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W6: Regional evaluation of secondary production observations and application of methodology in the North Pacific
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Traditional Approaches for Estimating Zooplankton Production Rate in a Neritic Area of the North Pacific

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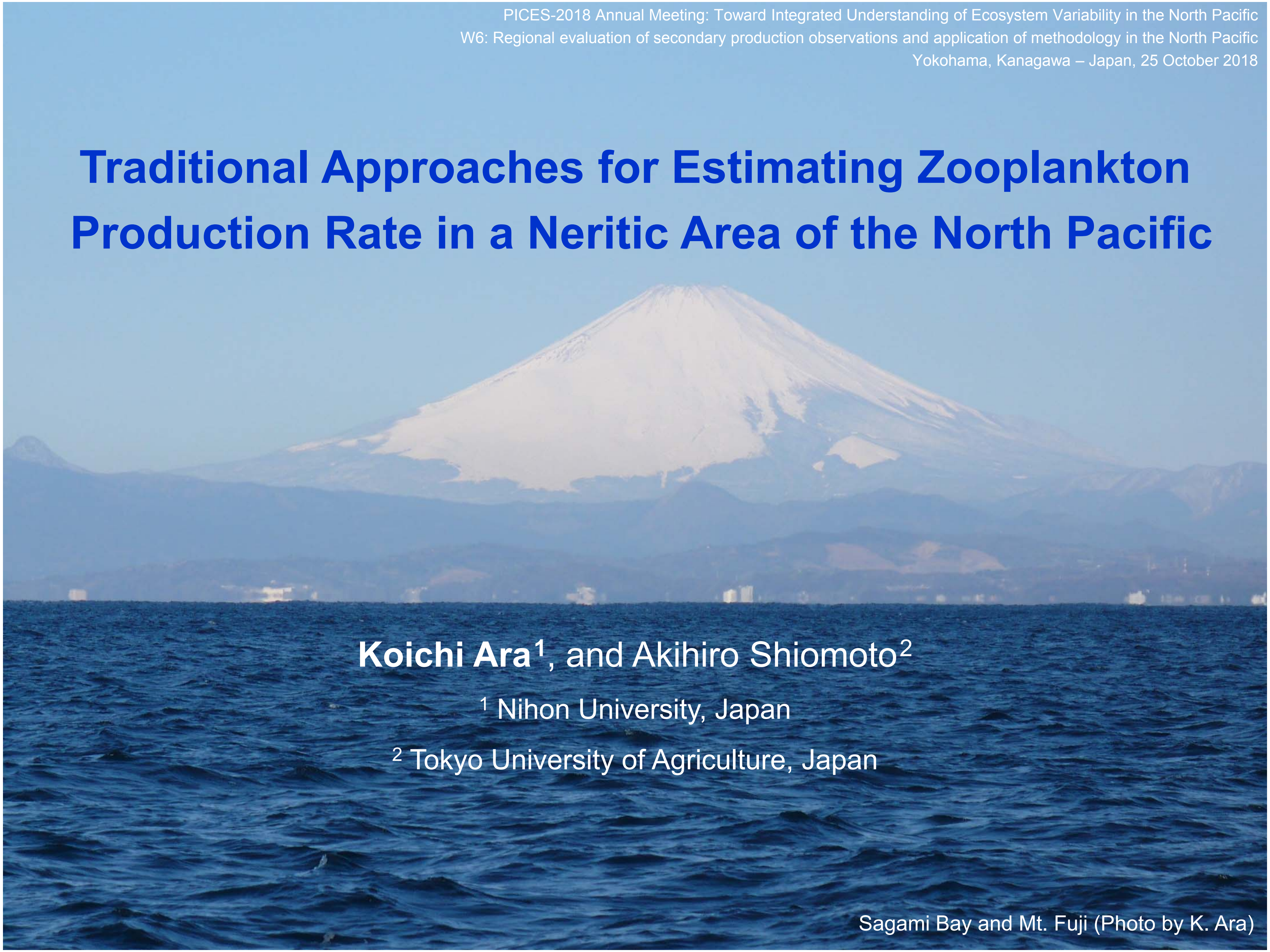


Sagami Bay and Mt. Fuji (Photo by K. Ara)

Introduction

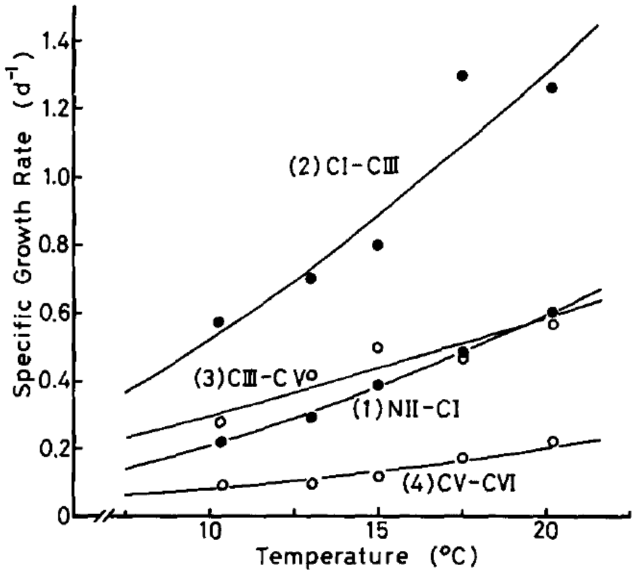
- Historically, the measurement of 2ndary production has been a primary goal for zooplankton research since the 1950s.
- Daily 2ndary production rate (***PR***) can be calculated as:

$$PR = \sum (Gi \times Bi) + Gf \times Bf$$

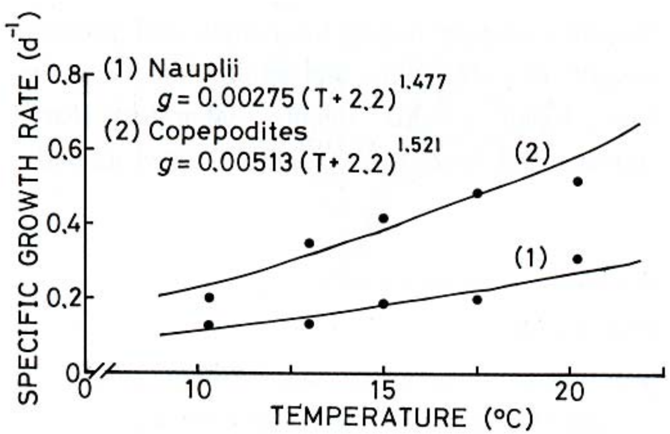
For mesozooplankton (0.2–20 mm), egg production rate and production rates of small juvenile stages (<20 mm) are not included.

where ***Gi***: the weight-specific growth rate (d^{-1}) of stage ***i***; ***Bi***: biomass of stage ***i*** (***Bi*** = ***Ai*** × ***Wi***, where ***A***: abundance; ***W***: individual weight); ***Gf***: egg production rate; ***Bf***: biomass of adult female.

- The weight-specific growth rate (***G***, d^{-1}) should be determined by incubation.



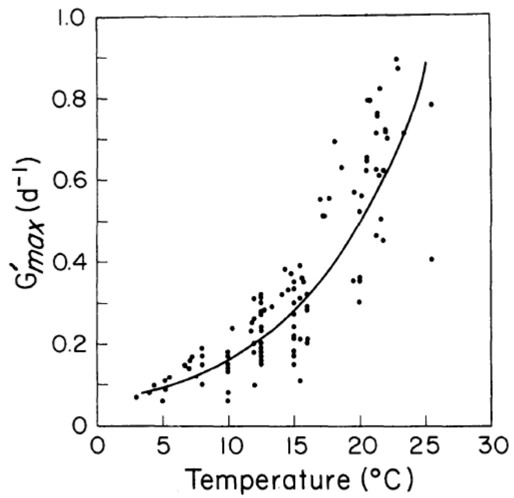
Uye (1988) *Calanus sinicus*



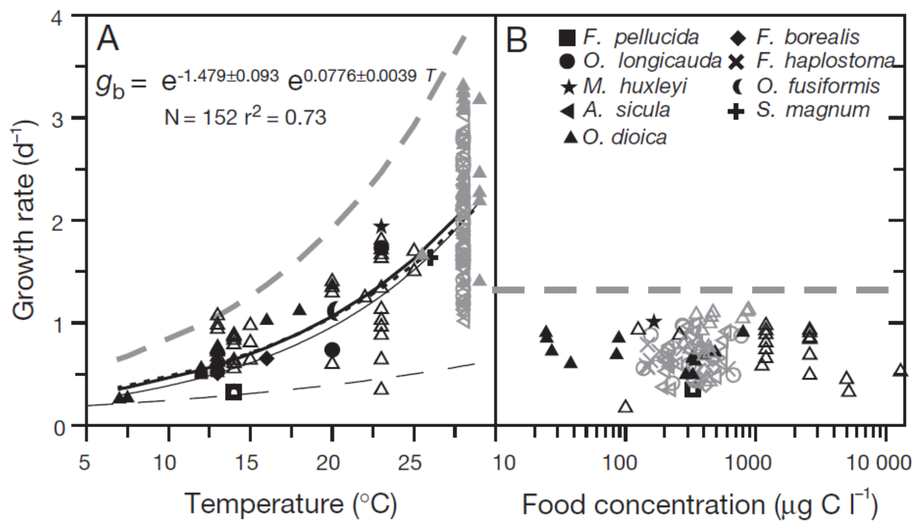
Uye (1991) *Paracalanus* sp.

Introduction

- When there is no available growth data, growth rate can be calculated using empirical growth models from a few easily measurable parameters (e.g. temperature, individual weight).



Huntley & Boyd (1984) Copepods



López-Urrutia *et al*. (2003) Appendicularians

Hirst & Bunker (2003) Copepods

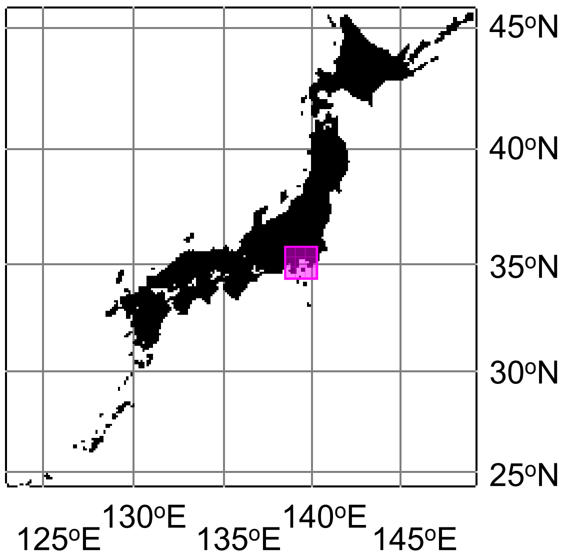
Table 6. Results from the regressions relating the dependent variable $\log_{10}$ weight-specific fecundity/growth (g, d^{-1}) to independent variables temperature (T, °C), $\log_{10}$ body weight (BW, μg C ind^{-1}), and total Chl *a* concentration (C_a, μg Chl *a* L^{-1}). For those data sets in which an independent variable did not statistically significantly add to prediction this was removed, and those remaining used in the formulation of a multiple linear regression.

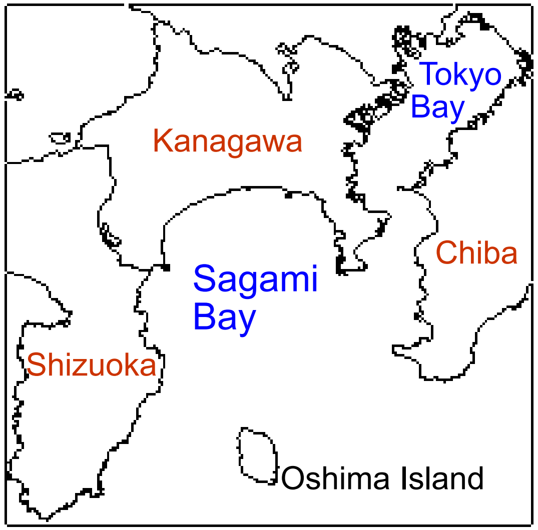
Group	Backward stepwise regression	Multiple linear regression $\log_{10} g = a[T] + b[\log_{10} \mathrm{BW}] + c[\log_{10} C_a] + d$						Multiple linear regression $\log_{10} g = a[\mathrm{var.}\ 1] + b[\mathrm{var.}\ 2] + c$						
		a	b	c	d	R^2	p (T; $\log_{10}$ BW; $\log_{10} C_a$)	a	b	c	var. 1; var. 2	R^2	p (var 1; var 2)	(n)
Adults														
Broadcasters	All included	0.0125	−0.230	0.729	−1.348	0.357	<0.001; <0.001; <0.001	—	—	—	—	—	—	(1,639)
Sac spawners	All included	0.0182	0.193	0.195	−1.591	0.113	<0.001; <0.001; <0.001	—	—	—	—	—	—	(320)
Juveniles														
Broadcasters	All included	−0.0143	−0.363	0.135	−0.105	0.392	<0.001; <0.001; <0.001	—	—	—	—	—	—	(644)
Sac spawners	C_a removed	—	—	—	—	—	—	0.0333	−0.163	−1.528	T; $\log_{10}$BW	0.595	<0.001; 0.003	(139)
All data	All included	0.0186	−0.288	0.417	−1.209	0.289	<0.001; <0.001; <0.001	—	—	—	—	—	—	(2,742)

Introduction

- Here, two questions arise:
  (1) Which empirical growth models are more applicable?
  (2) Are daily production rates estimated using empirical growth models reasonable?

- The aim of this study:
  (1) to compare and verify several empirical growth models for mesozooplankton (MZ), and
  (2) to assess carbon flow based on production rate and food requirement
  in the neritic area of Sagami Bay, Japan.

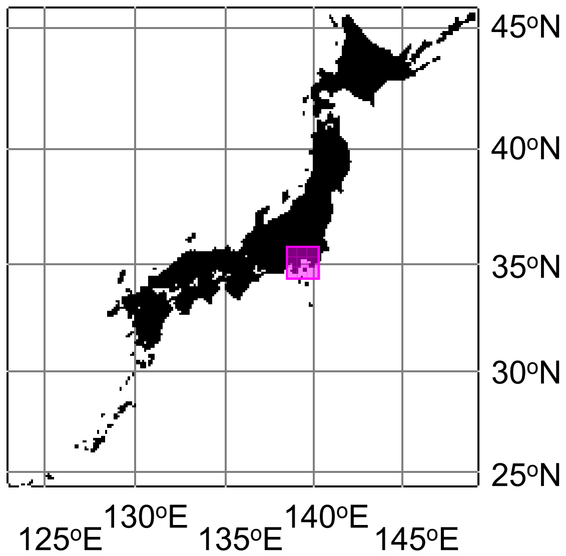


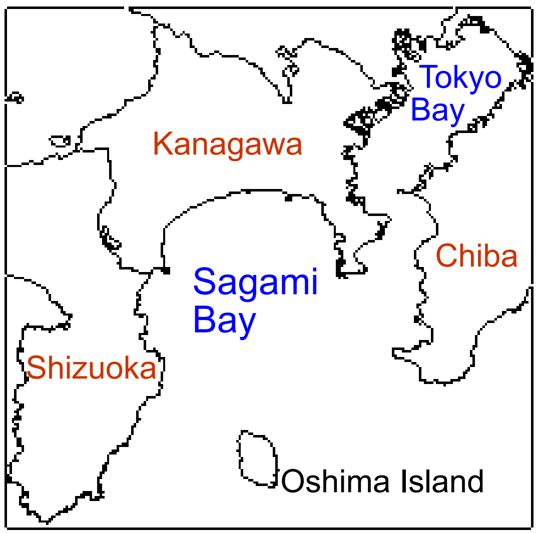


(1) Sagami Bay is traditionally well known for its beautiful natural environment and richness of marine organisms with high biodiversity.

(2) Since at least the 1960s until now, the total annual fishery capture in Sagami Bay has been maintained at ca. 30,000 tons wet weight per year, and most of this has been caught in the shallow (<250 m depth), coastal and neritic waters.





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湘 南

Project "*SHONAM*" (*Sagami Bay* – *Hydoroecology of Neritic Ambient*) in order to investigate physicochemical properties and plankton ecosystem in the neritic area of Sagami Bay.

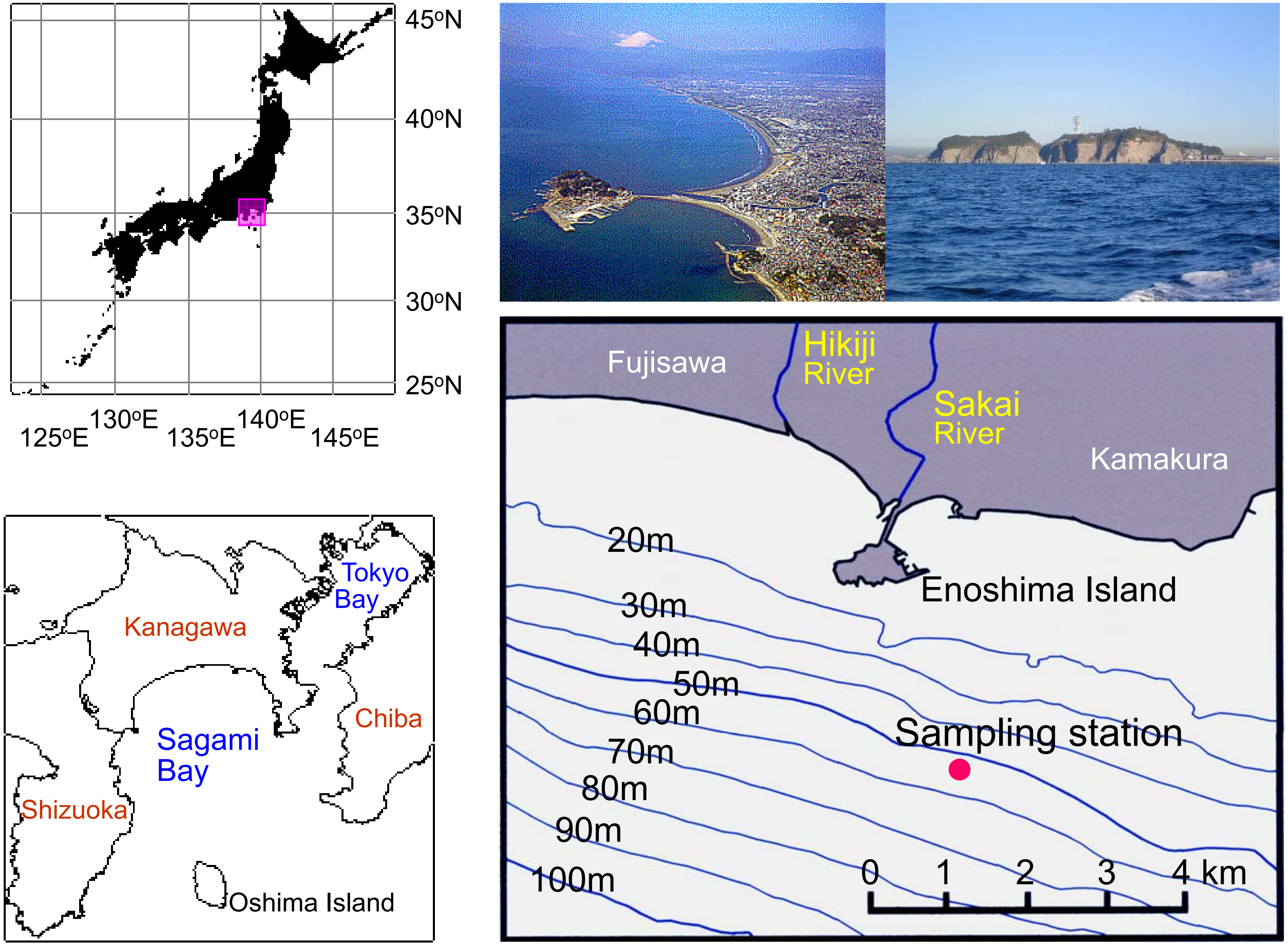


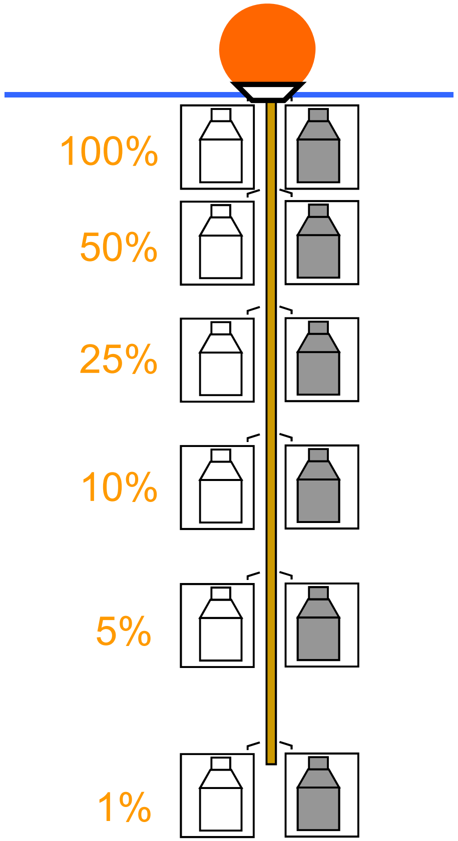
Figure 1 Map showing the study area in Sagami Bay.

Materials and methods

Sampling period and frequency	• Mostly every 2 weeks on 289 occasions • From January 2006 to December 2017
Water temperature and salinity	• Memory STD (Alec Electronics, AST1000-PK) • Every 1 m from the surface to the bottom
Primary production	• *In situ* ^{13}C incubation for 24 hrs (Hama *et al.* 1983)
Mesozooplankton	• Plankton net (mouth diameter: 45 cm, mesh opening size: 200 µm) equipped with a flowmeter (Rigosha) • Vertical tows from the bottom to the surface • Immediately preserved in 5–10% (final concentration) buffered formalin seawater solution • Identification Copepods: species, stage (CI–CVI) and sex Other non-copepods: taxonomic group • Count (>500 individuals) and measurement of body length

Primary production: *in situ* ^{13}C method

1. Water samples: from six depths (100, 50, 25, 10, 5 and 1% photon fluxes just above the sea surface), using a Niskin bottle.
2. Large zooplankton: removed by sieving through a 200 µm mesh.
   Seawater samples: into polycarbonate bottles (two light bottles and one dark bottle at each depth).
3. Add $NaH^{13}CO_3$ (ca. 10% of total inorganic carbon in ambient water).
   Bottles: placed at the same depths at which water samples were taken, and incubated *in situ* for 24 h.
4. Samples: filtered through pre-combusted (at 450°C for 4 h) filters.
   Filters: dried at 60°C for 1–2 h, fumed with HCl for 3 h, dried at 60°C, and stored in a desiccator.
5. $^{13}C/^{12}C$: determined using a quadruple mass-spectrometer (Europe Scientific ANCA-SL or SerCon INTEGRA-2).
6. Primary productivity: calculated according to Hama *et al*. (1983).
7. Depth-integrated primary production: as integral of primary productivities in the photic zone.



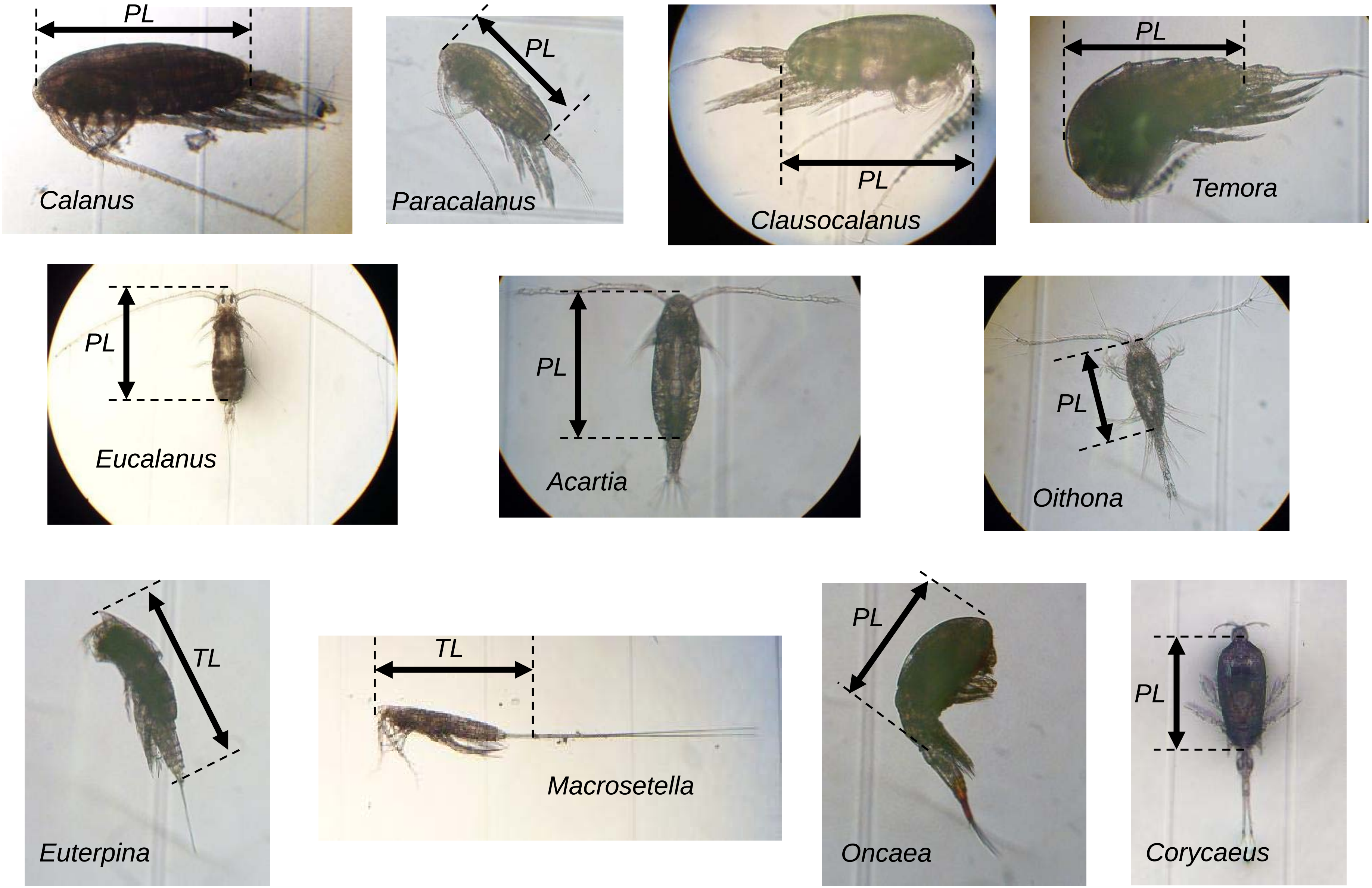


Figure 2 Measurements of body lengths for copepods (C1–C6). *PL*: prosome length; *TL*: total body length.

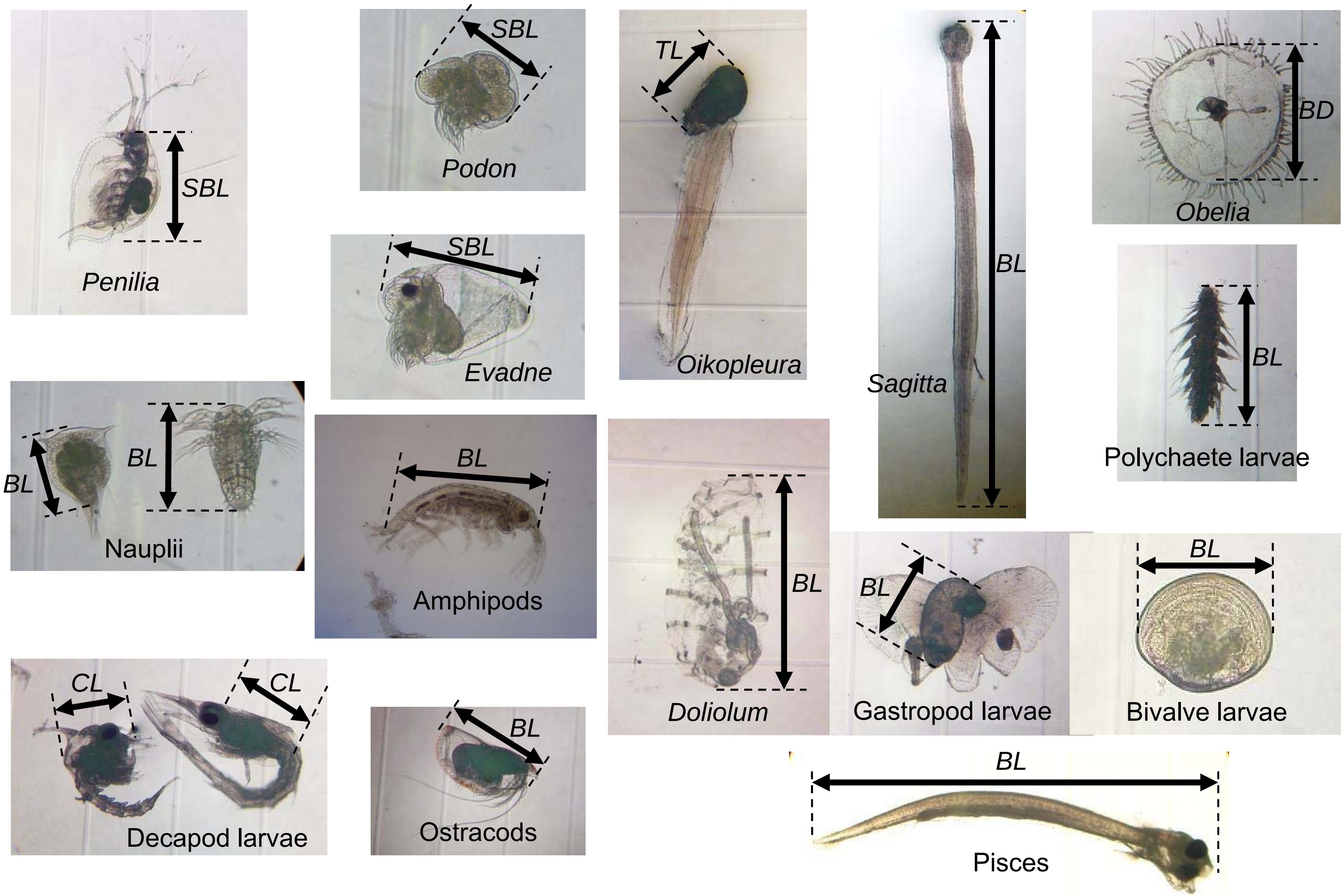
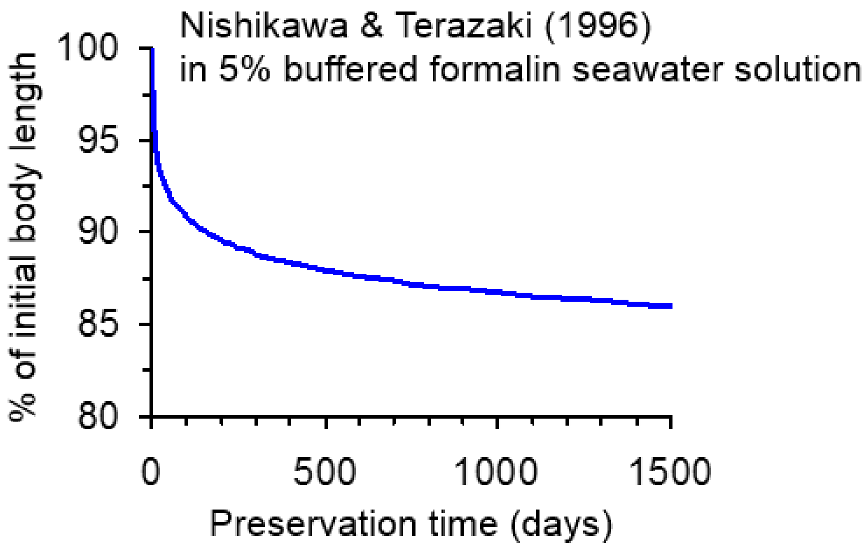


Figure 3 Measurements of body lengths for non-copepods. *BL*: body length; *SBL*: standard body length; *CL*: carapace length; *TL*: trunk length; *BD*: bell diameter.

Table 1 Shrinkage of body length due to preservation in formalin seawater solution.

Taxonomic group	Shrinkage rate or equation	Reference
Appendicularians	10%	Deibel (1988), Landry *et al*. (1994), Hopcroft & Robinson (1999)
Thaliaceans *Doliolum*	$L = 0.569 + 0.232 \log_{10} t + 0.911\ Pt$ L: body length of live specimen (mm), Pt: body length (mm) after preservation (day)	Nishikawa & Terazaki (1996)
Chaetognaths	5%	Murakami (1959)
Cnidarians	15%	Möller (1980)
Fish larvae	8%	Theilacker (1980), Kusakabe *et al*. (2007)



Calculations

- Abundance (A, ind. m^{-3})

- Biomass (B, mg C m^{-3}): $B = \sum A \times Wc$
  where Wc: individual weight (µg C).

- Daily production rate (PR, mg C m^{-3} d^{-1}): $PR = \sum A \times Wc \times G$
  where G: individual specific growth rate (d^{-1}).

- Food requirement (FR, mg C m^{-3} d^{-1}): $FR = Res / (As - Gr)$
  where Res: respiration rate (µL O_2 ind.$^{-1}$ h^{-1}); As (assimilation rate): 0.7 (Ikeda & Motoda 1978); Gr (gross growth efficiency): 0.3 (Ikeda & Motoda 1978); respiratory quotient: 0.97 (Gnaiger 1983).

  Appendicularians (T: 15°C): $\log_{10} Res = -1.38 + 0.81 \log_{10} W$ (Gorsky *et al*. 1987)
  Appendicularians (T: 20°C): $\log_{10} Res = -1.27 + 0.88 \log_{10} W$
  Appendicularians (T: 24°C): $\log_{10} Res = -1.27 + 0.88 \log_{10} W$
  where W: individual weight (µg DW); Q_{10}: 2.45 (15–20°C), 3.75 (20–24°C).

  Copepods: $\ln Res = 0.124 + 0.78 \ln Wc + 0.073T$ (Ikeda *et al*. 2001)
  Others: $\ln Res = 0.524 + 0.8354 \ln Wc + 0.0601T$ (Ikeda 1985)
  where Wc: individual weight (mg C); T: ambient water temperature (°C).

Table 2 Length-weight regression equations employed to estimate carbon weight for mesozooplankton (to be continued).

Taxonomic group	Regression equation	Units	Reference
Copepods			
Calanus	$Wc = 3.84 \times 10^{-10}\ PL^{3.378}$	µg C, µm	Uye (1988)
Paracalanus	$Wc = 3.54 \times 10^{-9}\ PL^{3.128}$	µg C, µm	Uye (1991)
Acartia	$Wc = 3.09 \times 10^{-9}\ PL^{3.08}$	µg C, µm	Uye (1982)
Centropages	$Wc = 6.46 \times 10^{-9}\ PL^{2.97}$	µg C, µm	Uye (1982)
Euchaeta	$Wc = 5.62 \times 10^{-7}\ PL^{2.45}$	µg C, µm	Uye (1982)
Oithona	$Wc = 1.83 \times 10^{-6}\ PL^{2.05}$	µg C, µm	Uye & Sano (1998)
Other calanoids, cyclopods and poechilostmatoids	$Wc = 4.27 \times 10^{-9}\ PL^{3.07}$	µg C, µm	Uye (1982)
Microsetella	$Wc = 2.65 \times 10^{-6}\ TL^{1.95}$	µg C, µm	Uye *et al.* (2002)
Other harpacticoids	$Wc = 8.51 \times 10^{-10}\ TL^{3.26} \times 0.457$	µg C, µm	Hirota (1986)
Crustacean nauplii	$Wc = 1.51 \times 10^{-5}\ BL^{2.94}$	ng C, µm	Uye *et al.* (1996)
Cladocerans			
Penilia	$Wc = 1.82 \times 10^{-13}\ TCL^{4.51}$	µg C, µm	Uye (1982)
Podon, *Evadne*	$Wc = 7.08 \times 10^{-12}\ TCL^{4.15}$	µg C, µm	Uye (1982)
Ostracods	$Wc = 7.08 \times 10^{-12}\ TCL^{4.15}$	µg C, µm	Uye (1982)
Decapod larvae	$Wc = 9.12 \times 10^{-9}\ CL^{3.28} \times 0.416$	µg C, µm	Hirota (1986)
Lucifer	$Wc = 3.09 \times 10^{2}\ PBL^{2.489} \times 0.1 \times 0.416$	µg C, mm	Vega-Pérez *et al.* (1996), Hirota (1986)
Mysids	$Wc = 6.81 \times 10^{-1}\ CL^{3.10}$	µg C, mm	Uye (1982)
Amphipods	$Wc = 4.85 \times 10^{-3}\ BL^{2.957} \times 0.3693$	mg C, mm	Ikeda (1990, 1991)

Table 2 Length-weight regression equations employed to estimate carbon weight for mesozooplankton (continued).

Taxonomic group	Regression equation	Units	Reference
Cirriped nauplii	$Wc = 2.88 \times 10^{-7}\ BL^{2.65} \times 0.434$	µg C, µm	Hirota (1986)
Appendicularians			
Oikopleura	$Wc = 2.62 \times 10^{-8}\ TRL^{2.83}$	µg C, µm	Sato *et al*. (2001)
Thaliaceans			
Doliolum	$Wc = 1.15 \times 10^{-7}\ BL^{2.54} \times 0.0782$	µg C, µm	Hirota (1986), Madin *et al*. (1981)
Chaetognaths	$Wc = 5.13 \times 10^{-2}\ BL^{3.16}$	µg C, mm	Uye (1982)
Bivalve larvae	$Wc = 2.00 \times 10^{-3}\ SL^{1.47} \times 0.177$	µg C, µm	Hirota (1986)
Gastropod larvae	$Wc = 7.94 \times 10^{-6}\ SL^{2.46} \times 0.177$	µg C, µm	Hirota (1986)
Polychaete larvae	$Wc = 2.09 \times 10^{-6}\ BL^{2.10} \times 0.512$	µg C, µm	Hirota (1986)
Cnidarians			
Hydrozoa *Obelia*	$Wc = 2.14 \times 10^{-8}\ BD^{2.75} \times 0.089$	µg C, µm	Hirota (1986), Larson (1986)
Siphonophora	$Wc = 20.47 \times BL^{0.834}$	µg C, mm	Lavaniegos & Ohman (2007)
Fish larvae	$Wc = 2.045 \times 10^{-4}\ BL^{3.385} \times 0.425$	mg C, mm	Shoji (2000), Uye (1982)

Table 3 Regression equations to estimate growth rate (G: d^{-1}) for copepods. T: temperature (°C); Wc: individual carbon weight (μg C); *Chl-a*: chlorophyll *a* concentration (μg L^{-1}).

Taxonomic group	Species	Regression equation	Reference
Copepods (C1–C6)	All	$G = 0.0542 \times e^{0.11T}$	Huntley & Boyd (1984)
Copepods (C1–C6)	All	$G = 0.0445 \times e^{0.111T}$	Huntley & Lopez (1992)
Copepods (C1–C6)	*Acartia*	$G = 0.059 \times e^{0.084T}$	Uye (1982)
	Calanus	$G = 0.08 \times e^{0.085T}$	Uye (1988)
	Centropages	$G = 0.099 \times e^{0.078T}$	Liang *et al*. (1996)
	Microsetella	$G = 0.0062 \times e^{0.12T}$	Uye *et al*. (2002)
	Oithona	$G = 0.025 \times e^{0.11T}$	Uye & Sano (1998)
	Paracalanus	$G = 0.094 \times e^{0.067T}$	Uye (1991)
	Others (Total)	$G = 0.078 \times e^{0.062T}$	Uye & Shimazu (1997)
Copepods (C1–C6)	All	$\log_{10}G = 0.0246T - 0.2962 \log_{10}Wc - 1.1355$	Hirst & Sheader (1997)
Copepods (C1–C6)	All	$\log_{10}G = 0.0208T - 0.3221 \log_{10}Wc - 1.1408$	Hirst & Lampitt (1998)
Copepods (C1–C6)	All	$\log_{10}G = 0.0345T - 0.128 \log_{10}Wc - 1.529$	Hirst et al. (2003)
Copepods (C1–C6)	All	$\log_{10}G = 0.0186T - 0.288 \log_{10}Wc + 0.417 \log_{10}Chl\text{-}a - 1.209$	Hirst & Bunker (2003)

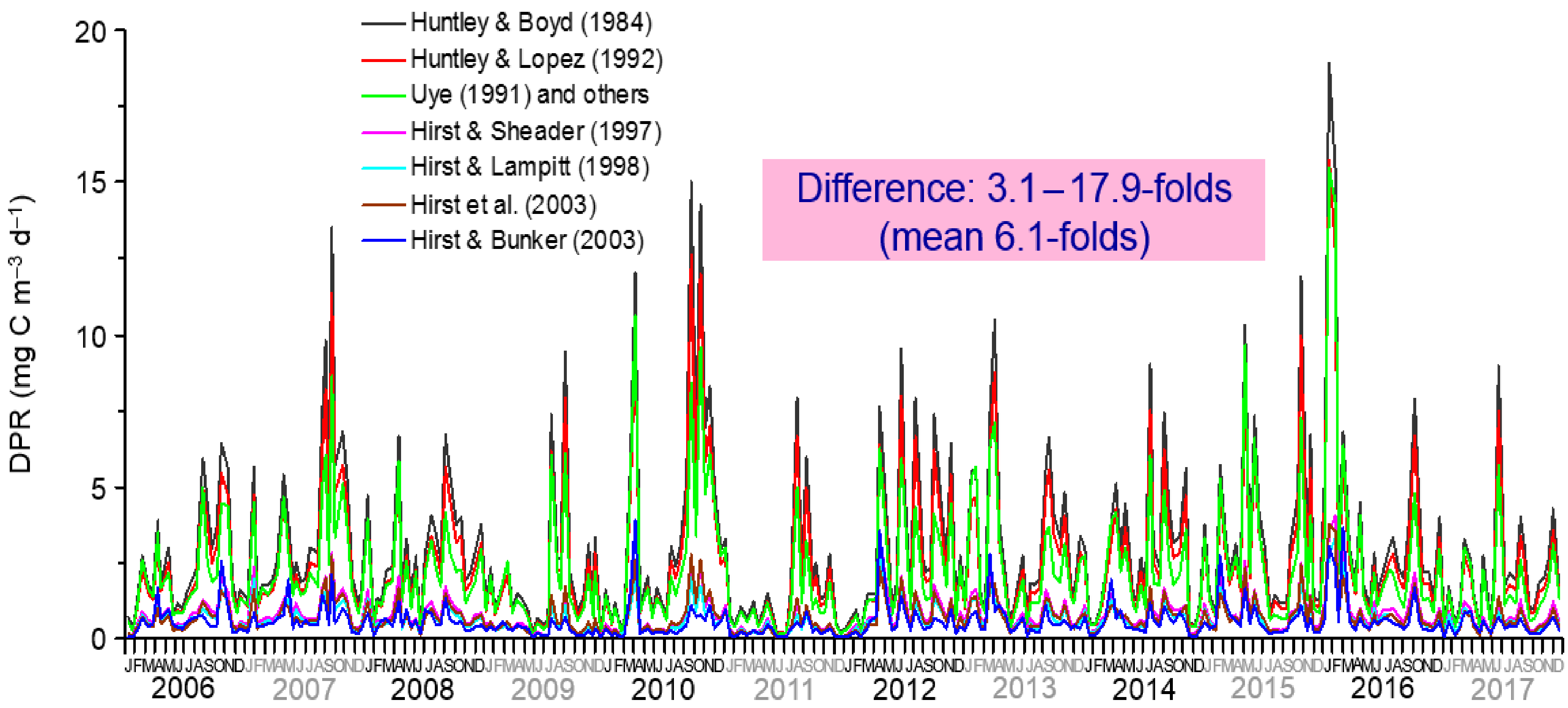


Figure 4 Temporal variations in daily production rate (DPR) of the total copepods in Sagami Bay, from January 2006 to December 2017.

- Which growth model is more reasonable and applicable?

Table 4 Regression equations to estimate growth rate (G: d^{-1}) for mesozooplankton. T: temperature (°C); Wc: individual carbon weight (µg C).

Taxonomic group	Body size or stage	Regression equation	Reference
Other crustaceans (Non-copepods)	Wc: ~10 µg C ind.$^{-1}$ Wc: 10–100 µg C ind.$^{-1}$	$\log_{10}G = -1.232 + 0.0246T$ $\log_{10}G = -1.405 + 0.0337T$	Hirst *et al*. (2003)
Appendicularians	All	$G = 0.21 \times e^{0.0815T}$	López-Urrutia (2003)
Thaliaceans	All	$\log_{10}G = 0.0645T + 0.138 \log_{10}Wc - 2.070$	Hirst *et al*. (2003)
Chaetognaths	All	$\log_{10}G = -1.851 + 0.0367T$	Hirst *et al*. (2003)
Others*	Wc: ~10 µg C ind.$^{-1}$ Wc: 10–100 µg C ind.$^{-1}$ Wc: >100 µg C ind.$^{-1}$	$\log_{10}G = -1.067 + 0.0206T$ $\log_{10}G = -1.406 + 0.0326T$ $\log_{10}G = -1.779 + 0.0364T$	Hirst *et al*. (2003)

Others*: molluscan (bivalve and gastropod) larvae, polychaete larvae, cnidarians and fish larvae.

- Are these empirical growth models reasonable and applicable?

- Ikeda & Motoda (1978) modified the basic balanced equations proposed by Winberg (1956), as follows:

$$FR = Res \,/\, (As - Gr) = Res \,/\, (0.7 - 0.3) = 2.5\ Res$$

$$PR = Gr \times Res \,/\, (As - Gr) = 0.3\ Res \,/\, (0.7 - 0.3) = 0.75\ Res$$

where ***FR*** is food requirement, ***PR*** is daily production rate, ***Res*** is respiration rate, ***As*** is assimilation rate (**0.7**, Ikeda & Motoda 1978), ***Gr*** is gross growth efficiency (**0.3**, Ikeda & Motoda 1978).

- Thus, the following equation holds:

$$PR = 0.3\ FR \quad \text{or} \quad PR \,/\, FR = 0.3$$

Table 6 The ratio of depth-integrated production rate to food requirement, *PR*/*FR* ratio (mean±SD), for copepods in Sagami Bay, from January 2006 to December 2017.

Taxonomic group	Species	Equation to estimate *G*	*PR*/*FR* (mean±SD)
Copepods (C1–C6)	All	Huntley & Boyd (1984)	1.11±0.24
Copepods (C1–C6)	All	Huntley & Lopez (1992)	0.93±0.20
Copepods (C1–C6)	*Acartia* *Calanus* *Centropages* *Microsetella* *Oithona* *Paracalanus* Others (Total)	Uye (1982) Uye (1988) Liang et al. (1996) Uye et al. (2002) Uye & Sano (1998) Uye (1991) Uye & Shimazu (1997)	0.82±0.17
Copepods (C1–C6)	All	Hirst & Sheader (1997)	0.29±0.02
Copepods (C1–C6)	All	Hirst & Lampitt (1998)	0.23±0.03
Copepods (C1–C6)	All	Hirst et al. (2003)	0.25±0.02
Copepods (C1–C6)	All	Hirst & Bunker (2003)	0.20±0.07

- The *PR*/*FR* ratio estimated using the Hirst & Sheader model is closer to 0.3.

Table 7 The ratio of depth-integrated production rate to food requirement, *PR*/*FR* ratio (mean±SD), for mesozooplankton in Sagami Bay, from January 2006 to December 2017.

Taxonomic group	Species	Equation to estimate *G*	*PR*/*FR* (mean±SD)
Copepods (C1–C6)	All	Hirst & Sheader (1997)	0.29±0.02
Crustacean nauplii	All	Hirst *et al*. (2003)	0.35±0.04
Cladocerans	All	Hirst *et al*. (2003)	0.37±0.06
Ostracods	All	Hirst *et al*. (2003)	0.40±0.05
Malacostracans	All	Hirst *et al*. (2003)	0.35±0.06
Appendicularians	All	López-Urrutia (2003)	0.33±0.05
Thaliaceans	All	Hirst *et al*. (2003)	0.40±0.17
Polychaet larvae	All	Hirst *et al*. (2003)	0.49±0.06
Mollucsan larvae	All	Hirst *et al*. (2003)	0.48±0.05
Chaetognaths	All	Hirst *et al*. (2003)	0.27±0.04
Cnidarians	All	Hirst *et al*. (2003)	0.47±0.04
Fish larvae	All	Hirst *et al*. (2003)	0.51±0.06
Others	All	Hirst *et al*. (2003)	0.34±0.06
Total mesozooplankton	All	Hirst & Sheader (1997) Hirst *et al*. (2003) López-Urrutia (2003)	0.33±0.03

- The *PR*/*FR* ratios for each taxonomic group and total mesozooplankton are close to 0.3.

Table 5 Feeding habits of mesozooplankton.

Feeding habit	Copepods	Non-copepods
Herbivorous (HER)	*Calanus, Acrocalanus, Calocalanus, Canthocalanus, Clausocalanus, Ctenocalanus, Eucalanus, Microcalanus, Nannocalanus, Rhincalanus, Paracalanus, Pseudocalanus, Calanoides, Pseudodiaptomus, Undinula, Clytemnestra, Euterpina, Macrosetealla, Microsetella*	Appendicularians, Cladocerans, Crustacean (non-copepod) nauplii, Molluscan (Bivalve and Gastropod) larvae, Polychaet larvae, Thaliaceans
Omnivorous (OMN)	*Acartia*, *Aetideus, Bradyidius, Centropages*, *Chiridius, Gaidius, Lucicutia, Metridia, Oithona, Oncaea*, *Pleuromamma, Scolecithricella, Scolecithrix, Scottocalanus*, *Temora*	Malacostracans (Decapod larvae, Mysids, Amphipods), Ostracods
Carnivorous (CAR)	*Calanopia*, *Candacia*, *Corycaeus, Copilia, Euchaeta*, *Paraeuchaeta*, *Heterorhabdbus, Labidocera*, *Pontellina, Phaenna, Farranula, Sapphirina*	Decapod *Lucifer*, Chaetognaths, Cnidarians, Fish larvae

Daily production rate (PR, mg C m^{-3} d^{-1})

- 2ndary production (PR_{2P}): $PR_{2P} = PR_{HER} + 0.5 \times PR_{OMN}$
- 3tiary production (PR_{3P}): $PR_{3P} = PR_{CAR} + 0.5 \times PR_{OMN}$

Food requirement (FR, mg C m^{-3} d^{-1})

- 2ndary producers (FR_{2P}): $FR_{2P} = FR_{HER} + 0.5 \times FR_{OMN}$
- 3tiary producers (FR_{3P}): $FR_{3P} = FR_{CAR} + 0.5 \times FR_{OMN}$

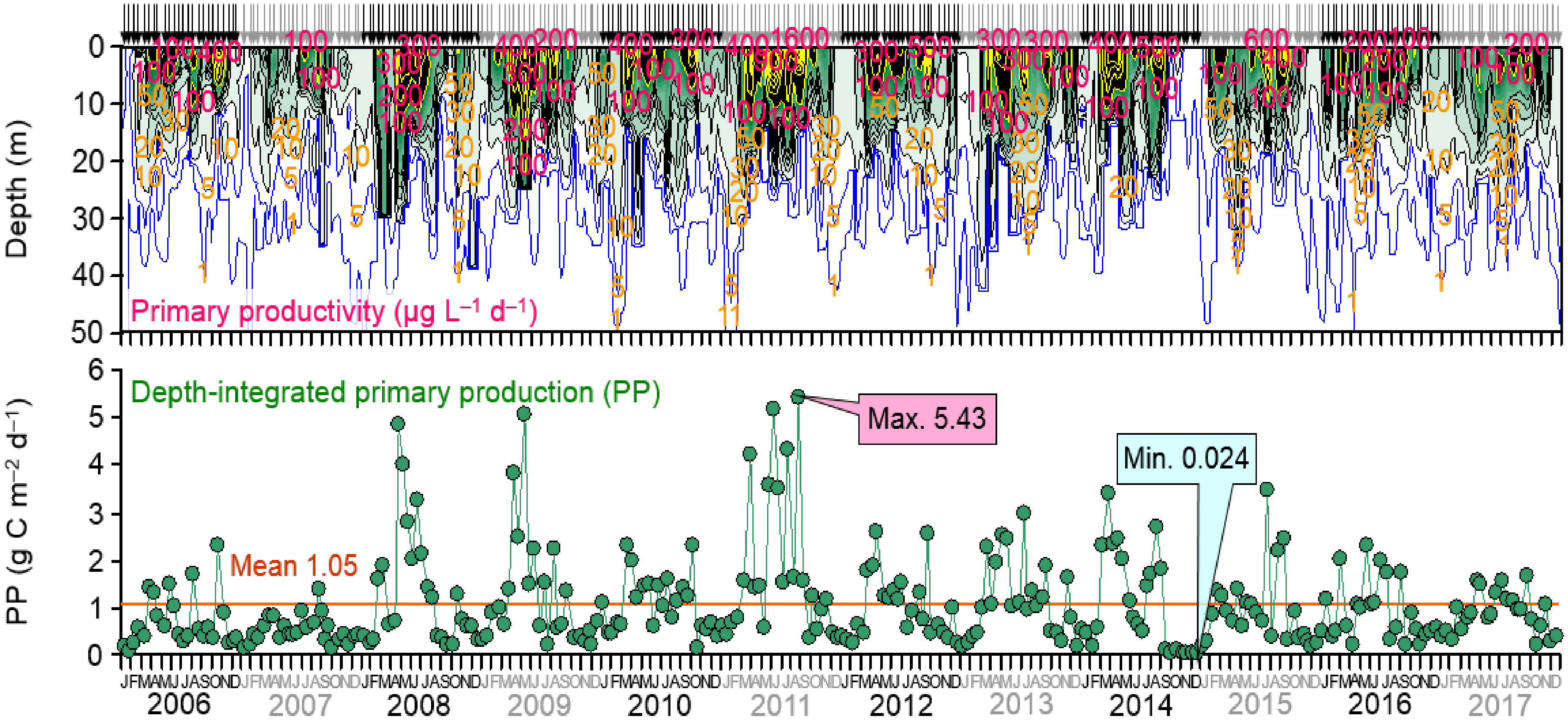


Figure 5 Temporal variations in vertical profiles of phytoplankton primary productivity (upper) and in depth-integrated primary production (PP) in the euphotic zone (lower) in Sagami Bay, from January 2006 to December 2017. Arrows denote sampling dates.

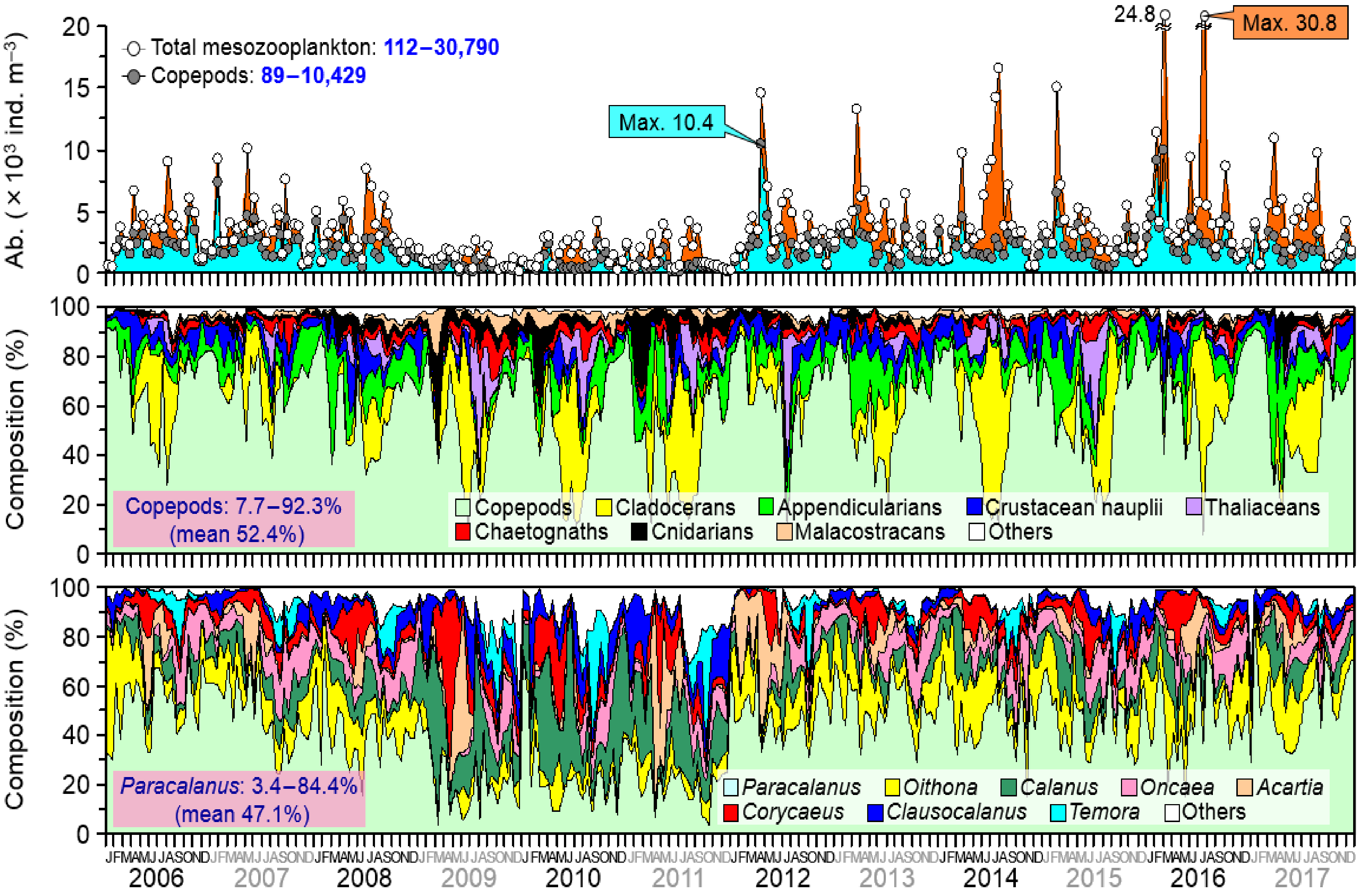


Figure 6 Temporal variations in abundance (Ab.) of the total mesozooplankton and copepods (upper) and in composition (middle and lower) in Sagami Bay, from January 2006 to December 2017.

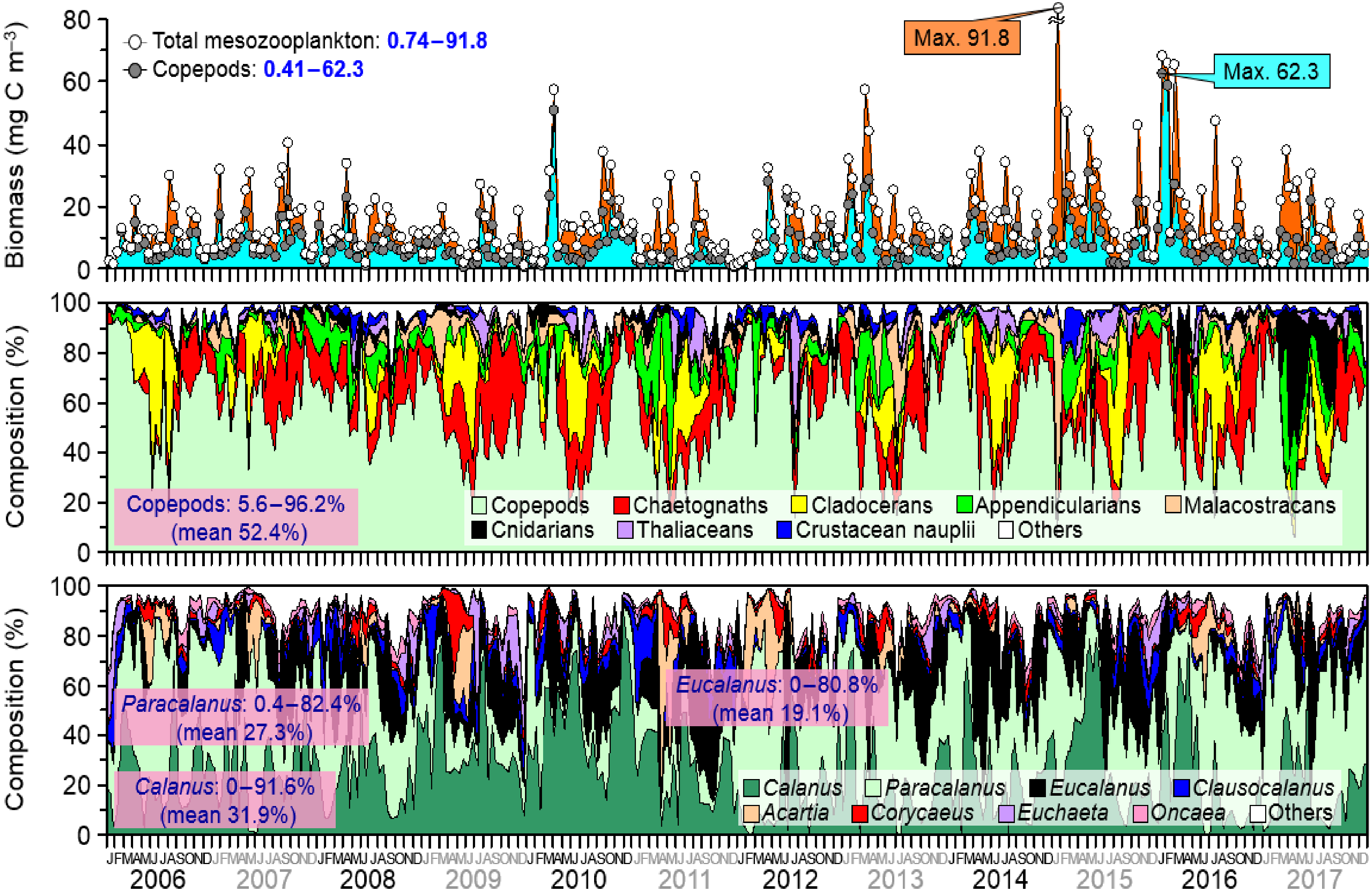


Figure 7 Temporal variations in biomass of the total mesozooplankton and copepods (upper) and in composition (middle and lower) in Sagami Bay, from January 2006 to December 2017.

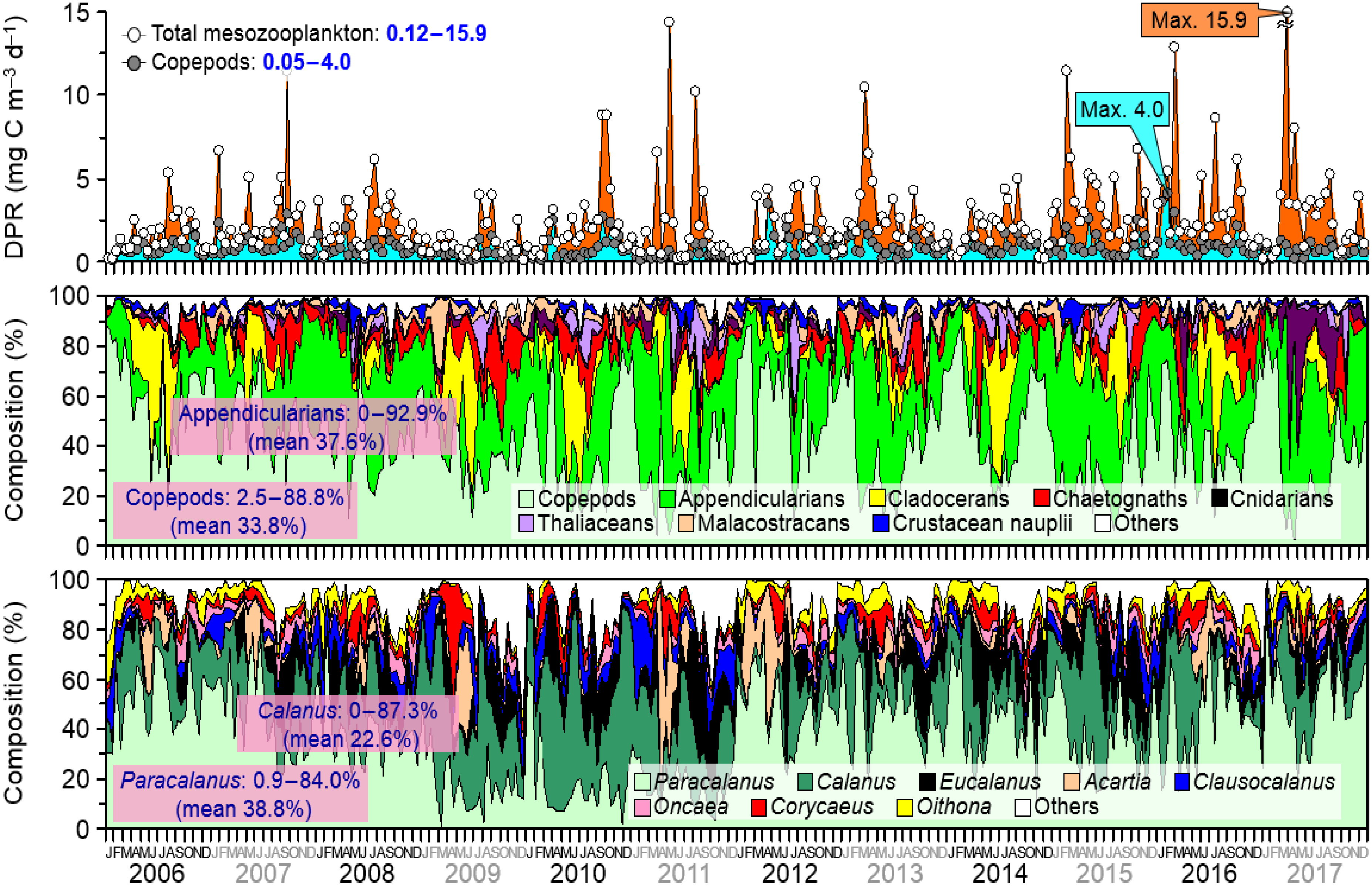


Figure 8 Temporal variations in daily production rate (DPR) of the total mesozooplankton and copepods (upper) and in composition (middle and lower) in Sagami Bay, from January 2006 to December 2017.

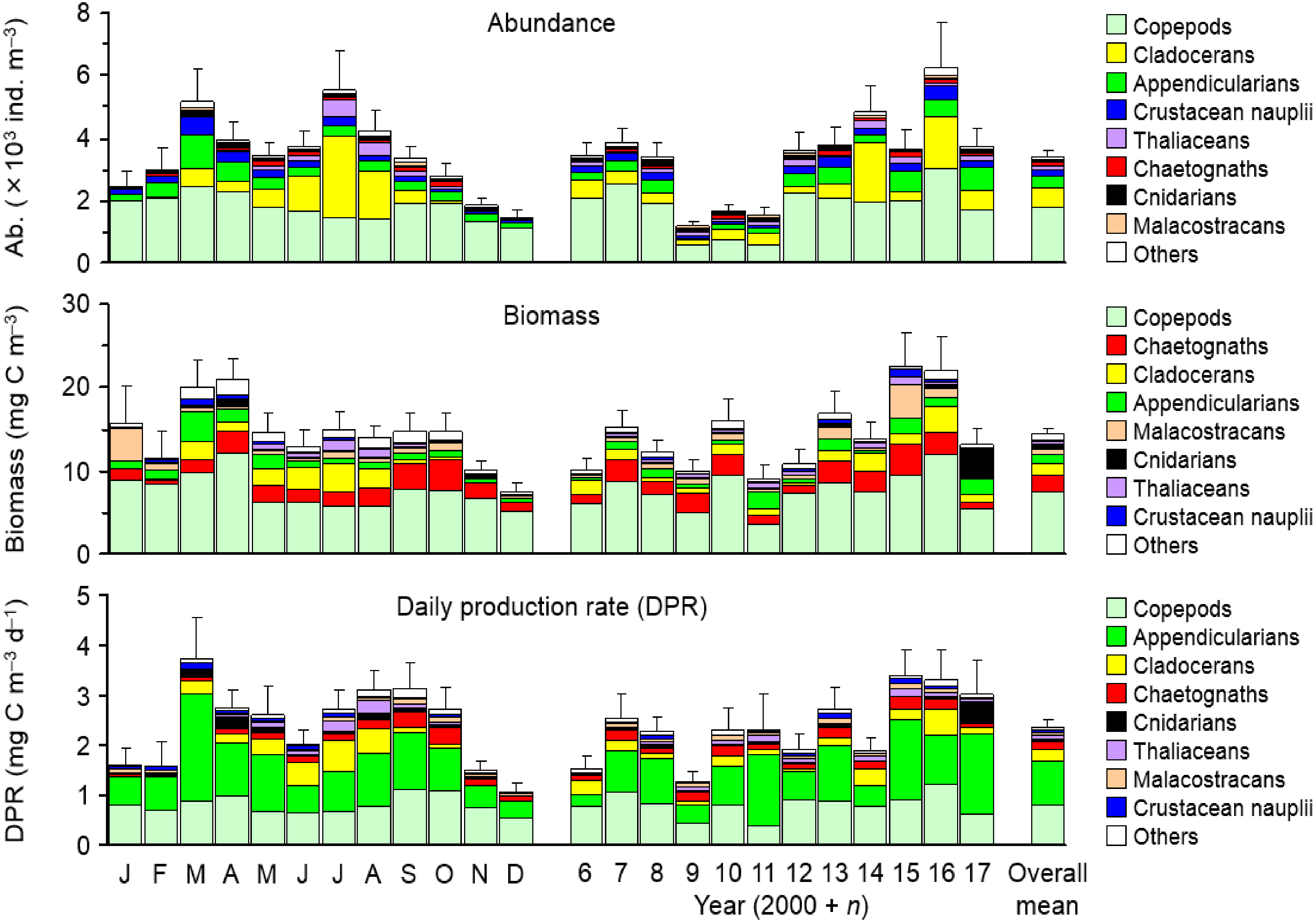


Figure 9 Mean MZ abundance, biomass and daily production rate (DPR) in Sagami Bay, from January 2006 to December 2017. Error bars indicates standard error (SE).

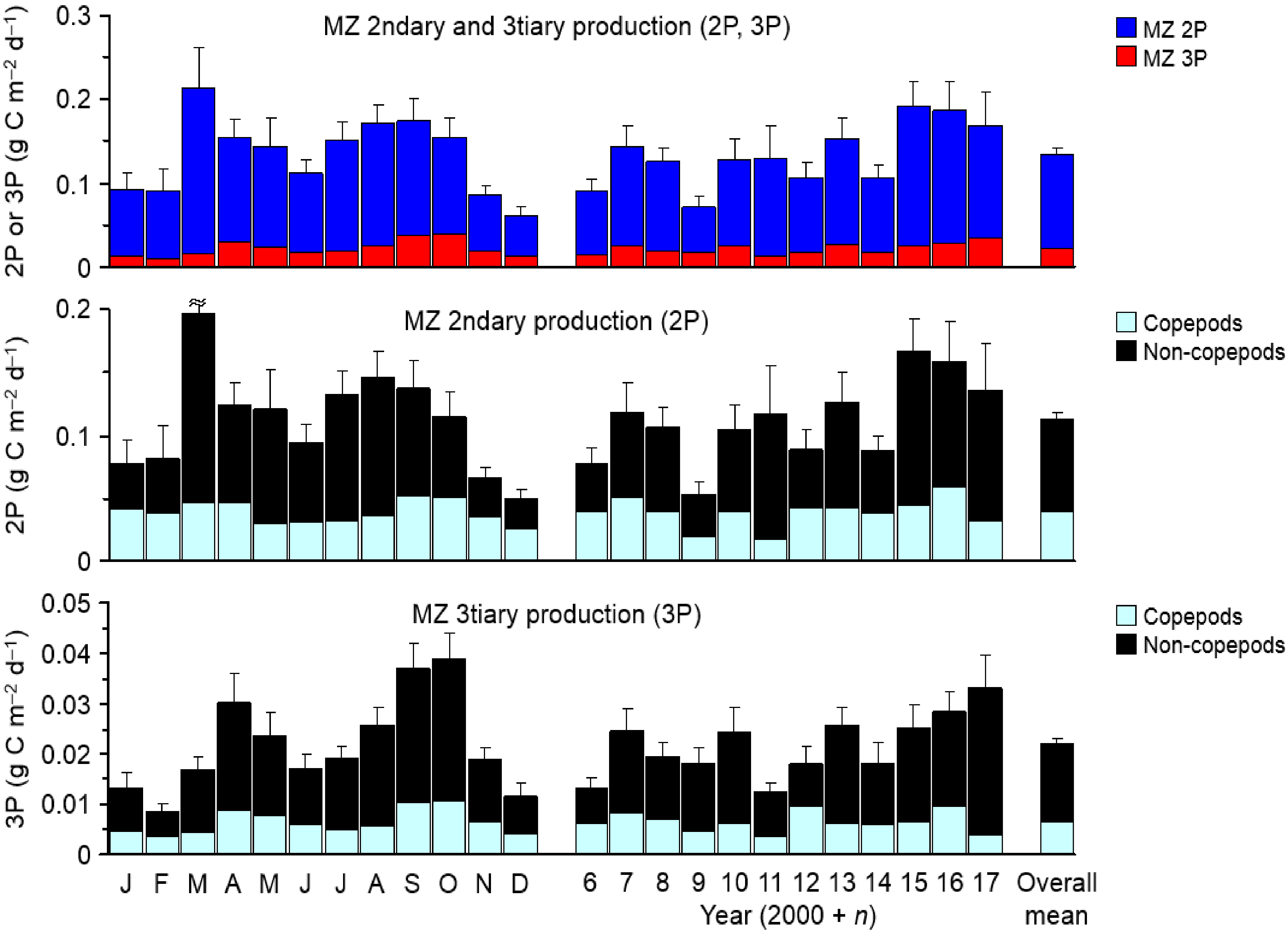


Figure 10 Mean depth-integrated MZ 2ndary and 3tiary production (2P, 3P) in Sagami Bay, from January 2006 to December 2017.

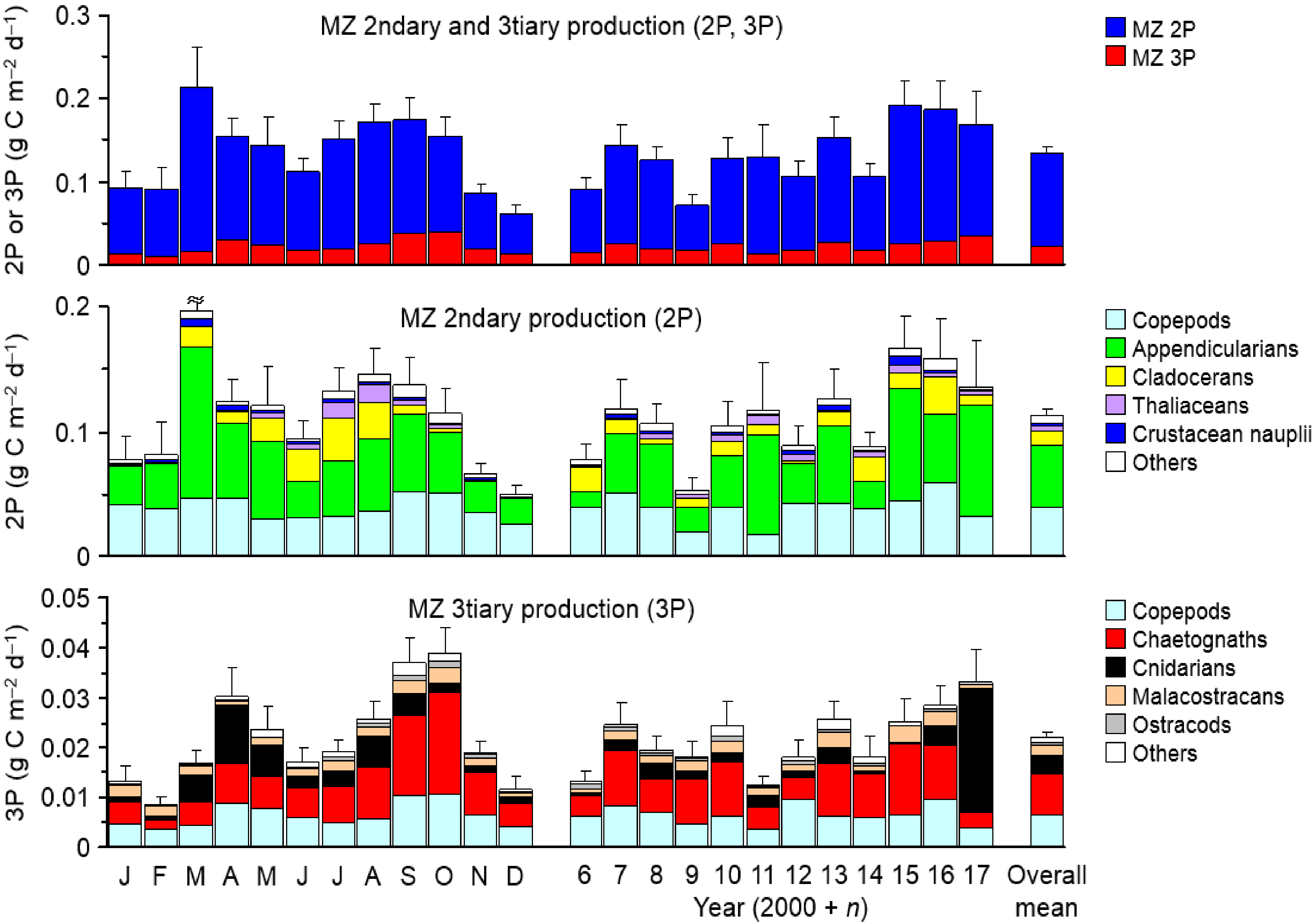


Figure 10 Mean depth-integrated MZ 2ndary and 3tiary production (2P, 3P) in Sagami Bay, from January 2006 to December 2017.

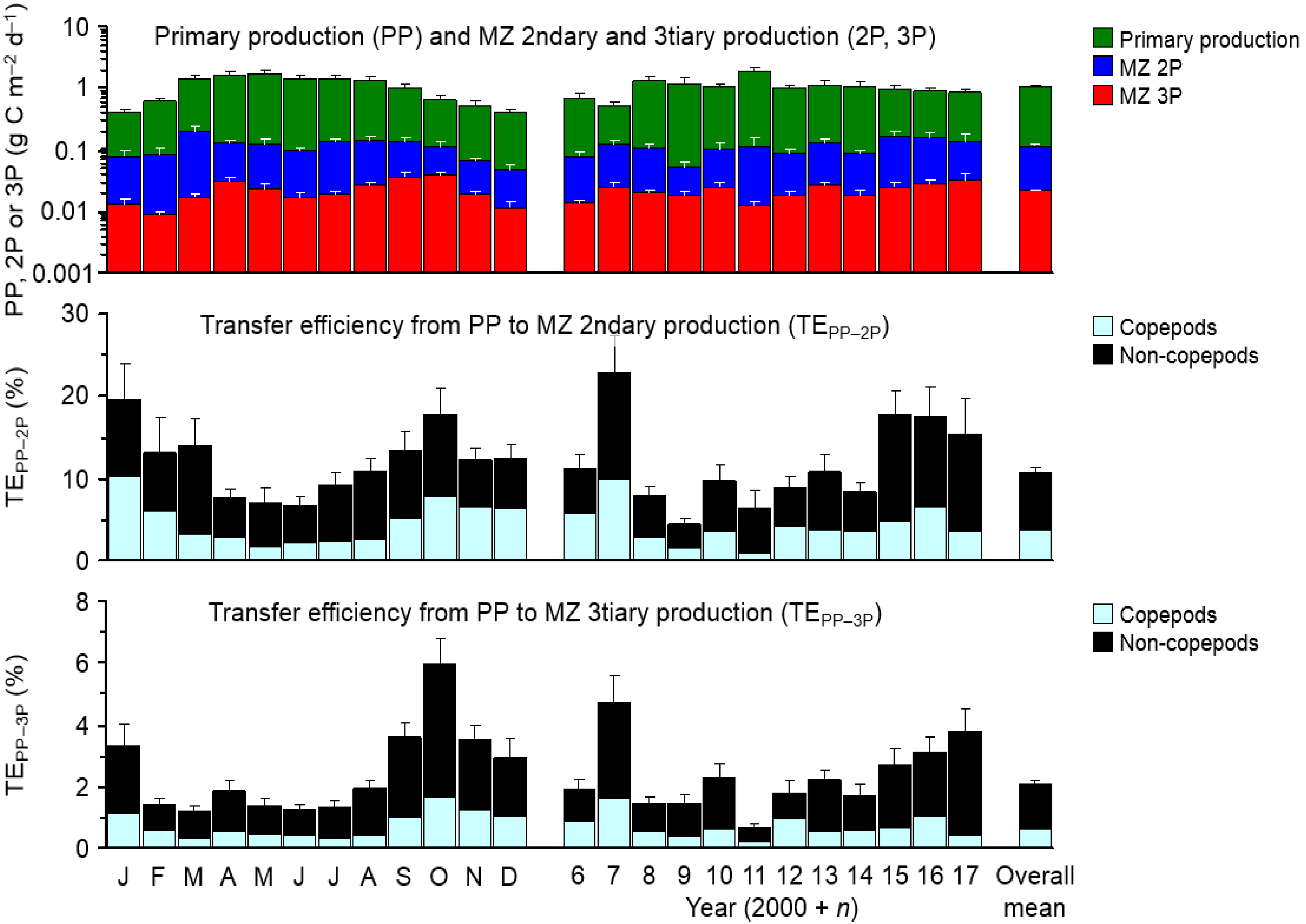


Figure 11 Mean depth-integrated production rate (PP, 2P, 3P) and transfer efficiency from PP to MZ 2ndary and 3tiary production (TE_{PP-2P}, TE_{PP-3P}) in Sagami Bay, from January 2006 to December 2017.

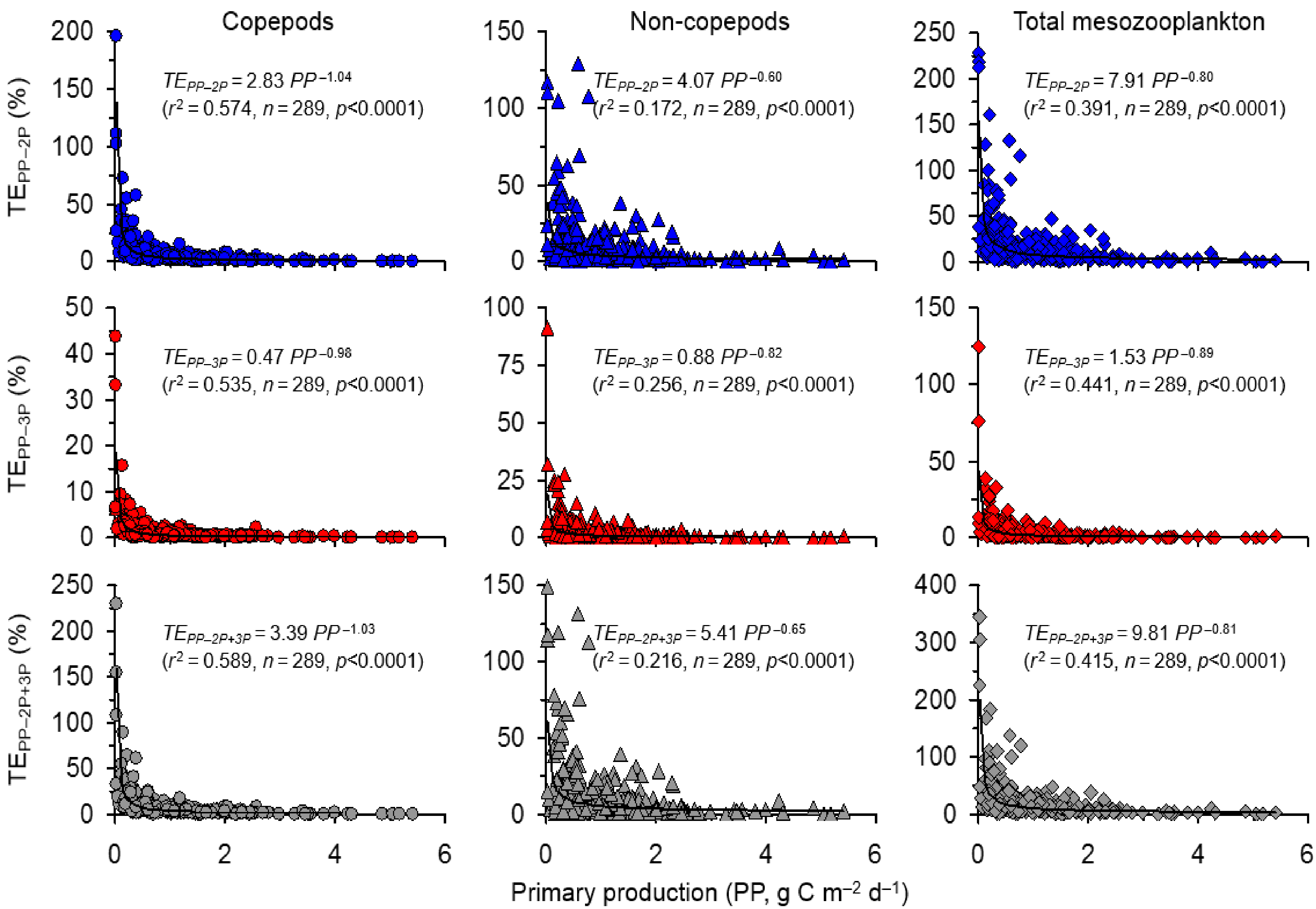


Figure 12 Relationships between primary production (PP) and transfer efficiency from PP to MZ 2ndary, 3tiary and total production (TE_{PP-2P}, TE_{PP-3P}, $TE_{PP-2P+3P}$) for copepods, non-copepods and total mesozooplankton in Sagami Bay, from January 2006 to December 2017.

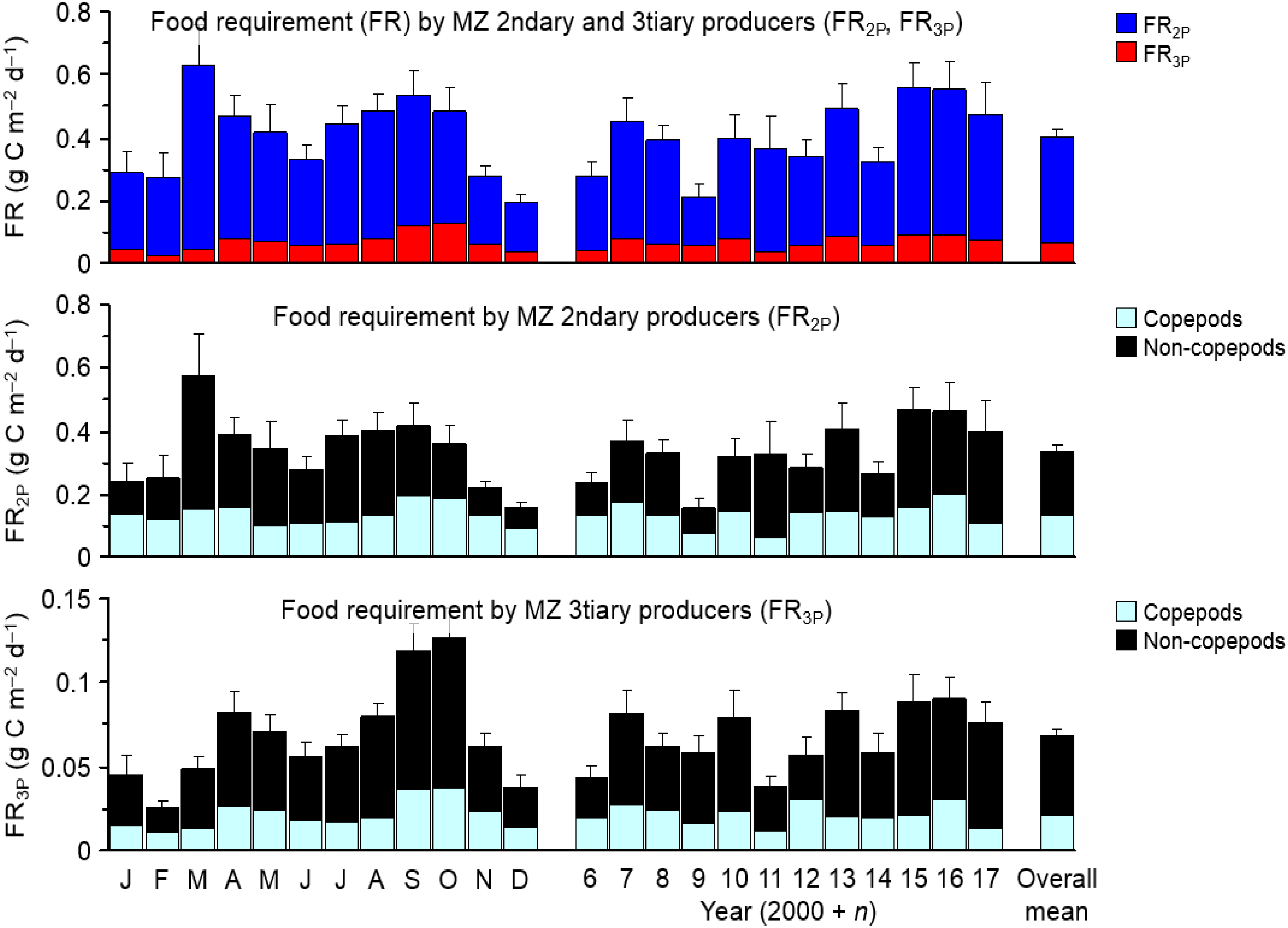


Figure 13 Mean depth-integrated food requirement (FR) by MZ 2ndary and 3tiary producers (FR_{2P}, FR_{3P}) in Sagami Bay, from January 2006 to December 2017.

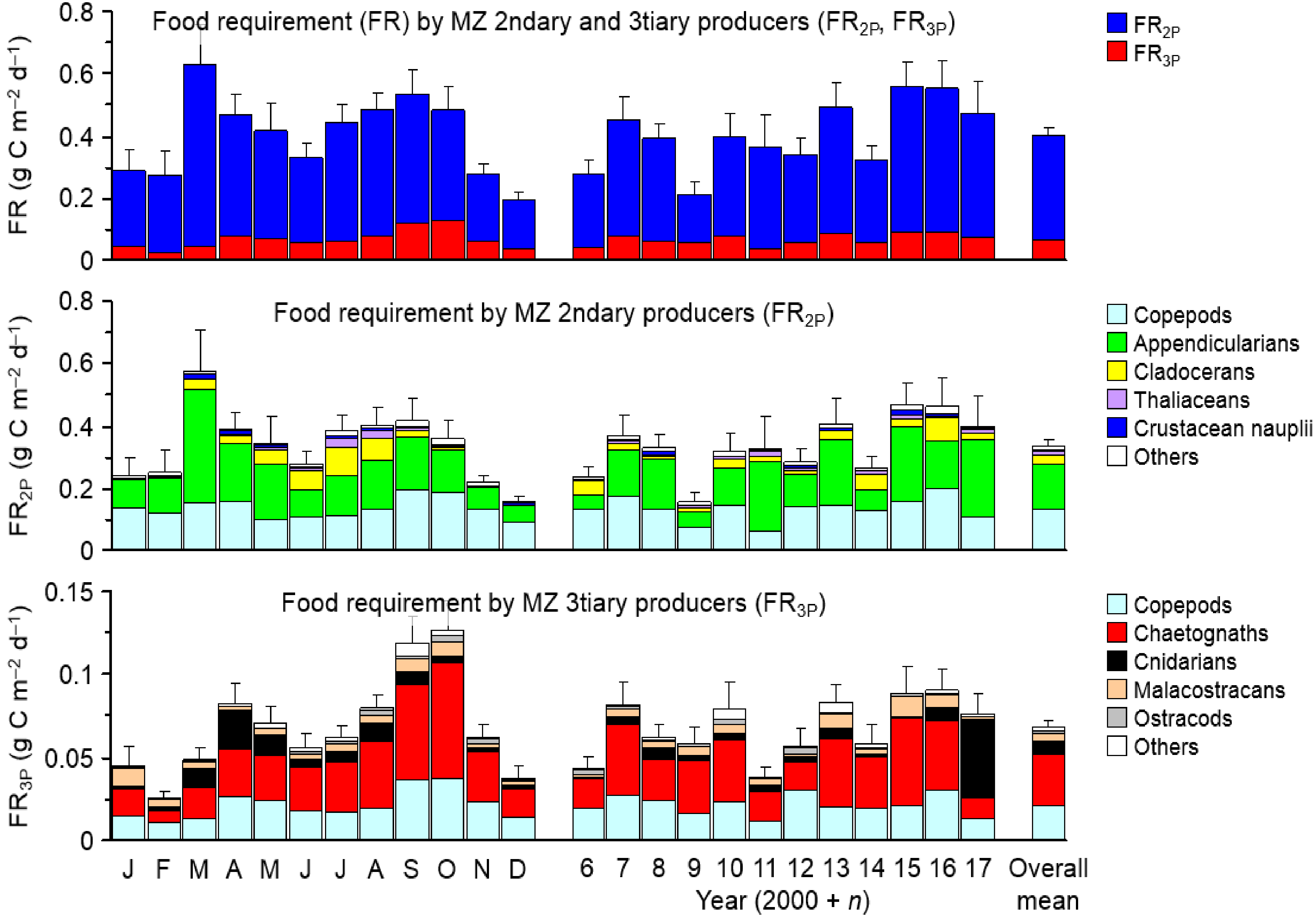


Figure 13 Mean depth-integrated food requirement (FR) by MZ 2ndary and 3tiary producers (FR_{2P}, FR_{3P}) in Sagami Bay, from January 2006 to December 2017.

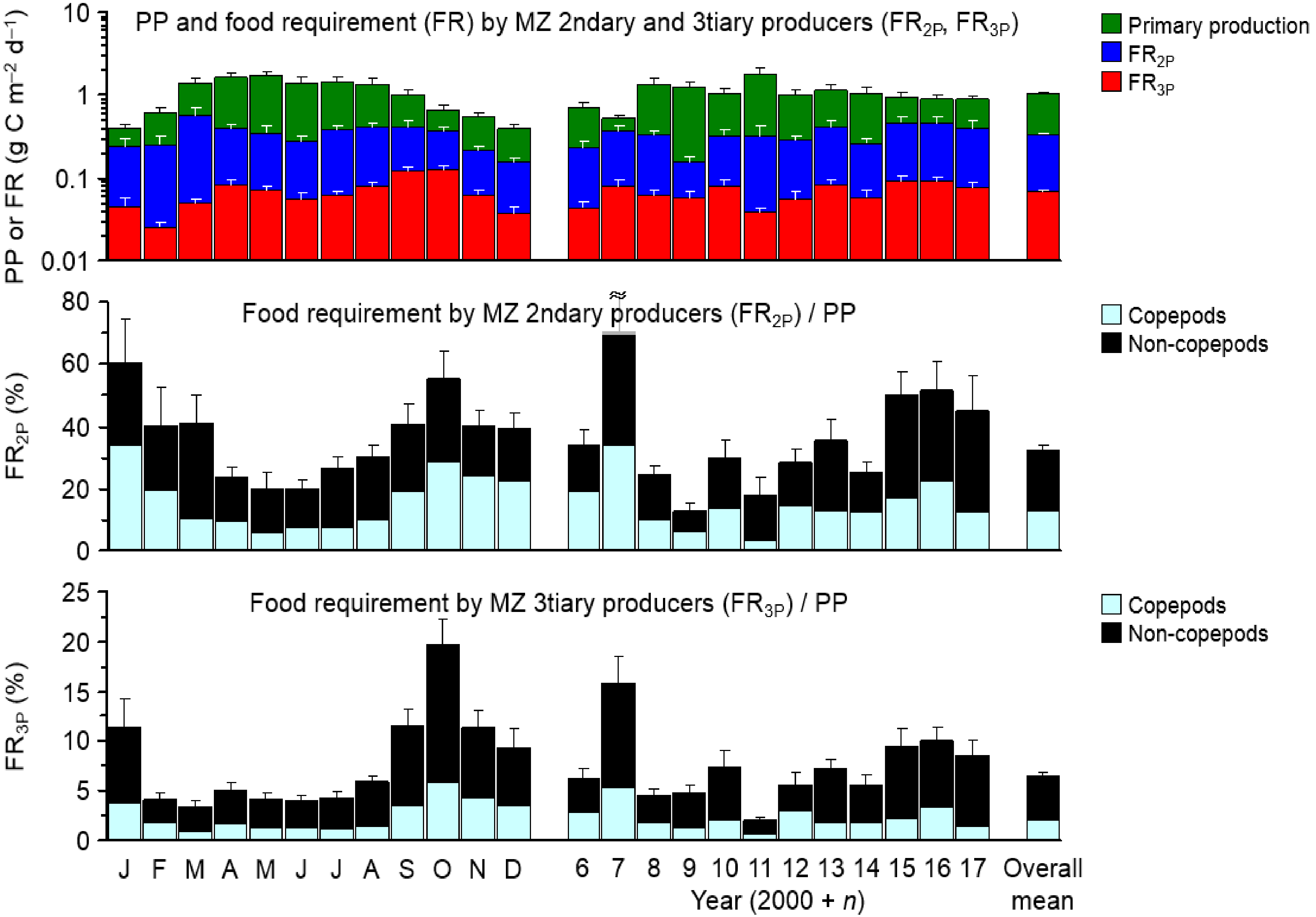


Figure 14 Mean depth-integrated primary production (PP) and food requirement (FR) by MZ 2ndary and 3tiary producers (FR_{2P}, FR_{3P}), and the ratio of FR_{2P} and FR_{3P} to PP in Sagami Bay, from January 2006 to December 2017.

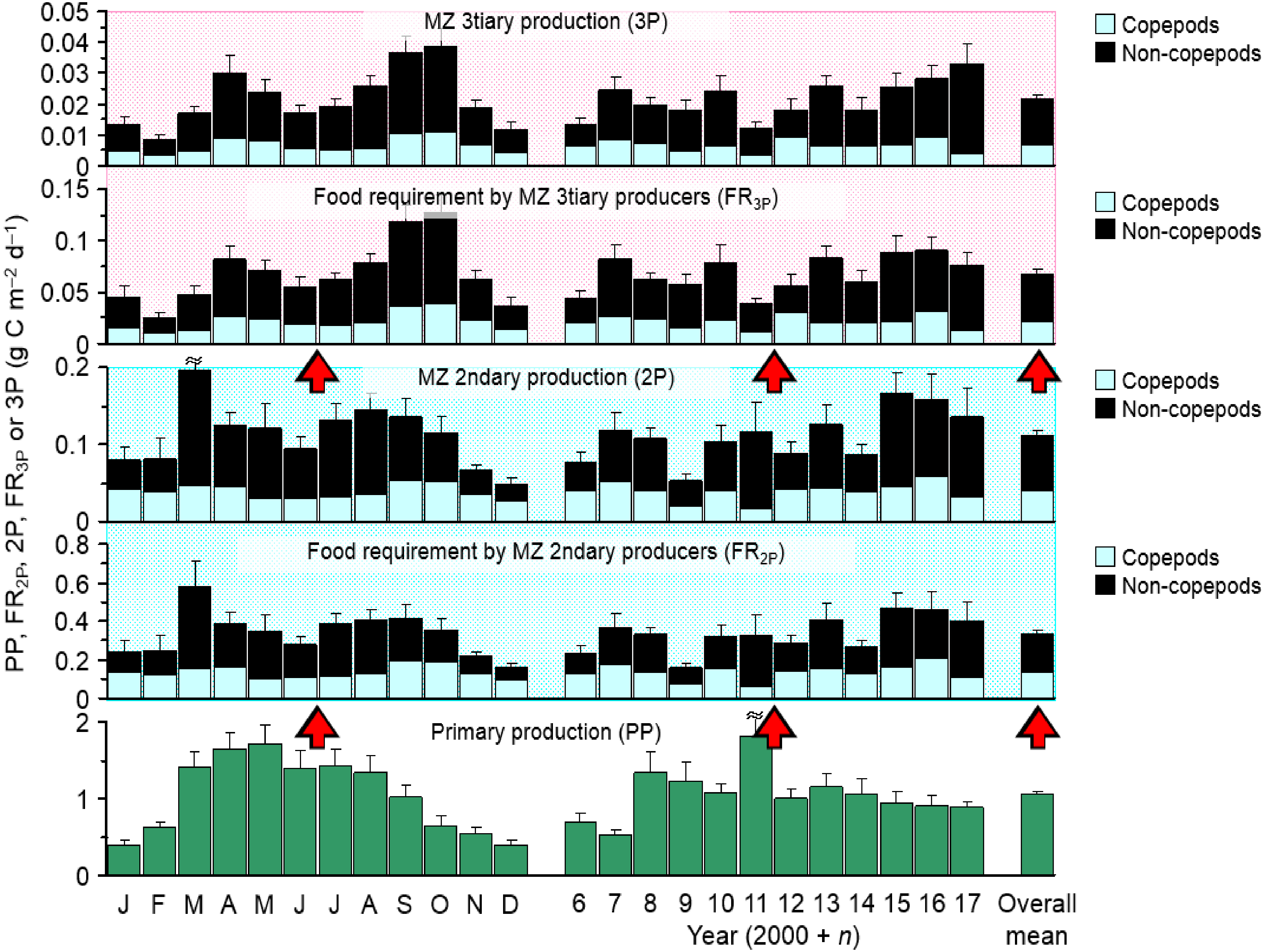


Figure 15 Trophodynamics in terms of carbon flow based on the depth-integrated production rate (PR) and food requirement (FR) from primary production (PP) to MZ 2ndary and 3tiary production (2P, 3P) in Sagami Bay.

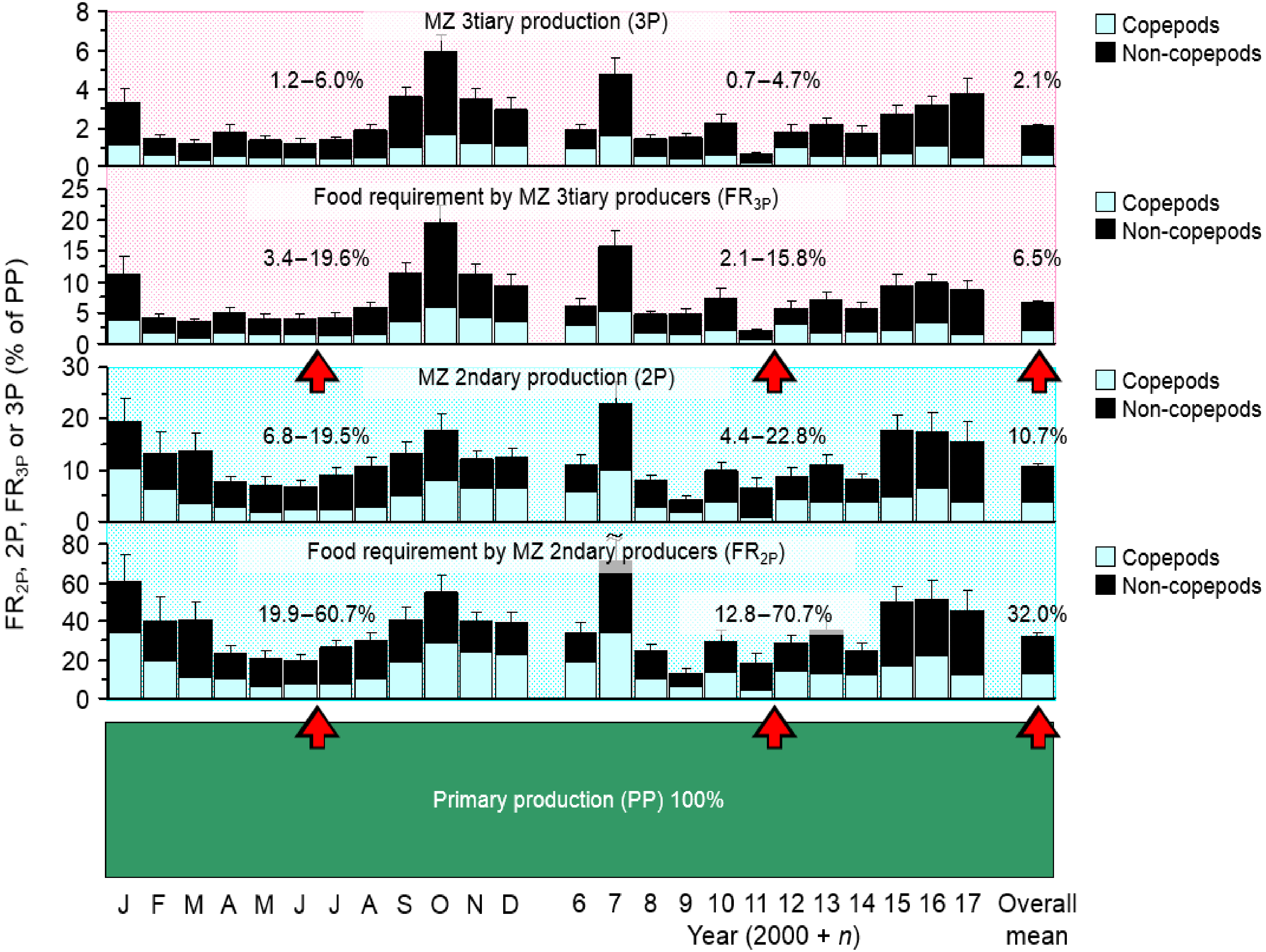


Figure 15 Trophodynamics in terms of carbon flow based on the depth-integrated production rate (PR) and food requirement (FR) from primary production (PP) to MZ 2ndary and 3tiary production (2P, 3P) in Sagami Bay.