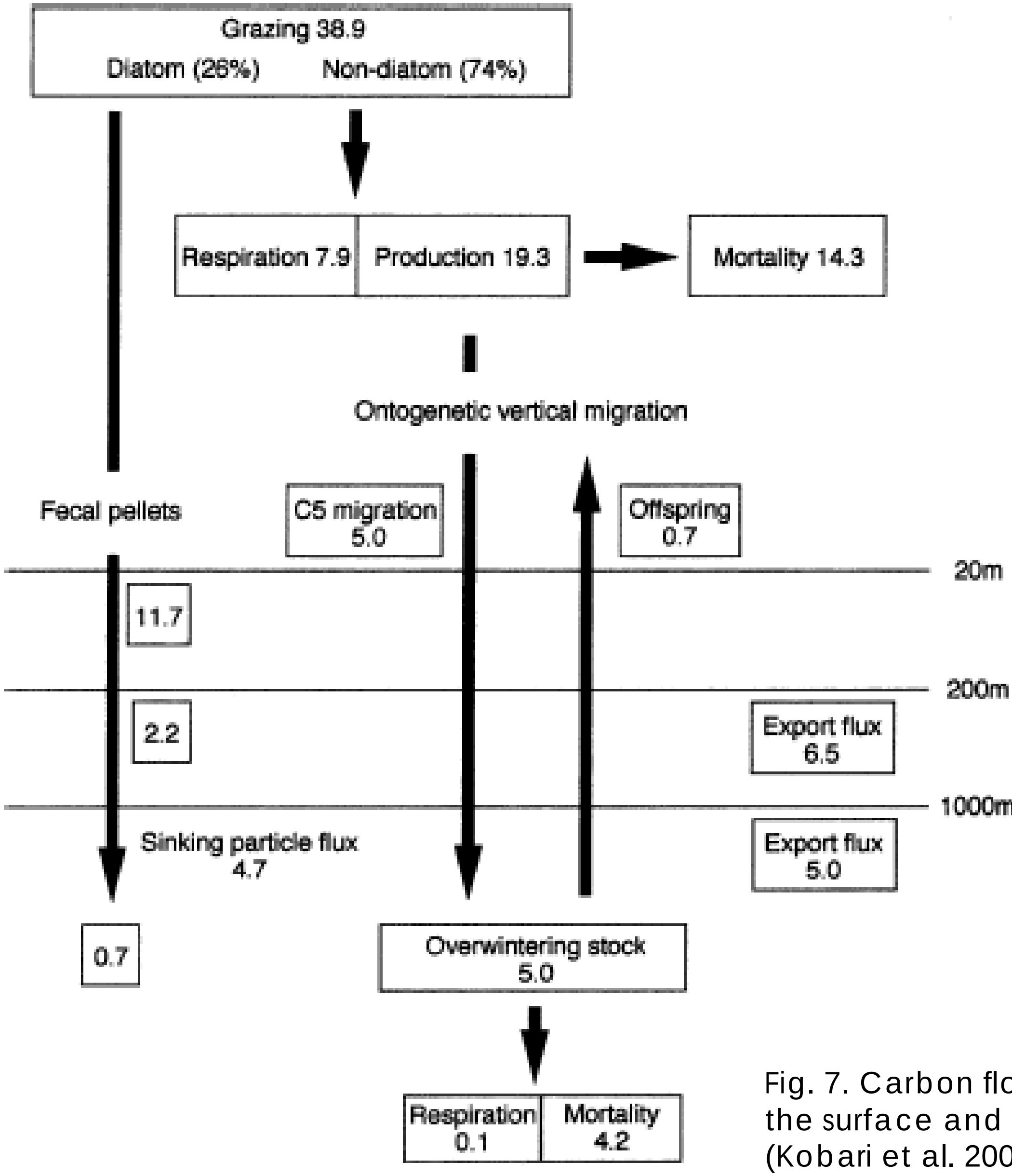
Feeding impacts on phytoplankton bloom

Table 1. Carbon budgets of the phytoplankton-copepod interaction in the top 150 m during the phytoplankton bloom season in the Oyashio region (March-April 2007). C/CHL ratio is assumed to be 21. Feeding rate is estimated from respiratory demand (6.5% of biomass: Dagg et al. 1982), 0.6 of assimilation efficiency and 0.3 of gross growth efficiency. ND: No data. *: Isada et al. (in prep).

Parameter	Source	9 Mar.	6 Apr.	19 Apr.	30 Apr.
Primary production* (PP: $gC\ m^{-2}$)		-	3.6	1.7	1.2
Copepod biomass ($gC\ m^{-2}$)		0.4	1.0	2.3	1.4
Feeding rate ($gC\ m^{-2}\ day^{-1}$)		0.2	0.4	1.2	0.7
Ratio ingested (%)	Phytoplankton	23.3	38.6	41.4	19.8
	Other POC	76.7	61.4	58.6	80.2
Ratio grazed on PP (%)		-	4.7	28.2	12.0
Carbon flux at 100 m (F_{100}: $gC\ m^{-2}\ day^{-1}$)		-	0.2	0.3	0.3
Contribution of feces to F_{100} (%)		-	47.8	78.3	53.6

- Major component of primary production during the bloom is micro-sized phytoplankton.
- In our observations, copepod feeding, by mostly late copepodides of *N. cristatus*, reach up to 28% of primary production.
- Copepod feeding on particles other than phytoplankton persists even though massive phytoplankton bloom occurred.
- Moreover, resultant fecal pellets production is equivalent to more than 50% of the POC flux at 100 m.
- These results suggest that the copepod community has significant impacts on phytoplankton bloom and important roles to channel phytoplankton and other POC into vertical carbon flux through their actively feeding.

Contribution to carbon flux



- Recently, it becomes evident that *Neocalanus* copepods contribute to vertical carbon flux through their ontogenetic vertical migration behavior in the western subarctic Pacific.
- According to our estimate, the exported carbon by the *Neocalanus* migration is 5.0 gC m^{-2} $year^{-1}$, which is comparable to that of sinking particle flux.
- Because the active carbon flux cannot be measured by sediment traps, our estimate of vertical flux may be underestimated.
- Considering wide distribution of *Neocalanus* copepods over the subarctic North Pacific, our estimate suggests their significant impacts on global carbon cycles in the ocean.
- More data covering all seasons of the year and mesopelagic biomass of *Neocalanus* in the PICES regions other than the western subarctic Pacific are needed in future study.

Fig. 7. Carbon flows (gC m^{-2} $year^{-1}$) by *Neocalanus* copepods in the surface and deep layers in the western subarctic Pacific (Kobari et al. 2003).

Response to climate change

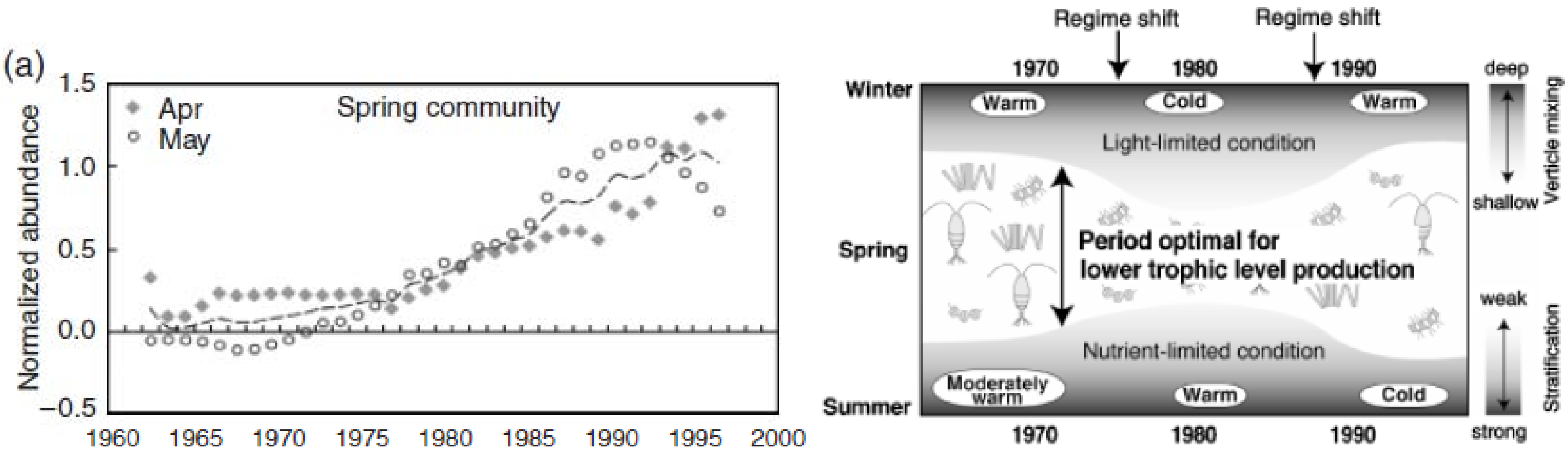


Fig. 9. Decadal changes in the abundance of spring copepod community represented by *N. cristatus/flemingeri* and diagram of the possible mechanism (after Chiba et al. 2006). White area shows the seasons for high primary production and surface development of *Neocalanus* copepods.

- Decadal fluctuations of the abundance, size and biomass of *Neocalanus* copepods have been observed in the Gulf of Alaska, central subarctic Pacific and Oyashio region in response to climate changes.
- For example, in the Oyashio region, the spring abundance of *Neocalanus* copepods show an increasing trend after mid-1970s.
- As causative mechanisms, Chiba et al. (2006) considered;

1. After 1970s, wintertime cooling is early terminated and summertime warming is rapidly progressed due to the Pacific Decadal Oscillation.
2. So, the subsequent spring bloom is early started after 1970s.
3. *Neocalanus* copepods shift the timings of surface development to the early-terminated phytoplankton bloom.
4. Thereby, *Neocalanus* copepods appear more abundantly during spring.

Conclusion

Neocalanus copepods as an integral component for ecological modeling in the PICES regions

1. These copepods are a vital rink between primary producer and animals at higher trophic levels, and have significant impacts on trophodynamics in food web.

2. These copepods occur abundantly over the PICES region and dominate zooplankton component.

3. These copepods undergo an extensive ontogenetic vertical migrations, implying important roles in biogeochemical cycles of the marine ecosystems of the PICES region.

4. The abundance, body size and life cycle timing of these copepods have been known as the influence of climate changes, and its mechanisms have been explored.

5. To advance our understanding, rate process (i.e. growth, mortality) is needed for ecological modeling.