Zooplankton Production and Metabolic Activity in the North Atlantic and Adjacent Seas

By

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Review

The ICES Working Group on Zooplankton Ecology: Accomplishments of the first 25 years

Peter H. Wiebe [a,*], Roger Harris [b], Astthor Gislason [c], Piotr Margonski [d], Hein Rune Skjoldal [e], Mark Benfield [f], Steve Hay [g], Todd O'Brien [h], Luis Valdés [i]

WGZE: ToR J (2015 – 2017)

Calculate zooplankton productivity and metabolic rates in the ICES area based on allometric approaches

Build a database of zooplankton individual species biomass, productivity and metabolic rate equations

Assessing the Zooplankton Metabolism & Productivity

1. Incubation methods

2. Biochemical methods

3. Calculations using empirical models mostly basing on 1

Comprehensive reviews by Runge and Roff and by Ikeda et al. in Zooplankton Methodological Manual ZMM (2000)

The principle

Formulas for metabolism and growth often base on KLEIBERs rule

– **A fundamental law in ecology** (Peters, 1983; Andersen et al., 2016)

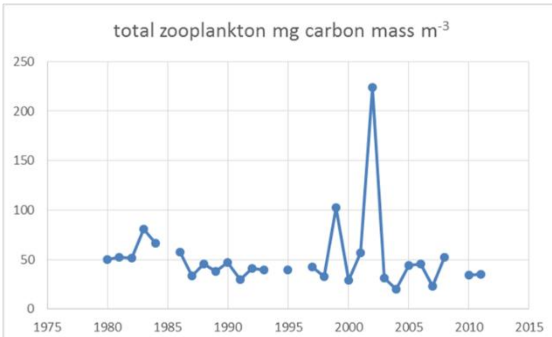
$$P = a * M^{b}$$

M - **body mass** , P=(Gross) productivity

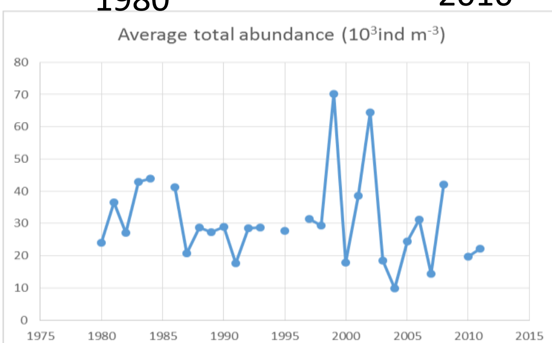
a - depend on **temperature**, **food** conc., other intrinsic and external factors
b - depend on the quantity of internal body parameter in relation to the entire organism (Kleiber, 1932, 1947, 1961; West et al., 1997, etc.)

Input

Biomass concentration

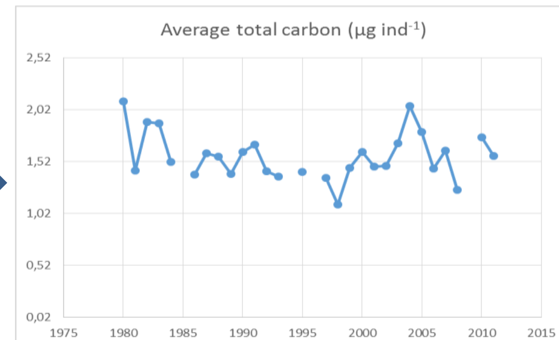


1980 2010



Abundance

Individual body mass



1980 2010

Baltic Sea, Bornholm Basin, 0-80m, July-August 1979 -2011

Output

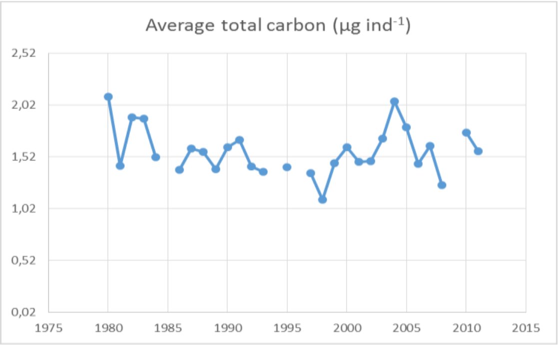
Banse and Mosher (1980)

- **Temperature ranges: 5 to 20°C**
- **Most measured values fall within 50 and 200 % of predicted values**

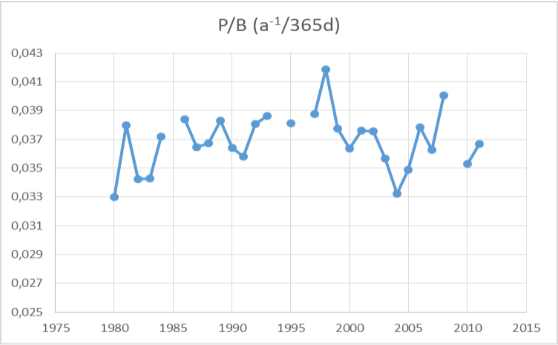
Invertebrates

$P/B = 0.65\ M_s^{-0.37}$

Individual body mass



Biomass specific Gross production

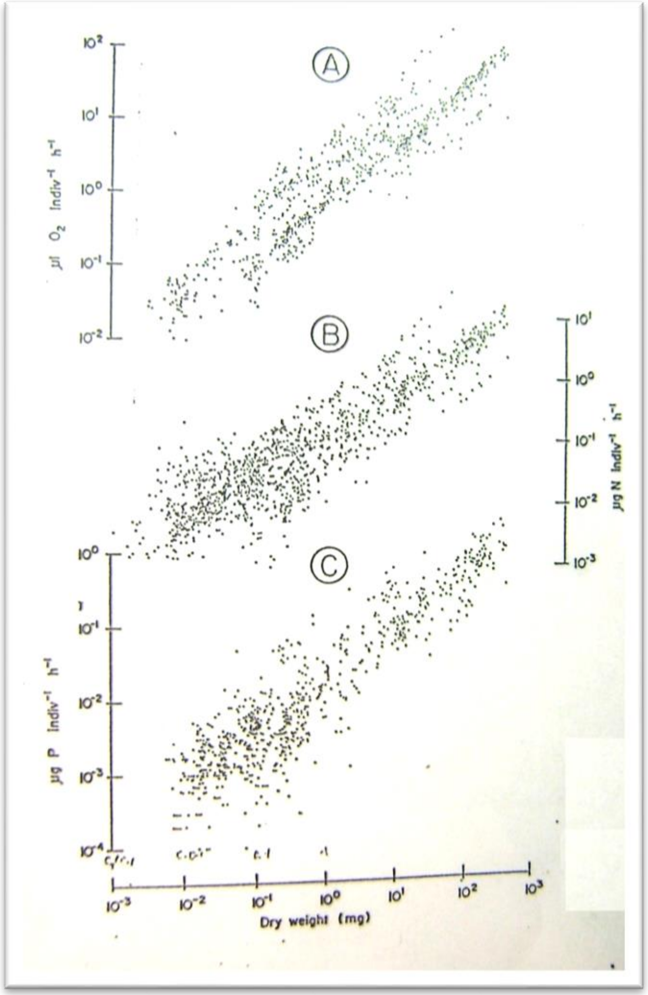


Baltic Sea, Bornholm Basin, 0-80m, July-August 1979 -2011

Principle can be used for metabolic rates as well:

- Respiration
- Ammonia excretion
- Phoshorus excretion

- Using formulas developed by Ikeda (1985)



Oxygen uptake rate
N = 721

Ammonia excretion rate
N = 1186

Phosphate excretion rate
N = 749

Habitat temperature -1,4° to 30°C

Ikeda (1985)

Calculation of respiration und excretion according to IKEDA (1985)

Temperate seas

$\ln R = - 0{,}2512 + 0{,}7886 \ln DM + 0{,}0490\, T$	DM / ind. [mg], T [°C], R [µl /ind./h]; NH_4^+ bzw. PO_4^{3-} [µg/Ind./h] Note: µg NH_4^+ / 14 = µM NH_4^+ µg PO_4^{3-} / 31= µM PO_4^{3-} µl O_2 / 22.4 =µM O_2
$\ln NH_4^+ = - 2{,}8900 + 0{,}7616 \ln DM + 0{,}0511\, T$	
$\ln PO_4^{3-} = - 4{,}3489 + 0{,}7983 \ln DM + 0{,}0285\, T$	

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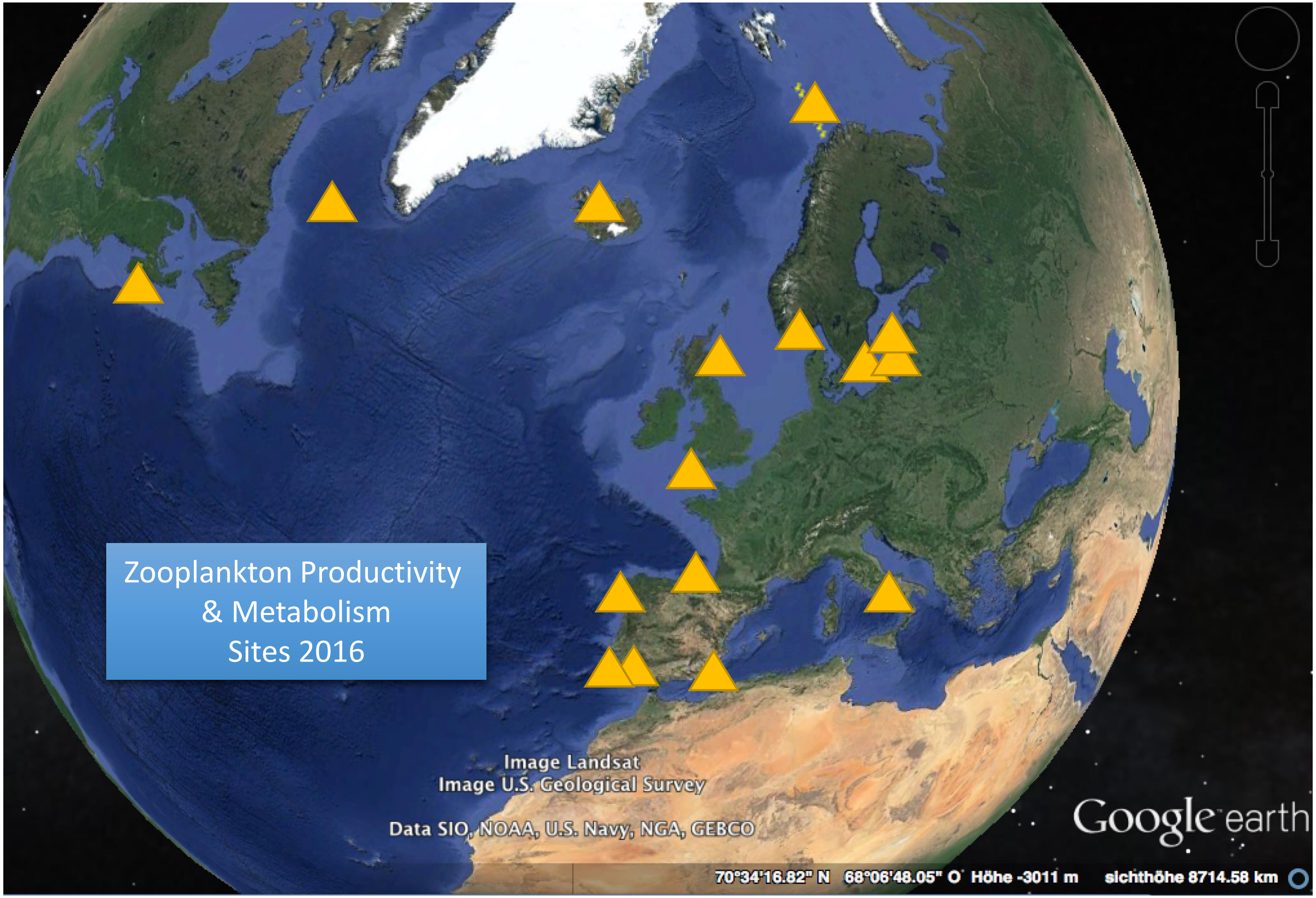
Following sites are included:

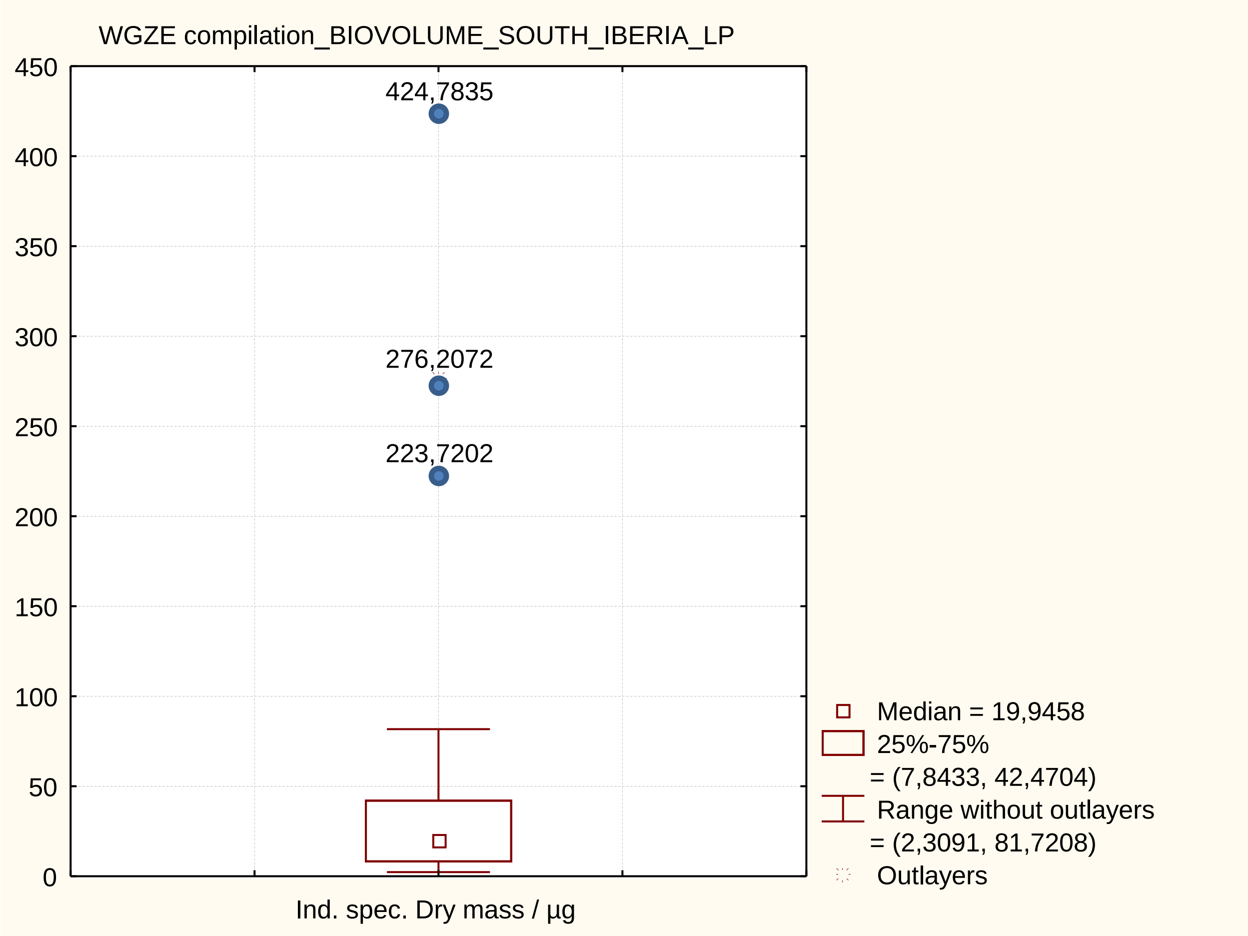


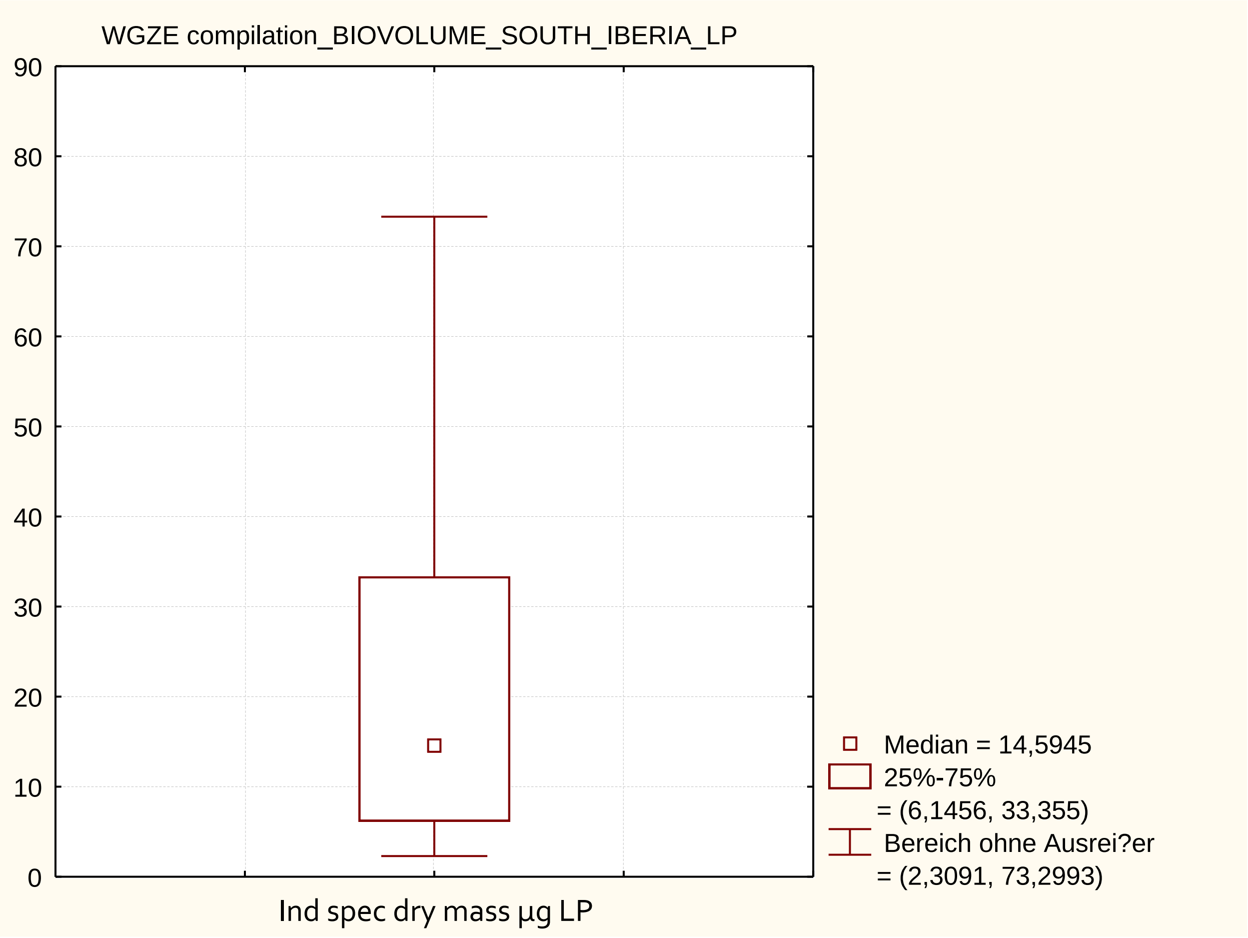
ZSR site		Partner	Period
Labrador Sea			
	Labrador Sea	Erica Head	1998 - 2006
Scotian Shelf			
	Halifax Line 2	Erica Head, Cathrine Johnson	1999 - 2012
Nordic & Barents Seas			
	Selvogsbanki Transect (South Iceland)	Astthor Gislason	2000-2013
	Siglunes Transect (North Iceland)		
	Fugløya-Bjørnøya Islands (FB) transect	Padmini Dalpadado	1995-2014
Baltic Sea			
	Bornholm Basin	Lutz Postel	1979 - 2012
	Bornholm Basin	Piotr Margonski, Alina Krajewska, Anna Grzyb	2008 - 2013
	Gdansk Basin		1986 - 2010
	Eastern Gotland Basin	Gunta Rubene (BIOR)	1960 - 2011
North Sea & English Channel			
	Stonehaven	Kathryn Cook	2007 - 2008
	Arendal Station 2	Tone Falkenhaug	1994 - 2010
	Plymouth L4	Elaine Fileman, Angus Atkinson	1993-1998
Bay of Biscay & western Iberian Shelf			
	Bilbao Estuary 35	Fernando Villate	1997
	Urdaibai Estuary 35	Arantza Iriarte	
	RADIALES Vigo St. 3	Ana Miranda	2010 - 2013
	Guadiana Lower Estuary	Maria Alexandra Teodósio	2009 - 2012
	Cascais watch	Antonina dos Santos Raquel Marques	2005 - 2014
Mediterranean Sea			
	Ecomalaga	Teodoro Ramírez, Dolores Cortés, Jesús M. Mercado, Lidia Yebra	1994-2000
	Gulf of Naples LTER-MC	Maria Grazia Mazzocchi	1984-90 1995-2014

Main problems to be considered:

- Outlier rejections
  (Organisms occasionally catched)
- Biomass conversion factors
- Which approach provides results
  of higher accuracy?

Individual specific dry mass [µg]:
Successive identification and removing of outliers

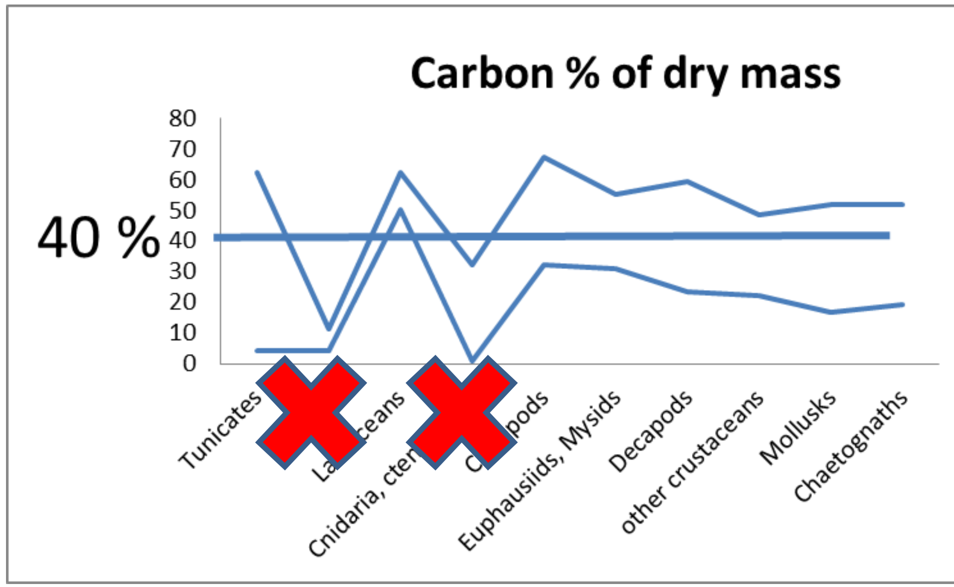




WGZE compilation_BIOVOLUME_SOUTH_IBERIA_LP
90
80
70
60
50
40
30
20
10
0
Median = 14,5945
25%-75%
= (6,1456, 33,355)
Bereich ohne Ausrei?er
= (2,3091, 73,2993)
Ind spec dry mass µg LP

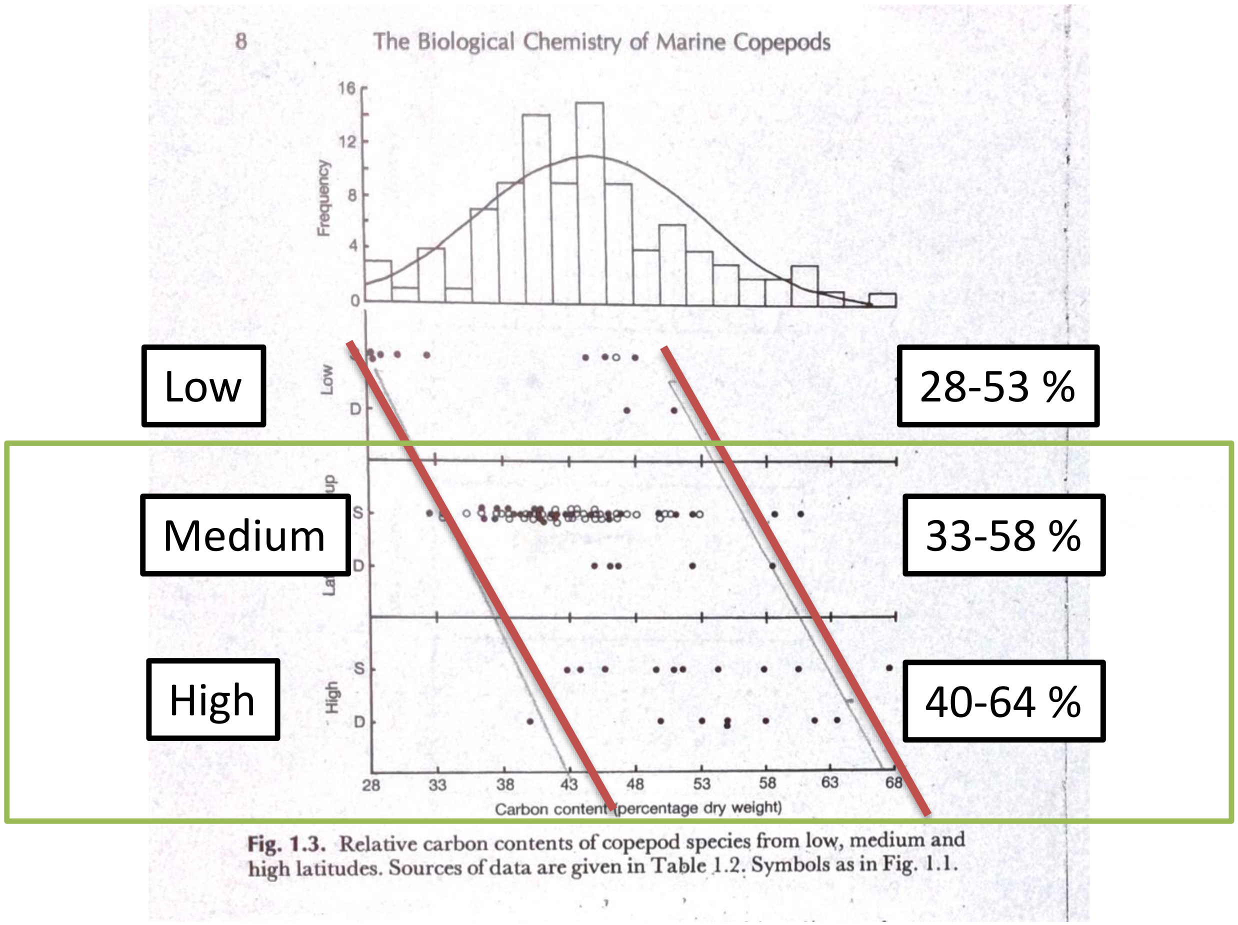
C content varies between taxa, ...

Hirst et al., 2003



Schneider, 1989, 1990

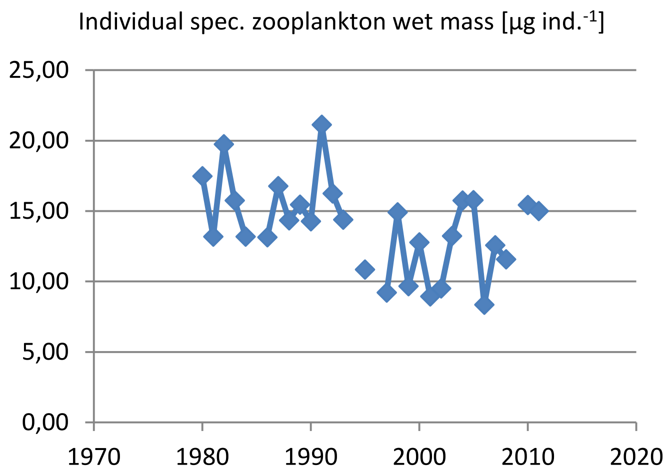
... and latitude

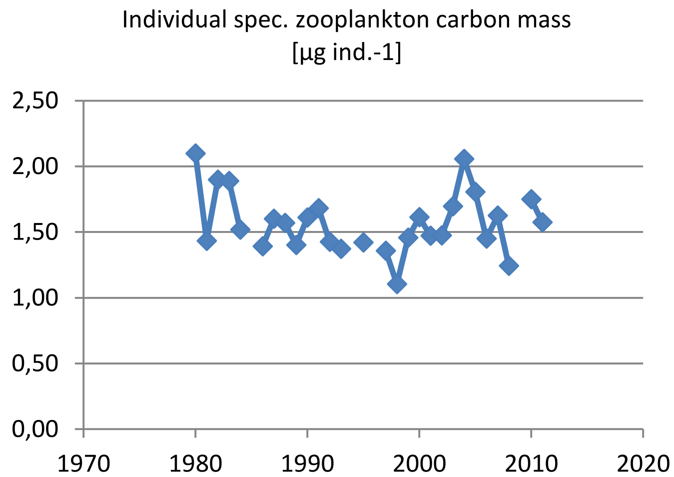


BAMSTEDT, U. 1986. Chemical composition and energy content, p. 1–158. In E. D. S. Corner and S. C. M. O'Hara [eds.], The biological chemistry of marine copepods. Oxford Scientific.

We checked the origin of conversion factors

Wet mass, factors of changing origin → Recalculation with carbon mass factors





Bornholm Basin (Baltic Sea): IOW

Conversion factors finally used:

Dry mass DM=	**0.2**	Wet mass WM	(ICES Terms…, 1958)
DM=	0.13 WM	(Mullin, 1969, basing on Beers,1966 and Lovegrove, 1966 respectively)	
C=	**0.4** DM	(Hirst, Roff and Lampitt, 2003, basing on Mullin, 1969, basing on Beers, 1966 and Lovegrove, 1966 respectively)	
DM=	**0,014**	Displacement volume DV (calculated after Bode et al. 1998)	
WM=	**0.12** C	(ICES Terms…, 1958)	

Interregional comparisons requires Standard-Procedure:

- One Plankton fraction: Mesozooplankton (0.2 – 2 mm)
  → i.e.: Similar gear and mesh size

- Preferably one method of biomass determination **(in our case mainly dry mass)** and of counting procedure

- Comparable seasonal conditions of metabolism →Checked by O:N ratio of respired/excreted components

ZSR site	Partner	Period	Net	Mesh size	Depth range [m]	Biomass determination
Labrador Sea						
Labrador Sea	Erica Head	1998 - 2006	Conical ring net, 0,44m^2	200 µm	0-100	Dry mass of Copepods [mg m^{-3}]
Scotian Shelf						
Halifax Line 2	Erica Head, Cathrine Johnson	1999 - 2012	Conical ring net, 0,44m^2	200 µm	0-150	Dry mass [g m^{-2}]
Nordic & Barents Seas						
Fugløya-Bjørnøya Islands (FB) transect	Padmini Dalpadado	1995-2014	WP 2 net, 0,25m^2	180 µm	0-59...480	Dry mass [g m^{-2}]
Baltic Sea						
Bornholm Basin	Lutz Postel	1979 - 2012	WP 2 net, 0,25m^2	100 µm	0-85	Carbon mass, calculated by factors
Bornholm Basin	Piotr Margonski, Alina Krajewska, Anna Grzyb	2008 - 2013	WP 2 net, 0,25m^2	100 µm	0-85	Wet mass, calculated by HELCOM factors
Gdansk Basin		1986 - 2010	WP 2 net, 0,25m^2	100 µm	0-102	
Eastern Gotland Basin	Gunta Rubene (BIOR)	1960 - 2011	Juday net, 0,11m^2	160 µm	Mostly 0-100	Wet mass, calculated by factors
North Sea & English Channel						
Stonehaven	Kathryn Cook	2007 - 2008	Bongo net, 0,1256m^2	200 µm	0-45m	Dy mass [mg m^{-3}]
Arendal Station 2	Tone Falkenhaug	1994 - 2010	WP 2 net, 0,25m^2	180 µm	0-50m	
Plymouth L4	Elaine Fileman, Angus Atkinson	1993-1998	WP 2 net, 0,25m^2	200 µm	0-50m	Dy mass [mg m^{-3}]
Bay of Biscay & western Iberian Shelf						
Bilbao Estuary 35	Fernando Villate	1997	Rig net, 0,25m^2	200 µm	5-20	Dry mass [mg m^{-3}]
Urdaibai Estuary 35					6-11	Dry mass [mg m^{-3}]
RADIALES Vigo St. 3	Ana Miranda	2010 - 2013	Bongo net, 0,50m^2	200 µm	0-58±8	Dry mass [mg m^{-3}]
Guadiana Lower Estuary	Maria Alexandra Teodósio	2009 - 2012	WP 2 net, 0,25m^2	200 µm	0.5-1	Displacement volume [ml m^{-3}]
Mediterranean Sea						
Gulf of Naples LTER-MC	Maria Grazia Mazzocchi	1984-90 1995-2014	Nansen net	200 µm	0-50	Dry mass [mg m^{-3}]

• Comparable seasonal conditions of metabolism (O:N ratio)→"Quality criteria"

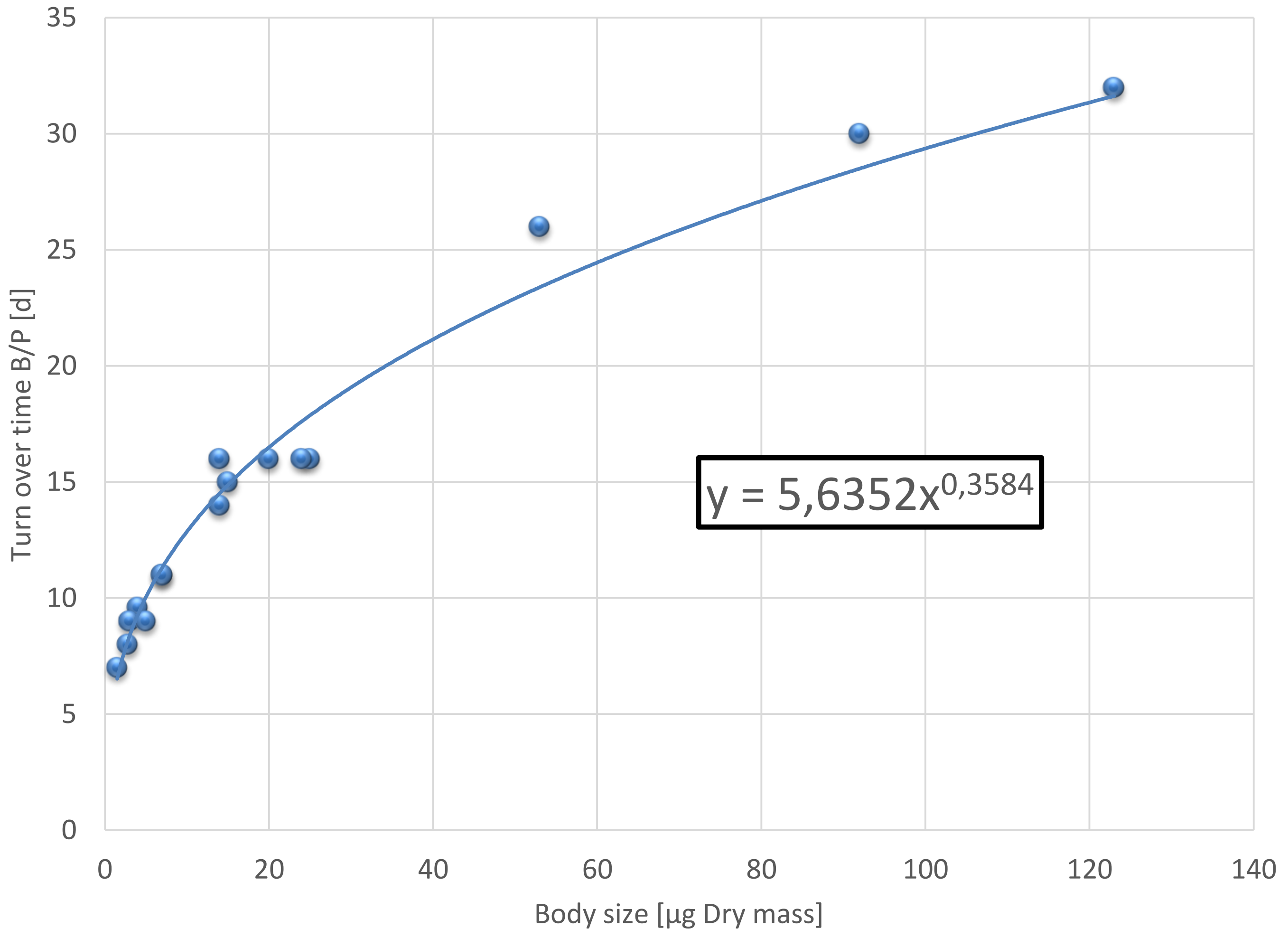
The atomic ratio of respiratory oxygen consumption rate to ammonia–nitrogen excretion rate (O:N ratio) is 7 **when only protein is metabolized,**
and is calculated, respectively, as 21 or 13 when protein-and-lipid or protein-and-carbohydrate
are catabolized in equal quantities simultaneously
(Table 10.3 in Ikeda et al. 2000).

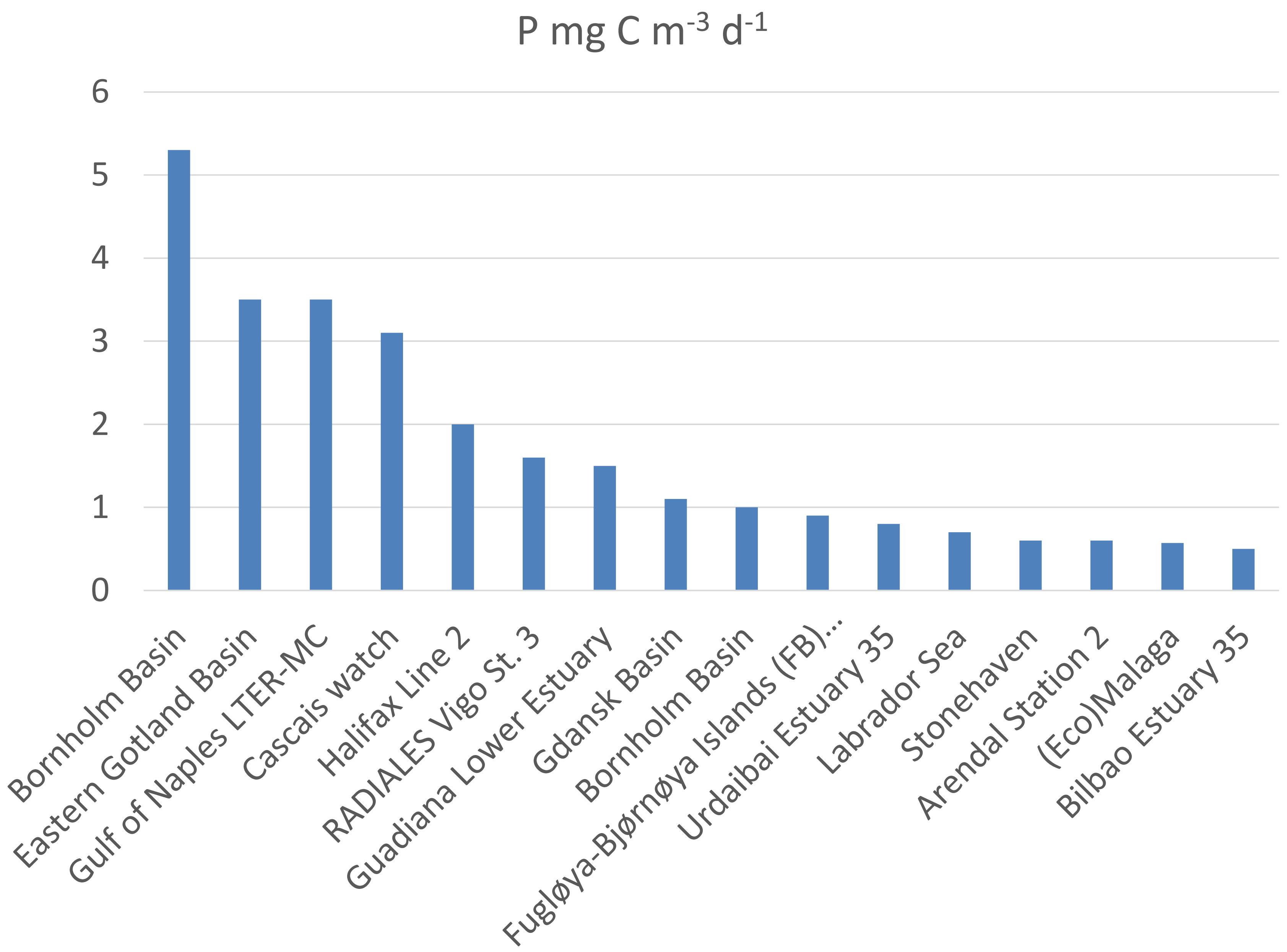
Ikeda, T. (2014) Respiration and ammonia excretion by marine metazooplankton taxa: synthesis toward a global-bathymetric model. Mar. Biol. 161:2753–2766

	Ind. spec. Dry mass [µg]	Turn over time B/P (d)	P mg C m^{-3} d^{-1}	O/N
Halifax Line 2	123	32	2	8,12
Labrador Sea	92	30	0,7	8,07
Fugløya-Bjørnøya Islands (FB) transect	53	26	0,9	7,96
Icelandic waters	43	22	1,4	7,86
(Eco)Malaga	30	20	0,6	7,64
Urdaibai Estuary 35	25	16	0,8	7,37
RADIALES Vigo St. 3	24	16	1,6	7,52
Guadiana Lower Estuary	20	16	1,5	7,51
Stonehaven	15	15	0,6	7,61
Arendal Station 2	14	14	0,6	7,57
Cascais watch	14	16	3,1	7,77
Plymouth L4	7	11	0,4	7,41
Gulf of Naples LTER-MC	7	11	0,3	7,33
Bilbao Estuary 35	5	9	0,5	7,2
Bornholm Basin	4	9,6	5,3	7,25
Eastern Gotland Basin	3	9	3,5	7,3
Bornholm Basin	2,8	8	1	7,45
Gdansk Basin	1,5	7	1,1	7,32

(O:N ratio) is 7 when only protein is metabolized

North Atlantic specific equations





P mg C m-3 d-1
6
5
4
3
2
1
0
Bornholm Basin
Eastern Gotland Basin
Gulf of Naples LTER-MC
Cascais watch
Halifax Line 2
RADIALES Vigo St. 3
Guadiana Lower Estuary
Gdansk Basin
Bornholm Basin
Fugløya-Bjørnøya Islands (FB)...
Urdaibai Estuary 35
Labrador Sea
Stonehaven
Arendal Station 2
(Eco)Malaga
Bilbao Estuary 35

Comparison with other Growth equations or models respectively

Garijo and Hernándes-León (2015) used

Two predictive equations considering
body mass, temperature and chl a
to determine the growth of the community through a single equation

- The purely empirical estimates by Hirst and Bunker (2003)

$$log_{10}\, g = 0{,}0186[T] + (-0.288)[log_{10}\, BM] + 0.417[log10C_a] + (-1.209)$$

g Growth rate [d^{-1}]
T Temperature [°C]
C_a Chlorophyll conc. [mg C m^{-3}]
BM Body mass [**µg** C ind^{-1}]

- The combined theoretical–empirical estimates by Zhou et al. (2010)

$$g(w, T, C_a) = 0.033\left(\frac{C_a}{C_a + 205e^{-0.125T}}\right)e^{0.09T}w^{-0.06}$$

Food dependence term considering Michaelis-Menten kinetics
(Half food saturation concentration)

g Growth rate [d^{-1}]
T Temperature [°C]
C_a Chlorophyll conc. [mg C m^{-3}]
w Body mass [**mg** C ind^{-1}]

We tested further:

Hirst et al. 2003 (COPEPODS)
Spindler and Gaedke (2000) (Fresh water ZOOPLANKTON)
Huntley and Lopez (1992) (ZOOPLANKTON)

The use of chlorophyll requires further conversion factors:

We used C:Chl =50 according to Garijo and Hernándes-León (2015).

However:

Pacific Science (1976), Vol. 30, No. 4, p. 317–327
Printed in Great Britain

Particulate Organic Carbon, Nitrogen, and Chlorophyll as Measures of Phytoplankton and Detritus Standing Crops in Kaneohe Bay, Oahu, Hawaiian Islands[1]

JOHN CAPERON,[2] WAYNE A. HARVEY,[3] AND FRANCES A. STEINHILPER[4]

STEADY STATE CONTINUOUS CULTURE CARBON TO CHLOROPHYLL-*a* AND NITROGEN TO CHLOROPHYLL-*a* RATIOS FOR *Thalassiosira pseudonana* (FORMERLY *Cyclotella nana*) AND VARIOUS GROWTH RATES UNDER NITRATE-LIMITING CONDITIONS

GROWTH RATE (hr^{-1})	CARBON: CHLOROPHYLL $\mu g:\mu g$	NITROGEN: CHLOROPHYLL $\mu g:\mu g$
0.0087	500	29.2
0.0176	333	31.1
0.0363	260	24.7
0.0402	138	17.8
0.0445	113	14.3
0.0478	68	11.2
0.0632	71	9.9
0.0708	55	10.2
0.0768	76	11.6

NOTE: See Caperon and Meyer (1972) for a full description of experiment.

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Intercomparison of zooplankton (net) sampling systems: Results from the ICES/GLOBEC sea-going workshop

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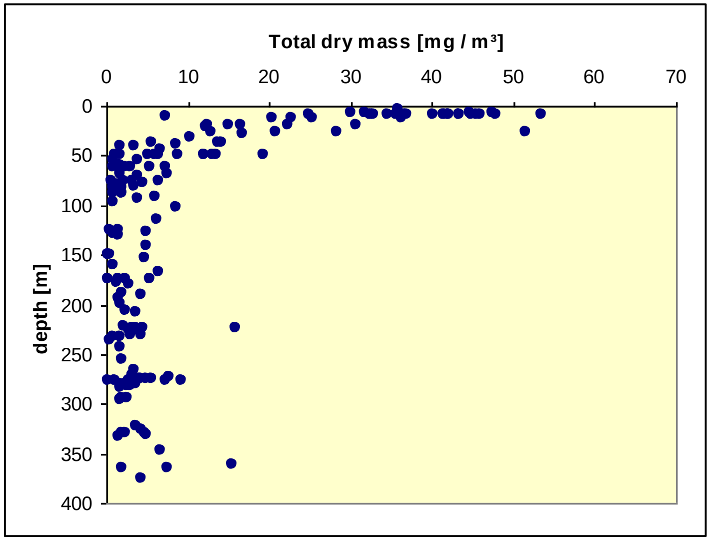
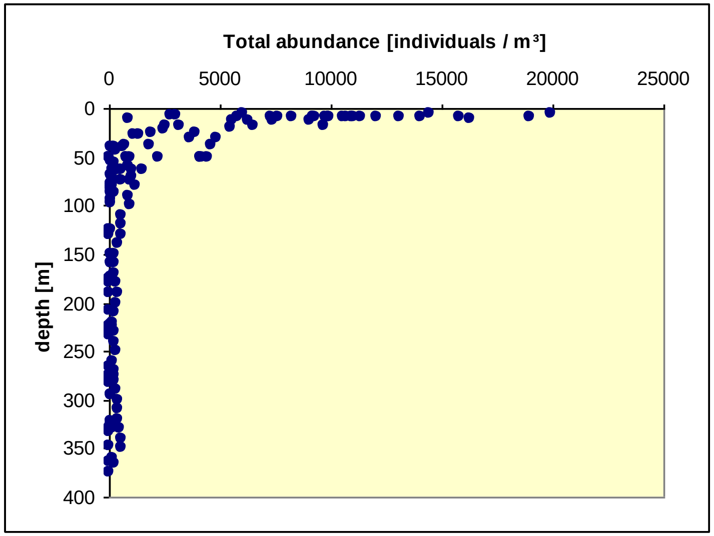
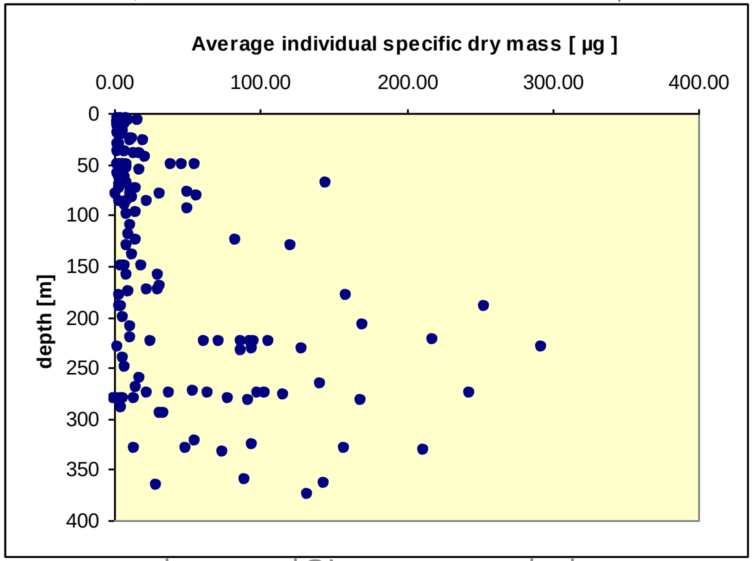
[b] Woods Hole Oceanographic Institution, Woods Hole, MA, USA
[c] Leibniz Institute for Baltic Sea Research, Warnemünde, Germany
[d] Department of Biology, University of Oslo, PO Box 1066 Blindern, 0316 Oslo, Norway
[e] Bedford Institute of Oceanography, Bedford, Nova Scotia, Canada

Storefjord June 1993





Skjoldal et al., 2013



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H.R. Skjoldal et al./Progress in Oceanography 108 (2013) 1–42

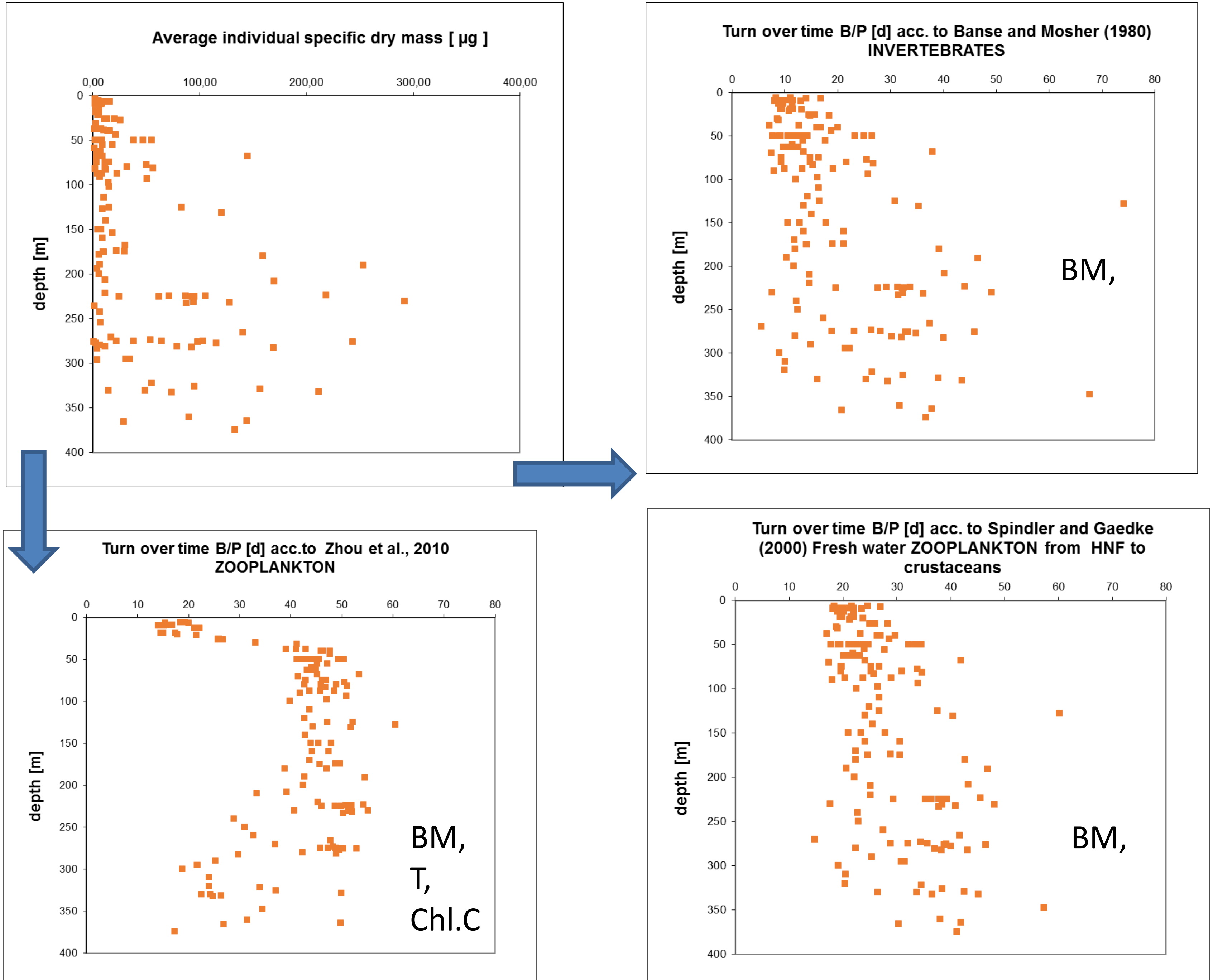
Fig. 3. Illustrations of the zooplankton samplers that were included in the sampling gear intercomparisons.

Mesh size [µm]	
Min	55
Max	400
AVG	**225**
STD	64
N	164

Body mass [µg C]	
Min	0,3
Max	356,2
AVG	**18,1**
STD	40,2
N	164

(Banse&Mosher, 1980)

Turnover rate P/B [d^{-1}]	
Min	0,013
Max	0,180
AVG	**0,071**
STD	0,033
N	164



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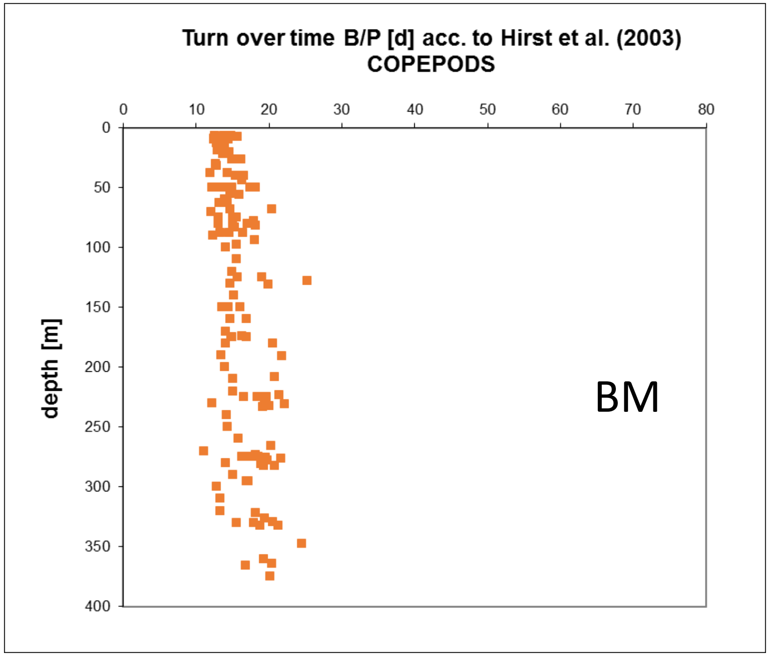
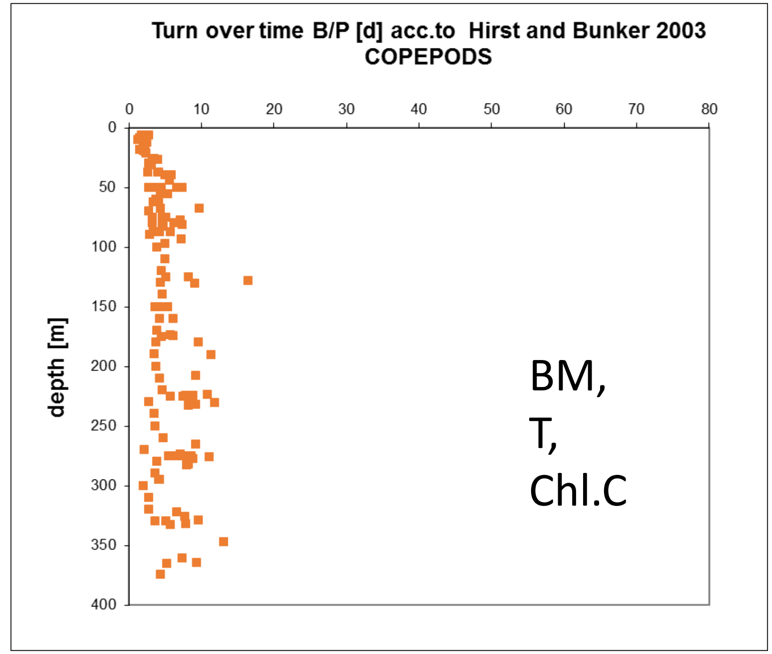
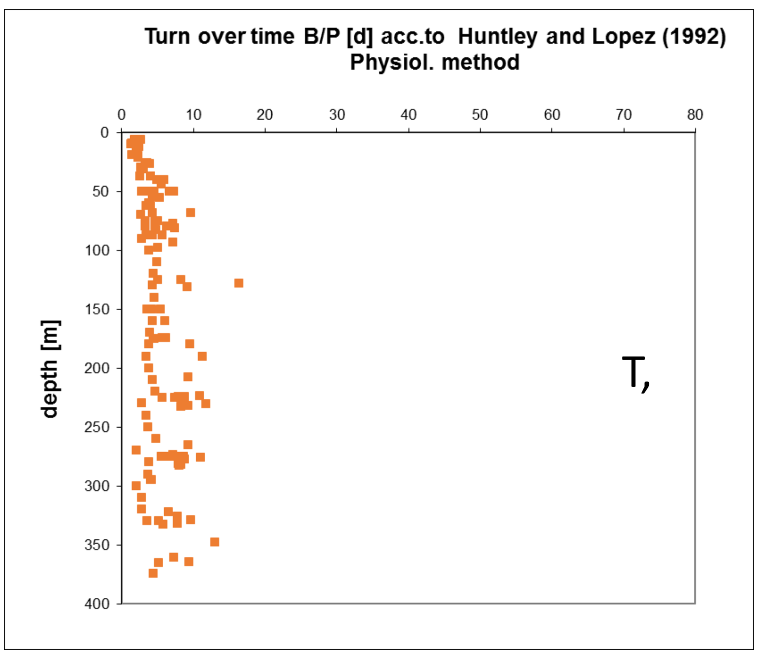
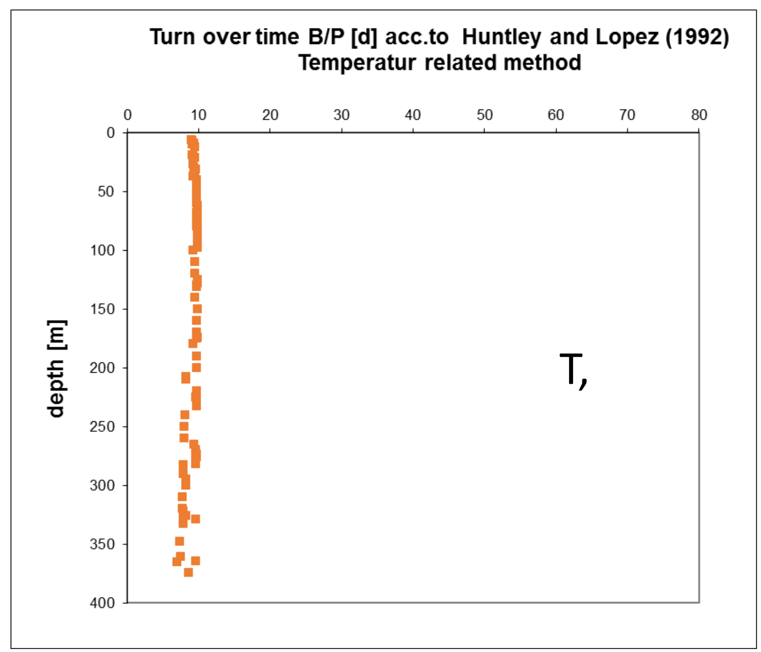

Turn over time B/P [d] acc. to Hirst et al. (2003)
COPEPODS
0 10 20 30 40 50 60 70 80
0 50 100 150 200 250 300 350 400
depth [m]
BM


Turn over time B/P [d] acc.to Hirst and Bunker 2003
COPEPODS
0 10 20 30 40 50 60 70 80
0 50 100 150 200 250 300 350 400
depth [m]
BM,
T,
Chl.C


Turn over time B/P [d] acc.to Huntley and Lopez (1992)
Physiol. method
0 10 20 30 40 50 60 70 80
0 50 100 150 200 250 300 350 400
depth [m]
T,


Turn over time B/P [d] acc.to Huntley and Lopez (1992)
Temperatur related method
0 10 20 30 40 50 60 70 80
0 50 100 150 200 250 300 350 400
depth [m]
T,

ICES Gear Intercomparison Storefjord JUNE 1993 (c.f. Skjoldal et al., 2013)

Turnover rate [d^{-1}]

	P/B [d-1] acc. to Zhou et al., 2010 ZOOPLANKTON	P/B [d-1] acc. to Spindler and Gaedke (2000) ZOOPLANKTON	P/B [d-1] acc. To Huntley and Lopez Physiol. method: $g=0.0222e^{0.094T}$ [d^{-1}]	P/B [d-1] acc. to Hirst et al. 2003 COPEPODS	P/B [d-1] acc. to Banse and Mosher, 1980 INVERTEBRATES	P/B [d-1] acc. To Huntley and Lopez T dep. method: $g=0.0452e^{0.110T}$ [d^{-1}]	P/B [d-1] acc. to Hirst and Bunker 2003 COPEPODS
Min	*0,017*	*0,017*	*0,044*	*0,040*	0,013	*0,101*	*0,061*
Max	*0,068*	*0,067*	*0,060*	*0,091*	0,180	*0,143*	*0,671*
AVG	***0,032***	***0,040***	***0,046***	***0,066***	***0,071***	***0,107***	***0,283***
STD	*0,016*	*0,011*	*0,003*	*0,011*	0,033	*0,008*	*0,163*
N	164	164	164	164	164	164	164

Developmental time [d]

Max	61	60	23	25	74	10	16
Min	15	15	17	11	6	7	1
AVG	***31***	***25***	***22***	***15***	***14***	***9***	***4***

	Average sampling depth [m]	Mesh size [µm]	Total numbers per m^3	Total biomass per m3 (mg DM m^{-3})	Total biomass per m3 (units are mg carbon m^{-3})	Body mass [µg C]	Body mass [µg Dry mass]	Average temperature (°C) of sample layer	Chla-C [mg m-3]
Min	6,25	55	0,9	0,2	0,1	0,3	0,8	*7,325*	*26,20*
Max	374,5	400	19957	53,4	21,3	356,2	890,5	*10,492*	*178,71*
AVG	***130,4***	***226***	***2406***	***11,3***	***4,5***	***18,1***	***45,3***	***7,809***	***49,42***
STD	111,6	65	4188	14,1	5,7	40,2	100,4	*0,642*	*40,59*
N	164	164	164	164	164	164	164	164	164,00

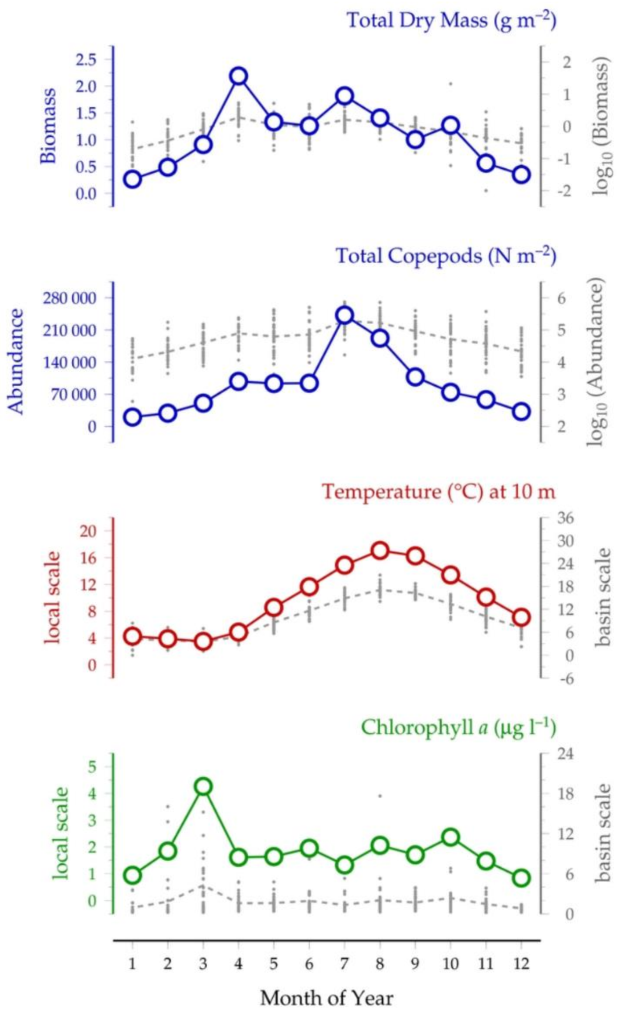
Planned deliverables ToRJ (WGZE)

2016:

- Submission of the manuscript

2017:

- Contribution to the next Zooplankton Status Report
- Implementation in the ZSR



Arendal Station 2

Latitude: 58.3830 ***Longitude:*** 8.8170

Associated Investigators:

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Lena Omli (Technician) [*lena.omli@imr.no*]

Associated Web Sites:

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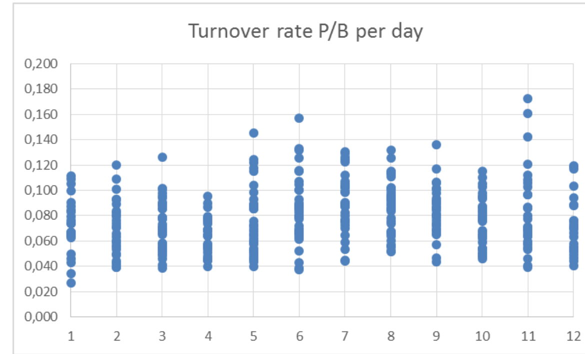

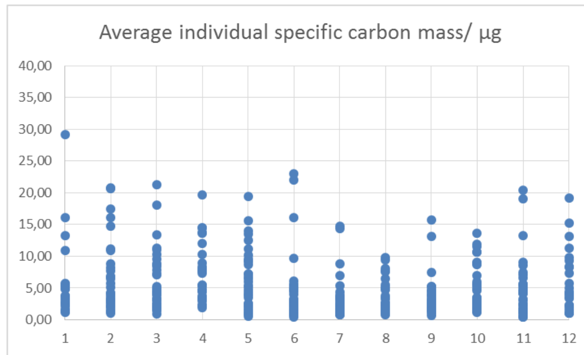

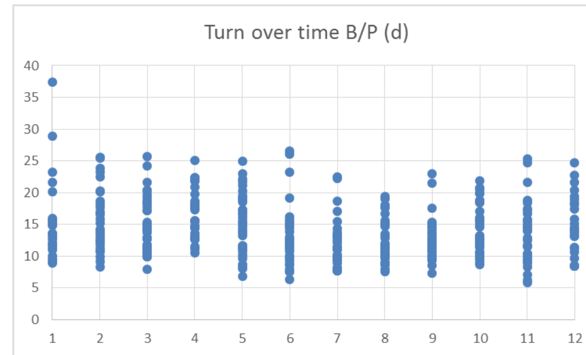

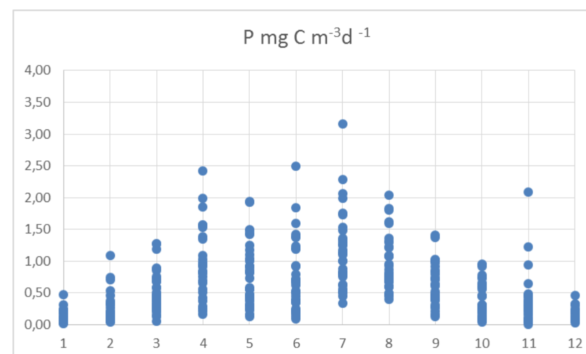

Seasonality

Halifax Line 2

Latitude: 44.2670 ***Longitude:*** -64.3170

Associated Investigators:

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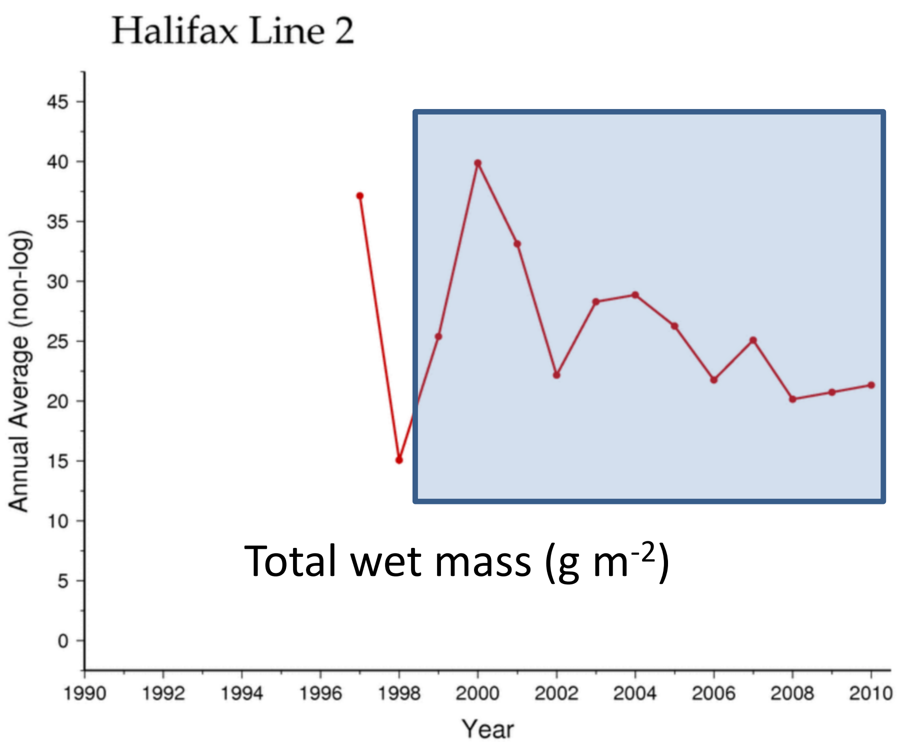
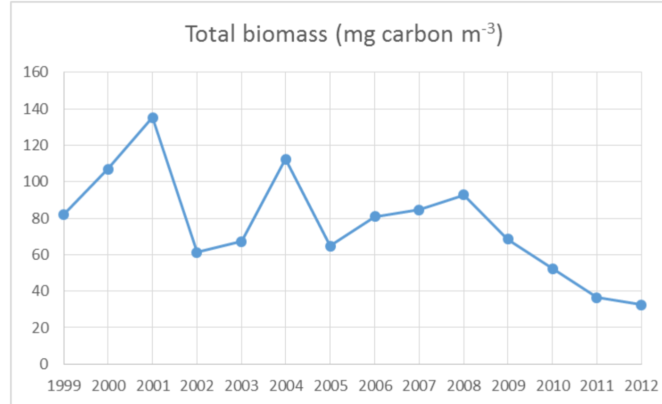
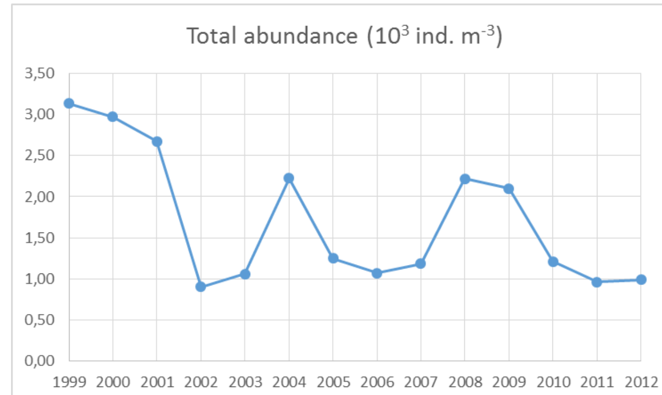
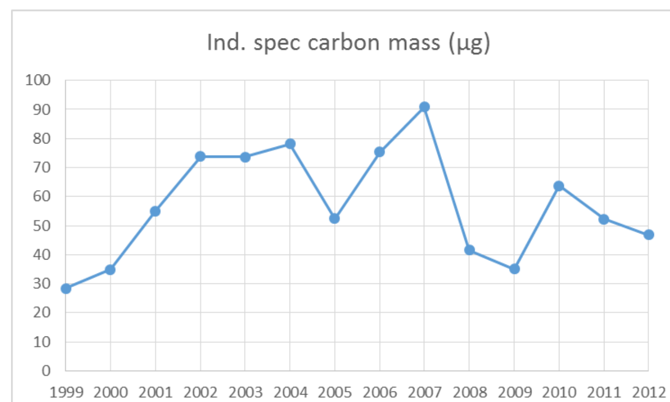
[www.dfo-mpo.gc.ca]







July-August



Interannual variability

Halifax Line 2

Latitude: 44.2670 ***Longitude:*** -64.3170

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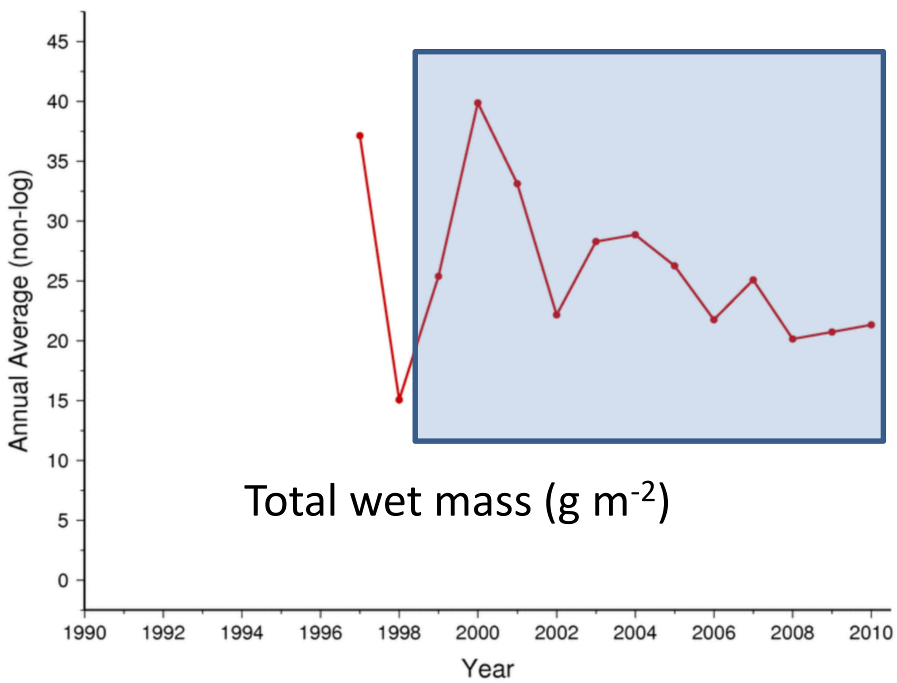
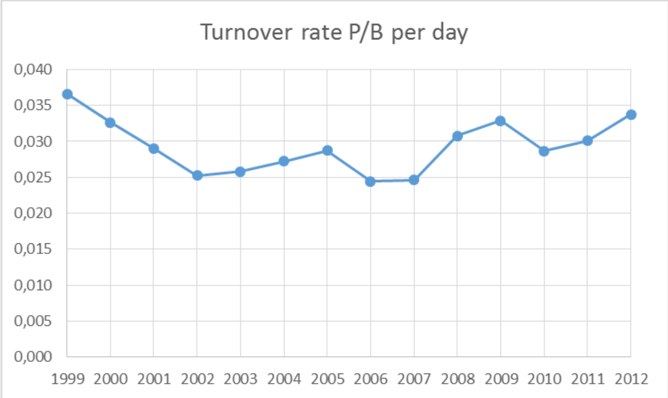
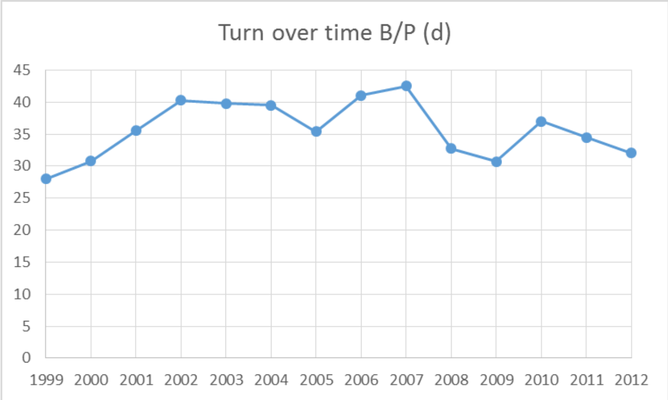
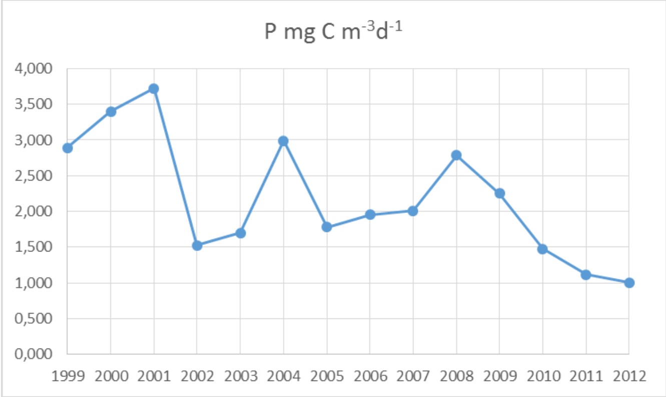
Halifax Line 2









July-August

Cont.

Halifax Line 2

Latitude: 44.2670 ***Longitude:*** -64.3170

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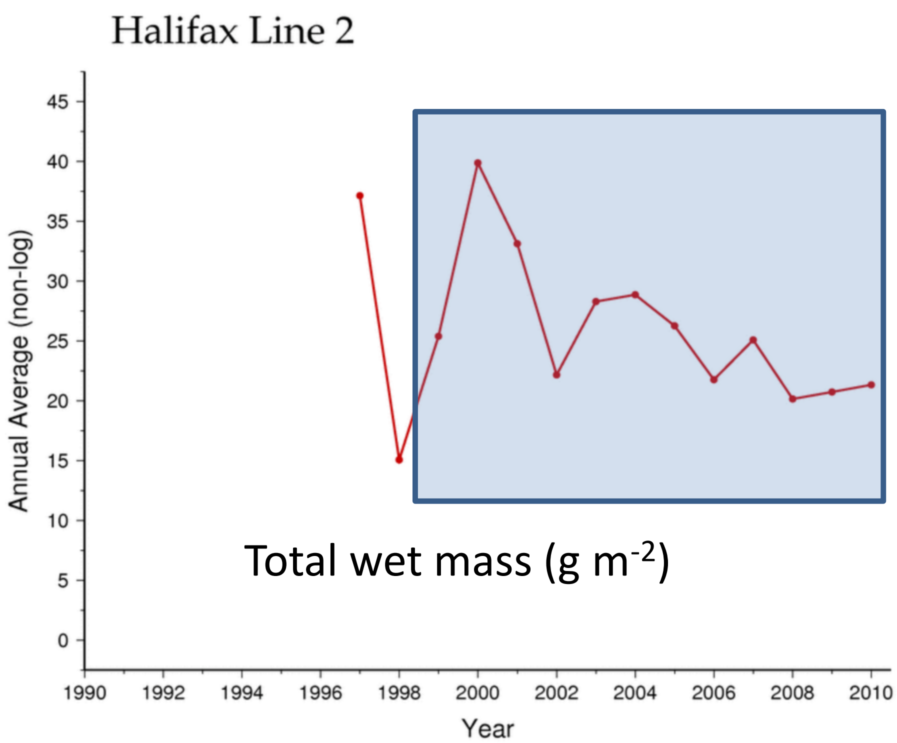
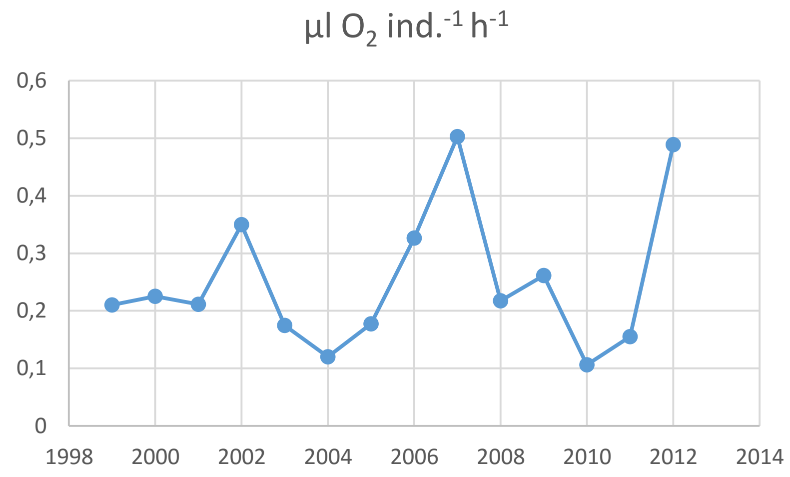
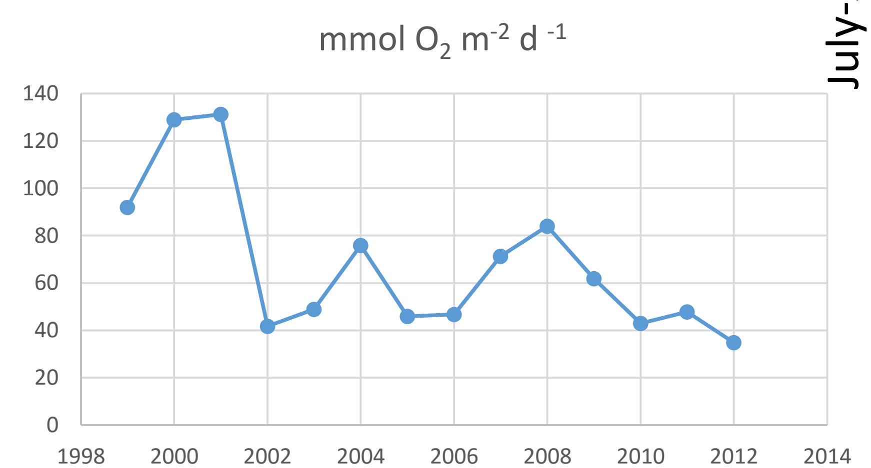




July-August



Cont.

Next steps:

- Include one or two data sets more
- Further tests of different calculation modes (e.g. Gillooly, 2000) including application of P formulas for single species in combination with application of sum formulas
- Regional studies in frontal zones
    - Island, Barent Sea,
- Comparison with measurements (e.g. Storefjord vertical ETS (respiration R) profile, converting R to P.
- Careful evaluating the literature for discussion
- Final recommendations

Comments?

Regional coverage

<u>ICES WGZE REPORT 2013</u>:

This ToR will continue next year to estimate zooplankton productivity and metabolic rates within the whole ICES area based on allometric approach and data collected in the ZSR." "… the Zooplankton Status Report (ZSR)… is covering 62 time series and 40 Continuous Plankton Recorder standard areas at the moment" (ICES WGZE Report 2013 / Executive Summary).

→ 25% achieved

Level of investigation	Method	Aim / result	Advantage	Disadvantage
Organisms, (ecosystem, compartments, population, size classes)	In vivo -Balance measurements -Isotopic techniques - Stress impact	-Metabolic balance estimation -Metabolism functioning -Ecological tolerance	**-Living organism (Regulation, etc.)**	-Mostly time consuming -Complexity of causes - black box - artifacts
Sub-cell structures (homogenates)	In vitro (Cell disintegration)	Enzyme / Co-enzyme reaction; Effect of substrates	**Allows data set of high frequency (ocean mapping)**	-Artificial system (substrate saturation) -Contact of various substances -loss of cell regulation
Molecular level	DNA /RNA ratio..	Growth		

Modified after Wieser “Bioenergetik” 1986

Calculations combine both advantages: characteristics of living organisms and “ocean mapping”. Required average body mass – easy to obtain.

Relative Importance of Somatic growth plus reproduction and Metabolism

Example:

Summary of a **363 day carbon budget of the *Themisto japonica*** (Crustacea: **Hyperiid Amphipod**) population, February 1990 to end of January 1991 in Toyanna Bay (Southern Japan Sea)

By: Tsutomu Ikeda and Naonobu Shiga, JPR 21(2) 1999:299-308

¼ of assimilated energy → Production, mainly P_g

	Percentage of Assimilation
Production P	**26.4**
Somatic P_g	**24.2**
Molt P_e	**2.2**
Metabolism M	**73.6**
$M_{routine}$	51.3
$M_{daily\ vertical\ migration\ (DVM)}$	22.3

Ikeda and Shiga (1999)

Median/Quart./Range.

This box plot describes the central tendency of the variable in terms of the median of the values (represented by the smallest box in the plot).

The spread (variability) in the variable values is represented in this plot by the quartiles (the 25th and 75th percentiles, larger box in the plot) and

the minimum and maximum values of the variable (the "whiskers" in the plot).

K. Y. Lin et al.: Copepod community growth rates: a test of metabolic theory of ecology

Biogeosciences, 10, 1877–1892, 2013

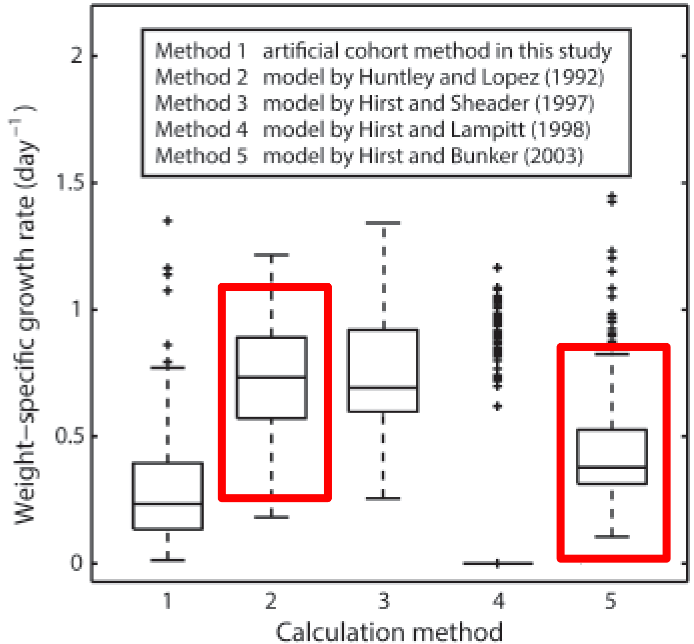


Fig. 8. Measured weight-specific growth rates compared to model-derived growth rates. The boxplots for each taxon indicate the values of medians, 25th and 75th percentiles, 95 % confidence intervals (whiskers), and outliers (crosses). The confidence interval for method 4 was narrow and most of the calculated values were close to zero.