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Review

Evaluation of trade-offs in traditional methodologies for measuring metazooplankton growth rates: Assumptions, advantages and disadvantages for field applications

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ABSTRACT

Zooplankton growth rates ultimately shape the functional response of marine ecosystems to regional and global climate changes, because they determine the quantity and distribution of matter and energy within the zooplankton community available to higher trophic levels. Despite the variety of techniques available for measuring zooplankton growth, no or few approaches have been universally applied to the natural zooplankton populations or community and there are only a limited number of comparisons among the methods. Here we review and compile data for the traditional methods for estimating metazooplankton weight-specific growth rates, describe the principles and underlying assumptions of each method, and finally their advantages and disadvantages. This review encompasses the analysis of time-series (i.e., Natural Cohort method), three experimental approaches (i.e., Artificial Cohort, Molting Rate and Egg Production) and several empirical models that have been applied to specific stages, populations or community guilds of metazooplankton in the field. Whereas, some methodological problems and their resolution have been proposed in the past, no single method adequately addresses the high biodiversity of metazooplankton communities and resolves our limited capacity determining rates. We recommend a more formal comparison of methodologies be undertaken that would allow for their direct cross-calibration to facilitate future cross-site synthesis.

1. Introduction

The impacts of anthropogenic activities on earth systems have been clearly articulated by the '5th Assessment Report of the Intergovernmental Panels on Climate Change' (AR5: IPCC, 2014). Zooplankton are important for understanding how marine ecosystems respond to natural and anthropogenic perturbations due to their fundamental role in ecosystem function (e.g., Walther et al., 2002; Edwards and Richardson, 2004; Boyce et al., 2010). In recent years, the development of a variety of ecosystem models (e.g., Kishi et al., 2007; Cornick et al., 2006; Link et al., 2010; Christensen and Walters, 2004) has contributed to an improved understanding of the complex responses of marine ecosystems (e.g., McKinnell and Dagg, 2010) to climate changes and anthropogenic perturbations. The accuracy and precision of these ecological models have been validated with comparisons against observed biomass measurements (e.g., Coyle et al., 2013; Coyle et al., 2019). However, relevant information on the trophodynamics (i.e., rates) of all lower trophic levels, but especially metazooplankton, used in models remains quite limited.

Metazooplankton communities are characterized by high taxonomic diversity with corresponding richness of behavioral, life-history and functional traits. Across biomes, this encompasses animals with generation times from days to years. Most of these organisms are the essential conduits of materials and energy through lower to higher trophic levels (Lalli and Parsons, 1993). Quantitative determination of their rate processes, particularly growth, are necessary for measuring "production", a proxy for the integrated output of the trophodynamics of lower food webs.

Metazooplankton production (*ZP*) represents the materials produced (through somatic and reproductive growth) by target individuals,

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Table 1
Application of Natural Cohort and modified Natural Cohort methods for estimating growth rate (g_{NC}) of zooplankton population and community. This table is modified from Huntley and Lopez (1992) and Kobari (2010). Equations to measure growth rate are indicated in text. Asterisks indicatethat growth rates are not available but production rates were estimated with the modified Natural Cohort method. C: copepodite stage. N: naupliar stage.

Taxon	Target groups	Location	g_{NC} (day^{-1})	Source
Copepods				
	Acartia clausi	Loch Striven, Scotland	0.15–0.19	McLaren (1978)
		Texel, the Netherlands	0.19–0.26	Klein-Breteler et al. (1982)
		Onagawa Bay	*	Uye (1982)
	Acartia omori	Fukuyama Bay, Japan	N: 0.11–0.38 C: 0.11–0.39	Liang and Uye (1996a)
	Acartia tonsa	Chesapeake Bay, USA	0.34–0.58	Heinle (1966)
	Calanus finmarchicus	Loch Striven, Scotland	0.21	McLaren (1978)
		Clyde Sea, Scotland	0.06–0.23	Nicholls (1933)
		Balsfjorden, Norway	0.05	Tande (1982)
		North Atlantic	0.05–0.06	Hirche et al. (2001)
	Calanus glacilis	Fram Strait	0.03	Hirche and Bohrer (1987)
		Barents Sea	0.03	Slagstad and Tade (1990)
	Calanus marshallae	Bering Sea	0.10	Vidal and Smith (1986)
	Calanus sinicus	Inland Sea, Japan	*	Huang et al. (1993)
	Centropages abdominalis	Fukuyama Bay, Japan	N: 0.12–0.30 C: 0.16–0.41	Liang et al. (1996)
	Centropages hamatus	Texel, the Netherlands	0.25–0.29	Klein-Breteler et al. (1982)
	Centropages velificatus	off Kingston, Jamaica	0.49–0.95	Chisholm and Roff (1990)
	Eucalanus bungii	Bering Sea	0.10	Vidal and Smith (1986)
	Eurytemora herdmanni	Texel, the Netherlands	0.15–0.29	Klein-Breteler et al. (1982)
	Metridia pacifica	Toyama Bay, Japan	*	Ikeda et al. (2002)
	Microsettela norvegica	Fukuyama Bay, Japan	N: 0.00–0.39 C: 0.02–0.18	Uye et al. (2002)
	Neocalanus cristatus	Bering Sea	0.05–0.06	Vidal and Smith (1986)
		Oyashio, Western North Pacific	0.06–0.09	Kobari et al. (2003)
	Neocalanus plumchrus	Bering Sea	0.09	Vidal and Smith (1986)
		Strait of Georgia, Canada	0.08–0.09	Fulton (1973)
	Oithona davisae	Fukuyama Bay, Japan	N: 0.08–0.35 C: 0.06–0.45	Uye and Sano (1998)
	Oithona nana	Kaneohe Bay, USA	0.22	Newbury and Bartholomew (1976)
		Bering Sea	0.09–0.22	Vidal and Smith (1986)
	Paracalanus aculeatus	off Kingston, Jamaica	0.30–1.39	Chisholm and Roff (1990)
	Paracalanus sp.	Kaneohe Bay, USA	0.92	Newbury and Bartholomew (1976)
		Fukuyama Bay, Japan	N: 0.06–0.19 C: 0.10–0.36	Liang and Uye (1996b)
	Pseudocalanus minutus	Loch Striven, Scotland	0.11	Marshall (1949)
	Pseudocalanus sp.	Texel, the Netherlands	0.22–0.23	Klein-Breteler et al. (1982)
	Pseudodiaptomus marinus	Inland Sea, Japan	0.24	Uye et al. (1983)
		Fukuyama Bay, Japan	N: 0.05–0.50 C: 0.02–0.41	Liang and Uye (1996c)
	Sinocalanus tenellus	Fukuyama Bay, Japan	0.06–0.61	Kimoto et al. (1986)
	Temora turbinata	off Kingston, Jamaica	0.28–0.65	Chisholm and Roff (1990)
Mixed copepods guild				
		Sagami Bay, Japan	*	Ara and Hiromi (2009)
		Sagami Bay, Japan	*	Ara and Hiromi (2006)
Appendicularians				
	Oikopleura dioica	Inland Sea, Japan	0.26–3.00	Uye and Ichino (1995)
	Oikopleura longicauda	Toyama Bay, Japan	*	Tomita et al. (1999)
Euphausiids				
	Euphausia pacifica	Toyama Bay, Japan	*	Iguchi and Ikeda (1999)
Amphipods				
	Temisto japonica	Toyama Bay, Japan	*	Ikeda and Shiga (1999)
	Temisto pacifica	Oyashio	*	Yamada and Ikeda (2006)
	Temisto japonica		*	
	Primno abyssalis		*	
	Cyphocaris challengeri		*	
Mixed zooplankton guild				
		Coral reef, Japan	*	Nakajima et al. (2017)

populations or communities over a defined period of time as follows (Clarke, 1946; Mullin, 1969; Edmondson and Winberg, 1971; Downing and Rigler, 1984; Kimmerer, 1987; Hirst and McKinnon, 2001):

$$ZP = SP + EP + EX \quad (1)$$

where *SP* is somatic production represented by incremental change in body mass, *EP* represents biomass (eggs or spermatophores) produced by adults (see Egg Production Method), and *EX* indicates the mass of molted exoskeletons (exuviae) by crustaceans or the mass of mucus houses produced by appendicularians. The *EX* term has been largely ignored because it is either assumed to be negligible, goes unidentified, or is indistinguishable from other detrital materials in the water column. Note, however, that *EX* is not negligible for some taxonomic groups. For instance, appendicularian house production can be of a similar magnitude if not higher than somatic production (see Hopcroft and Roff, 1998a; Tomita et al., 1999; Sato et al., 2008).

Somatic production can be calculated from the product of meta-zooplankton biomass (*ZB*) and weight-specific instantaneous growth rate (*g*). The value of *g* is calculated as the increase of body mass of a target individual, population or community over a defined period.

According to Omori and Ikeda (1984):

$$g = [\ln(W_t) - \ln(W_o)]/t \quad (2)$$

where W_o and W_t represent body mass at the beginning and end of a defined period, respectively. The duration of that period is defined by t (days).

A variety of techniques for measuring zooplankton growth rates have been proposed and applied to metazooplankton populations and communities over the course of the last half century (Omori and Ikeda, 1984; Runge and Roff, 2000; Yebra et al., 2017). Relative to methodologies for measuring phytoplankton growth rates (i.e. isotopically-labeled carbon uptake; Steemann Nielsen, 1952; Hama et al., 1983), we have no routine and globally applicable method for measuring metazooplankton growth rates, due to: 1) the wide range of metazooplankton taxonomic groups; and 2) the lack of knowledge of methodological intercalibration. Metazooplankton production rates have been measured using traditional approaches such as the Natural Cohort Method (e.g., Heinle, 1966), Artificial Cohort Method (Kimmerer and McKinnon, 1987), Molting Rate Method (Burkill and Kendall, 1982) and Egg Production Method (McLaren and Corkett, 1981; Berggreen et al., 1988). Empirical models (e.g., Ikeda and Motoda, 1978; Huntley and Lopez, 1992; Hirst and Sheader, 1997; Hirst and Bunker, 2003) have also been applied for research on regional to global comparisons of metazooplankton growth and the potentially regulatory role of environmental variables. Over the past two decades, indices of metazooplankton growth have been developed using biochemical approaches, such as those using nucleic acids (e.g., Dagg and Littlepage, 1972; Ota and Landry, 1984; Wagner et al., 2001) and enzyme activities (e.g., Sastri and Roff, 2000; Oosterhuis et al., 2000; Yebra and Hernández-Léon, 2004). The biochemical approaches have been reviewed recently (Yebra et al., 2017), however, a comparable review of traditional approaches given the most recent advances, published after the ICES Zooplankton Methodology Manual (Harris et al., 2000), are scattered in the literature.

Here, we review the traditional methods of measuring metazooplankton growth rates that includes information arising from the last two decades of research, and compiles growth rate estimates by application of method type. Our goal is to provide a practical description of each method, in terms of principles, procedures, advantages, and disadvantages, and then recommendations for identifying the most suitable methods for particular metazooplankton populations and communities in field studies.

2. Natural Cohort method

2.1. Principle

The basic approach for estimating weight-specific growth rate is to identify a population clearly defined by one or more developmental stages (i.e., natural cohorts) and to estimate the stage-specific mass increment and stage duration. The Natural Cohort method (hereafter NC method) for metatzooplankton was first employed on copepods (Heinle, 1966). It relies on three major assumptions, 1) intermittent recruitment of traceable cohorts, 2) tracking of the same assemblage (i.e. no immigration or emigration), 3) mortality (or vulnerability to capture) is not size-dependent, and 4) sampling at intervals relatively short compared to generation times. Cohorts can be identified by temporal changes in developmental stage composition and/or of size distributions of body length and mass in time-series samples (see 2.3.2. Identification of cohorts). Growth rates are represented by change in per capita biomass for the subject cohort between sampling intervals. Growth measurements by the NC method are the most common among the traditional methodologies, and they have been applied to many taxonomic groups throughout the world oceans (Table 1).

2.2. Advantages and disadvantages

The NC method may have the simplest principles and procedures among the traditional methods. It requires no manipulation or incubation of animals. Materials required are common and inexpensive. It's most obvious advantage, at least theoretically, is a wide applicability to any group or population. Disadvantages are that identification of cohort developmental progress can be laborious and problematic, if not impossible, for those taxonomic groups with continuous recruitment and short generation times, such as small coastal or subtropical to tropical species. For small species, microscopic identification is time-consuming. Even for populations with a clearly identifiable cohort structure, it can be difficult to follow their growth progress at sites affected by extensive mixing of different water masses and/or by strong advection. At remote oceanic sites, it is generally difficult to secure sufficient ship time for suitable sampling intervals. Another disadvantage is that somatic growth and size-selective mortality are confounded.

2.3. Procedures

2.3.1. Field collection of target species

Sampling should be frequent enough to census the target group multiple times over the generation time but long enough between samples to have a detectable change in size (and developmental stage). Target species should be sampled by net tows through the vertical ranges of their diel and seasonal migrations. To minimize both net avoidance and extrusion, towing speeds and mesh sizes need to be selected to capture and retain the target body sizes. Once collected, zooplankton are gently transferred into plastic bottles and preserved with a fixative (e.g., buffered formalin, ethanol).

2.3.2. Identification of cohort

The abundance of each development stage is counted (usually with stereomicroscope magnification) and/or size distributions (in terms of body length or mass) are determined for the target group within time-series of zooplankton samples. Cohorts can be identified with the Steepest Increase Method, which finds the time of the peaks in abundance of each developmental stage, of body length or of mass measures (see Omori and Ikeda, 1984). Note that peaks for target groups can be influenced by any factor that creates synchrony in molting cycles and are also affected by within-stage mortality. Cohorts can be also distinguished by the Median Development Time Method, which estimates the times required for half the population to advance from one stage to the next. The method is based on shifts in the relative compositions of the target group's developmental stages or size classes (see Hirche et al., 2001).

2.4. Calculation

When obvious cohorts are identified in the time-series of zooplankton samples, mass-specific growth rate (g_{NC}: day^{-1}) is calculated by the following equation.

$$g_{NC} = \ln(MW_{i+1}/MW_i)/D \quad (3)$$

where MW_i and MW_{i+1} are the average body mass at developmental stage/size group i and that of the next stage or size group, respectively. Development time (D: days) is determined by following the peak times of successive stages of the cohort. Dry or carbon mass is the preferable representation of mass due to large variability of water and organic content among developmental stages and taxonomic groups. Note that, in practice, MW_i and MW_{i+1} are the mass of the mean sized individual. Use of mass should be that of geometric rather than arithmetic mean. Some attention needs to be given to how these averages (MW_i and MW_{i+1}) represent the changes within a stage since some taxonomic groups do not increase their masses linearly over the stage (Miller,

2008).

2.5. Notes and comments

Despite the limitations mentioned above, the NC method has been applied to small species with short generation times (e.g., Liang et al., 1996; Liang and Uye, 1996a, b, 1997; Uye et al., 2002), continuous recruitment (e.g., Jerling and Wooldridge, 1991; Webber and Roff, 1995) or at remote oceanic sites (e.g., Hirche et al., 2001). One solution to difficulties in estimating development time is to compare the development or generation times for cohorts evaluated in the time-series to those derived from laboratory incubations, generating a modified NC method (e.g., Uye, 1982; Uye and Sano, 1998; McLaren et al., 1989). The NC method had been applied at sites affected by the mixing of water masses or by strong advection, by following populations using tracers for the constituent water masses (e.g., Kobari et al., 2010).

3. Artificial Cohort method

3.1. Principle

The Artificial Cohort method (hereafter AC method) is applicable to most taxonomic groups in metazooplankton communities. This method was first employed for coastal copepods in the Westernport Bay, Australia (Kimmerer and McKinnon, 1987). Artificial cohorts composed of target size/stage ranges are created by gentle sieving and incubating during a defined period of time. Growth rates are represented by the increase in size, stage and/or biomass per unit time between the beginning and the end of the incubation. This method relies on several major underlying assumptions (Kimmerer et al., 2007; Liu et al., 2013), 1) each artificially-created cohort includes a relatively restricted range of size/development stages, 2) growth and development rates proceed as in nature (i.e., food and temperature remain as *in situ*), 3) members of cohorts are randomly distributed in their position within the molt cycle (i.e., there is no synchrony in molting cycles), 4) mortality is not size/stage-dependent, 5) the sampling intervals are long enough to detect a change in size/stage/mass, but still remain short compared to generation times, 6) adults are a small component of any initial cohort (since they do not express somatic growth) and 7) larger individuals of target size range have been removed from the incubation water prior to setup. The AC method has been applied to diverse taxonomic groups over the world oceans as well as in the laboratory (Table 2).

3.2. Advantages and disadvantages

A detailed summary of the advantages and disadvantages of the AC method are presented by Liu et al. (2013). In brief, the AC method can be applied to various groups of metazooplankton, such as specific developmental stages or size groups, populations and also whole communities. Another advantage is that it is applicable to animals with continuous recruitment, short generation times, or no metamorphosis. Growth measurements can be done for several species or groups at the same time within a single incubation. Disadvantages include, the need for incubations, and that identification of incubated animals is laborious and can be difficult, in particular, for small animals. At each of the many steps of the procedures, special care is required in the collection, handling and incubation of cohort samples, because measured growth of target animals should be representative of those in the field.

3.3. Procedures

3.3.1. Collecting seawater for incubating target animals

The seawater used incubations and providing food for target animals is all collected from a representative environment (i.e., close to animal collection depths) using Niskin bottles or low-pressure pumps. Supplies for collecting and storing seawater might be cleaned (Landry et al., 1995) in oligotrophic or micronutrient-limited waters where metals and toxic compounds may exert negative effects on phytoplankton (e.g., Fitzwater et al., 1982; Williams and Robertson, 1989) and protozoans (e.g., Price et al., 1986). Seawater containing the prey assemblage is prescreened through a suitable sized mesh sock placed over the end of a silicon tube to remove contaminating individuals under the high density while siphoning dilution water into containers. Since turbulence and air bubbles destroy some phytoplankton and particularly protozoans in the prey assemblage, the water should be gently siphoned and the draining tube should contact the bottom of the receiving bottle.

3.3.2. Collecting metazooplankton and creating artificial cohorts

Metazooplankton are collected using a finer mesh plankton net (i.e., 50–150 μm) with an enlarged non-filtering cod-end. Since development is inhibited for fragile crustaceans and gelatinous forms damaged by netting, slow towing speed (e.g., 0.5 m sec^{-1} or less) or drifting with the vessel is recommended. Metazooplankton retained in the cod-end is gently transferred and diluted into containers filled with the prescreened seawater including ambient food resources. Mixtures of target development stages or size groups (i.e., artificial cohorts) are created by multiple sequential passages through submerged screens of the appropriate mesh-size that covers one end of a cylindrical pipe. The AC created in the cylindrical pipe is repeatedly washed with prescreened water by gentle raising and lowering of the submerged screen. The AC is then gently siphoned or backwashed into prescreened water and stored at ambient temperature until all AC size-fractions have been created. The water passing through the screen is reconcentrated by reverse filtration (i.e. submerging a 50 μm cylinder as above into the fraction and siphoning the water out of it). The process is then repeated with the next-finest mesh-size in the series. This constant dilution and reconcentration of the target community is essential to maintain normal oxygen concentrations and prevent the buildup of metabolic wastes. Once all size-fractions have been created, each is divided into aliquots, with duplicates or triplicates preserved as time zero and the others diluted into the incubation bottles or containers. As recommended by Kimmerer et al. (2007) and Liu and Hopcroft (2006a), the number of target metazooplankton incubated should be at least 40 and up to 300, but it may be difficult to control the number on deck. If optical methods such as Optical Plankton Counter and ZooSCAN are used for estimating abundance and biomass, the number of organisms needed for incubation experiments is smaller and precision is maintained.

3.3.3. Incubating artificial cohorts

The incubation bottles or containers are put into a temperature-controlled or temperature-recording water bath. Temperature is often regulated by continuous water exchange with the ocean. Ideally, incubation bottles should be floating or at neutral buoyancy to keep target animals and their prey from sinking out. Ship movement provides ideal constant jostling and internal mixing of the incubation bottles or containers. If conditions are quiescent and settling is a concern, then a turning wheel may be used in the laboratory. Incubation should proceed under partially-reduced light that mimics normal diurnal cycles. It is important that the AC are not unduly concentrated (compared to ambient abundances) during incubation or they will exhaust their food (and potentially their oxygen). The artificial cohorts should be incubated for more than multiple 24 h and harvested during daytime to avoid impact of any diel molting cycles (see *4.3.3. Incubation*). Target organisms are harvested using a concentrator (typically a mesh), preserved with fixative, and then identified as with the NC method.

3.4. Calculation

Artificial cohorts are identified as a mixture of target developmental stages or size groups in the samples preserved at the beginning and end

Table 2
Application of Artificial Cohort method for estimating growth rate (g_{AC}) of zooplankton population or community. This table is modified from Kimmerer et al. (2007) and Kobari (2010). Equations to measure growth rate are indicated in text. C: copepodite stage. N: naupliar stage.

Taxon	Target groups	Location	g_{AC} (day^{-1})	Source
Copepods				
	Acartia fancetti	Westernport Bay, Australia	0.03–0.26	Kimmerer and McKinnon (1987)
	Acartia bifilosa	France	0.03–0.14	Irigoien and Castel (1995)
	Acartia longiremis	Skagerrak, North Sea	0.15–0.24	Peterson et al. (1991)
	Acartia spp.	off Kingston, Jamaica	0.25–1.43	Hopcroft et al. (1998b)
	Calanus agulhensis	Agulhas Bank	0.19–0.46	Peterson and Hutchings (1995)
	Calanus finmarchicus	Skagerrak, North Sea	0.01–0.14	Peterson et al. (1991)
		George Bank, USA	C: −0.09 to 0.31 N: −0.07 to 0.20	Campbell et al. (2001)
		North Atlantic	−0.07 to 0.22	Yebra et al. (2006)
	Calanus helgolandicus	English Channel, UK	0.05–0.29	Yebra et al. (2005)
	Calanus marshallae	Alaska coast, USA	0.05–0.29	Liu and Hopcroft (2007)
	Calanus pacificus		0.03–0.29	
	Centropages typicus	Skagerrak, North Sea	0.24–0.77	Peterson et al. (1991)
		Alboran Sea	< 0.01–0.27	Calbet et al. (2000)
	Centropages velificatus	off Kingston, Jamaica	0.70–1.00	Hopcroft et al. (1998b)
	Corycaeus spp.		0.10–0.36	
	Eurytemora affinis	San Francisco Estuary, USA	0.07–0.30	Kimmerer et al. (2014)
	Metridia pacifica	Alaska coast, USA	< 0.01–0.29	Liu and Hopcroft (2006a)
	Neocalanus flemingeri/plumchrus		< 0.01–0.24	Liu and Hopcroft (2006b)
	Oithona davisae	Laboratory	N, C: 0.05–0.45	Almeda et al. (2010)
		Laboratory	N, C: 0.06–0.27	Yebra et al. (2011)
	Oithona simplex	off Kingston, Jamaica	0.17–0.53	Hopcroft et al. (1998b)
	Oithona nana		0.40–0.91	
	Paracartia grani	Laboratory	N: −0.01 to 0.85	Herrera et al. (2012)
	Paracalanus aculeatus		0.25–1.26	
	Paracalanus parvus	Skagerrak, North Sea	0.16–0.48	Peterson et al. (1991)
	Pavrocalanus crassirostris	off Kingston, Jamaica	0.44–1.08	Hopcroft et al. (1998b)
	Pseudocalanus spp.	Skagerrak, North Sea	0.12–0.35	Peterson et al. (1991)
		Alaska coast, USA	0.00–0.16	Liu and Hopcroft (2008)
	Pseudodiaptomus forbesi	San Francisco Estuary, USA	0.01–0.17	Kimmerer et al. (2014)
			0.23–0.53	Kimmerer et al. (2018b)
	Temora longicornis	Skagerrak, North Sea	0.15–0.56	Peterson et al. (1991)
		Norway	0.00–0.32	Hernández-León et al. (1995)
	Temora turbinata	off Kingston, Jamaica	0.34–1.23	Hopcroft et al. (1998b)
Mixed calanoid guild				
		Indian Ocean	C: 0.38 N: 0.43	McKinnon and Duggan (2003)
		Great Barrier Reef, Australia	C: 0.12–0.53	McKinnon et al. (2005)
Mixed cyclopoid guild				
		Indian Ocean	C: 0.28 N: 0.38	McKinnon and Duggan (2003)
		Great Barrier Reef, Australia	C: 0.16–0.48	McKinnon et al. (2005)
Appendicularians				
	Appendicularia sicula	off Kingston, Jamaica	1.20–3.00	Hopcroft and Roff (1998a)
	Fritillaria borealis		1.22–2.10	
	Fritillaria haplostoma		1.60–2.42	
	Oikopleura longicauda		1.20–2.80	
	Oikopleura dioica		2.00–3.02	
Mixed zooplankton guild				
	50–80 μm	East China Sea	0.04–1.35	Lin et al. (2013)
	100–150 μm		0.01–0.79	

of the incubations. Mass-specific growth rate (g_{AC}: day^{-1}) is calculated by the following equation (Kimmerer and McKinnon, 1987).

$$g_{AC} = \ln(W_t/W_o)/t \quad (4)$$

where, W_o and W_t are the mean mass of the target cohorts (i.e., mixture of development stages or size groups) at the beginning and end of the incubation, respectively. The incubation period (days) is represented by t. Dry or carbon mass would be preferable as with the NC method. In practice, masses are often predicted from LW relationships, and the mass of an individual of mean length at each time period is used to calculate growth rate. If available, some optical methods such as Optical Plankton Counter and ZooSCAN have several advantages such as faster measurements, less error-prone, more precise than measuring mass per individual and further measurements for the saved samples (personal communication with Dr. Wim Kimmerer). Volume of the target cohorts can be directly determined and then calibrated to mass using the length-weight relationships. Growth is calculated as the slope of a linear regression of log-transformed mass to several time-steps of the incubation time. In addition, the growth rate can be calculated from the median mass rather than the mean, which reduces the influence of individuals at the upper end of the size range. Since the choice of density, incubation time, and container size are often made without much knowledge of the extant conditions to support growth (e.g., food availability), taking more than one time point to terminate the incubations helps to assure that incubation times are not excessive, or reduce the number of time points if the longest incubations are too long. Such variations on the method are described in Kimmerer et al. (2018a).

3.5. Notes and comments

Despite the multi-step procedures and time-consuming microscopic

identifications, the AC method has been most used for growth rate measurements among the incubation techniques. However, satisfying assumptions of the method are not guaranteed without extreme care in applying the methodological protocol. For example, some animals from outside of the target group may leak into the artificial cohort by incomplete sieving (Kimmerer et al., 2007; Kobari, 2010). Inclusion of non-target animals may introduce error into growth rate calculations. This is of particular concern when incubations focus on a single stage/size class, but incubation of multiple stages/size fractions can be used to identify and exclude non-target animals from calculations. Despite the large number of target stages or size classes required to minimize the sampling variability, there is some "art" involved in determining a suitable density to dilute the target animals at the beginning of the incubation. This is often determined by the total number of containers available to dilute the size-fractions into, for example, Liu and Hopcroft (2006a,b, 2007, 2008) typically used up to 36 20L-carboys per community experiment. Some crustaceans and gelatinous forms are fragile and excessive handling can inhibit development or lead to death. The estimated growth of the target animals can fluctuate due to the poor reproducibility of the experiments, particularly if the number of target animals in a size-fraction is low. Also, as Kimmerer et al. (2007) mention, potential errors (both under- and overestimation) arising from incorrect assumptions about growth connected with the shifts of age-within-stage for the incubated animals. While tradeoffs between optimal measurements and the logistics of obtaining them are often required, some recommendations are provided for the AC method, including: 1) use direct measurements of biomass for the target animals; 2) choose incubation periods to secure anticipated growth or stage development times; and 3) seek constant growth in the incubation by minimizing food limitation (e.g., through reduced incubation time and/or increased volume of the incubation). Note, however, that directly weighing individuals is destructive making them unavailable for retrospective identification and/or body size/stage determination and decisions to do so should be made with some practical consideration.

4. Molting rate method

4.1. Principle

The Molting Rate method (hereafter MR method) can be applied for crustaceans, the predominant group in metazooplankton communities throughout the world oceans. This method was proposed by Burkill and Kendall (1982), who first employed it in the Bristol Channel for the copepod, *Eurytemora affinis*. They incubated sorted batches of a single developmental stage of *E. affinis* during defined periods and estimated the proportion (i.e., MR) of animals molting to the next developmental stage. Since the reciprocal of MR is assumed equivalent to stage duration, growth rate can be calculated as the difference of body mass between the two stages divided by 1/MR. This method relies on three major requirements: 1) no bottle effect on molting, 2) steady-state molting and mass increment between two consecutive stages, and 3) nearly equal age-within-stage distribution for target animals. In the last three decades, growth measurements by the MR method have been conducted for copepods and euphausiids (Table 3).

4.2. Advantages and disadvantages

The main advantage of the MR method is a simpler experimental design and protocol than the AC method. Materials required are common and not expensive. The MR method is applicable to continuously reproducing populations and large crustaceans. In terms of disadvantage; the MR method is based on sorted samples of specific stages and applicable only to crustaceans. Identification of developmental stages at sea for incubation is often difficult due to their constant swimming plus ship motion, in particular for small crustaceans. Moreover, identifying and sorting large numbers of incubating animals are required to minimize the sampling variability of proportions molted for the target crustaceans with the long development time (i.e., low frequency of molting). Recently, Hirst et al. (2014) have challenged this approach (see below) for methodological reasons.

4.3. Procedures

4.3.1. Field collection of seawater containing prey assemblages

Seawater containing natural prey assemblages is collected from the field as per the AC method description (see 3.3.1).

4.3.2. Field collection of target crustaceans

Target crustaceans are collected by plankton nets with appropriate mesh size and large cod-end volume. Similar to the AC method, since molting is likely inhibited for crustaceans with damaged appendages, antennules or mouthparts, slow towing speed and fine mesh nets are recommended. Crustaceans collected in this way are gently transferred into plastic buckets and diluted with filtered water to avoid damage to appendages and antennae when under high density. After sorting of a developmental stage of interest using a dissecting microscope, batches of that stage are transferred into cleaned bottles with the prey assemblage. Healthy individuals (i.e., undamaged) are recommended (as with the AC method). The number of individuals per bottle is dependent on the size of the target crustacean and incubation volume (see below). Total numbers should be large enough to reduce statistical variation of estimated MR yet small enough to limit crowding effects.

4.3.3. Incubation

Bottles containing target crustaceans are incubated under temperature-controlled or temperature-measured conditions as with the AC method (see 3.3.3. Incubating artificial cohorts). Incubation periods depend on stage duration of the target crustaceans, but should employ 24 h increments for duration. Incubation should ideally be started and stopped during daytime since molting generally occurs most commonly during nighttime (e.g., Fowler et al., 1971; Ambler et al., 1999). Individuals incubated are collected using a sieve and their development stages are identified under dissecting microscopes.

As an alternative, animals are incubated individually and checked regularly (under dim light) for the presence of exuviae. The frequency of checking is informed by knowledge of expected stage duration. The cumulative number molting is then plotted to determine the time at which 50% of the experimental population have molted, with that time doubled to estimate the stage duration.

4.4. Calculation

Molting rate (MR: day^{-1}) is calculated by the following equation (Runge et al., 1985).

$$MR = N_{i+1}/N_i/t \quad (5)$$

where N_i and N_{i+1} are the number of developmental stage i at the beginning of the incubation and the next stage at the end of the incubation, respectively. The duration of the incubation in days is denoted by t. As mentioned above, stage duration (D: days) can be approximated as the reciprocal of the molting rate (i.e. $1/MR$). Thus, mass-specific growth rate (g_{MR}: day^{-1}) is calculated by:

$$g_{MR} = \ln(MW_{i+1}/MW_i)/D \quad (6)$$

where, MW_i and MW_{i+1} are the average body masses of developmental stage i at the beginning of the incubation and the next stage ($i + 1$) at the end of the incubation, respectively. Dry or carbon mass is preferable as with other approaches.

4.5. Notes and comments

The incubation duration should be shorter than the stage duration

Table 3
Application of Molting Rate method for estimating growth rate (g_{MR}) of zooplankton population or community. This table is modified from Hirst et al. (2005) and Kobari (2010). Equations to measure growth rate are indicated in text. C: copepodite stage. N: naupliar stage.

Taxon	Target groups	Location	g_{MR} (day^{-1})	Source
Copepods				
	Calanoides acutus	South Georgia, Southern Ocean	0.01–0.24	Shreeve and Ward (1998), Shreeve et al. (2002)
	Calanus agulhensis	Southern Benguela, South Africa	C: 0.00–0.81 N: 0.40–0.66	Richardson and Verheye (1998)
	Calanus chilensis	Antofagasta coast, Chile	0.05–0.35	Escribano and McLaren (1999)
	Calanus finmarchicus	Skagerrak, North Sea	0.01–0.14	Peterson et al. (1991)
	Calanus marshallae	Oregon coast, USA	0.05–0.20	Peterson et al. (2002)
	Centropages velificatus	off Kingston, Jamaica	0.53–0.76	Hopcroft et al. (1998b)
	Eucalanus bungii	Oyashio, Japan	0.04	Kobari et al. (2010)
	Euchaeta marina	Discovery Bay, Jamaica	0.24–0.38	Webber and Roff (1995)
	Eurytemora affinis	Bristol Channel, UK	0.01–0.20	Burkill and Kendall (1982)
	Limnoithona tetraspina	San Francisco Estuary, USA	0.02–0.05	Gould and Kimmerer (2010)
	Neocalanus cristatus	Oyashio, Japan	0.06	Kobari et al. (2010)
	Neocalanus flemingeri	Oyashio, Japan	0.03–0.10	
	Neocalanus flemingeri/plumchrus	Alaska coast, USA	< 0.01–0.22	Liu and Hopcroft (2006a)
	Neocalanus plumchrus	Oyashio, Japan	0.02–0.03	Kobari et al. (2010)
	Oithona plumifera	Discovery Bay, Jamaica	0.04–0.31	Webber and Roff (1995)
	Paracalanus/Clausocalanus spp.		0.12–0.91	
	Pseudodiaptomus forbesi	San Francisco Estuary, USA	0.03–0.27	Kimmerer et al. (2018a)
	Pseudodiaptomus hessei	Algoa Bay, Southern Africa	0.11–0.38	Jerling and Wooldridge (1991)
	Pseudocalanus elongatus	Southern North Sea, Germany	0.02–0.31	Renz et al. (2008)
	Rhincalanus gigas	South Georgia, Southern Ocean	0.01–0.06	Shreeve and Ward (1998), Shreeve et al. (2002)
	Temora turbinata	off Kingston, Jamaica	0.36–0.75	Hopcroft et al. (1998b)
	Undinula vulgaris	Discovery Bay, Jamaica	0.17–0.49	Webber and Roff (1995)
Euphausiids				
	Euphausia pacifica	Oregon coast, USA	−0.03 to 0.13	Shaw et al. (2010)
		Gulf of Alaska, Eastern North Pacific	0.00–0.01	Pinchuk and Hopcroft (2007)
	Thysanoessa inermis		−0.00 to 0.02	
	Thysanoessa spinifera		−0.00 to 0.03	

of the target crustaceans (i.e., $t < D$) given requirements of proportions molted for MR (i.e., $1 \leq N_{i+1} < N_i + N_{i+1}$). While crustacean molting is likely more independent of food (Miller et al., 1984) than mass increase, molting rate would be overestimated under molting burst or during nighttime (Miller et al., 1984). Number and size of incubation bottles should be commensurate with size and density of the incubated animals, particularly for large crustacean swimmers like euphausiids and amphipods due to bottle effects on molting. As with the AC method, large numbers of incubating animals are recommended due to the sampling variability of age-within-stages, in particular for the animals with long stage duration. There are obvious trade-offs in sample volumes, numbers incubated and experimental duration. On the other hand, Hirst et al. (2005, 2014) suggested probable errors (both under- and overestimation) underlying the MR method. These errors propagate from steady-state assumptions on stage duration and mass increment between two consecutive stages, as well as normal distribution of age within stage for field collected individuals. Such errors are particularly pronounced for some stages where the next stage has different rate of body mass increment or is not actively molting such as mature or dormant copepods. These errors can be corrected using the new Modified Molt Rate (MMR) equations proposed by Hirst et al. (2005), which require additional measurements and computations. In essence, they argued that while the MR approach does reasonably estimate the durations of a stage, the masses employed are typically determined from individuals in the ambient population. These masses represent the average for the mid-point of each stage, and not that at the stage's beginning and end, thus errors are introduced if stage duration and/or growth are not constant across stages. This criticism can be partly resolved by taking the initial mean mass at stage from the ambient population and the final mean mass from the animals incubated, then using experimental duration as the divisor. Since the probable errors are likely variable depending on the target species, life stage and type of mass (Hirst et al., 2014), the original MR method has not been recommended. Alternatively, Hirst et al. (2014) recommended to apply the two methods, either MMR method across the two stages or stage-specific method (see their Fig. 1). The major shortcoming of the MMR method is requiring knowledge of stage duration of each adjoining stage, becoming impossible to estimate the growth rate for C5 stage often dominating the secondary production. It might be also impossible to get the initial and final mean masses of a stage of a small and rapidly developing crustacean with currently available technology.

5. Egg production method

5.1. Principle

Some traditional methodologies are not applicable to adult males and females with little or no somatic growth; however, the Egg Production method (hereafter EP method) can be applied to adult females producing eggs. Berggreen et al. (1988) first applied McLaren and Corkett (1981) suggestion using the EP method on *Acartia tonsa* in laboratory experiments. Adult females of the target species are incubated, usually 24 h to avoid diel periodicity, and the number of eggs spawned is counted. Growth rate can be estimated as the mass of eggs produced during the incubation. This method relies on two major assumptions: 1) the body mass of an incubated female is steady-state (i.e., no storage of ingested materials) and 2) the assimilated energy is all used for egg production. During the last four decades, the EP method has been the most widely used to measure copepods growth (> 85% of the copepod growth data compiled by Hirst et al. (2003) were from EP experiments) (Table 4).

5.2. Advantages and disadvantages

The obvious advantage of the EP method is that it is only concerned with reproductive (mature) developmental stages. Mature animals are generally the easiest to pick out of a sample since they are the largest among the life stages, and the stage most confidently identified to species. The EP method is employed by many researchers due to the simplest experimental design, minimal handling, and the simplest

Table 4
Application of Egg Production method for estimating growth rate of zooplankton population. Equations to measure growth rate (g_{EP}) are indicated in text. This table is modified from Hirst et al. (2003) and Dvoretsky and Dvoretsky (2014).

Taxon	Target groups	Location	g_{EP} (day^{-1})	Source
Copepods				
	Acartia clausi	Ebrie Lagoon, Gulf of Guinea	0.01–0.05	Pagano et al. (2004)
	Acartia longiremis	Skagerrak, North Sea	0.03–0.13	Peterson et al. (1991)
		Sandsfjord, Norway	0.00–0.09	Nielsen and Andersen (2002)
		Barents Sea	0.01–0.07	Dvoretsky and Dvoretsky (2014)
	Acartia steueri	Ilkwang Bay, Korea	0.02–0.07	Jung et al. (2004)
	Acartia tonsa	Laboratory	−0.13 to 0.45	Berggreen et al. (1988)
		Limfjord, Denmark	0.03–0.22	Sørensen et al. (2007)
	Calanus finmarchicus	Skagerrak, North Sea	0.09–0.17	Peterson et al. (1991)
	Calanus helgolandicus	English Channel, UK	0.01–0.37	Yebra et al. (2005)
	Calanus marshallae	Alaska coast, USA	0.07	Liu and Hopcroft (2008)
	Calanus pacificus		0.07	Liu and Hopcroft (2008)
	Calanus sinicus	Inland Sea, Japan	~0.09	Uye and Murase (1997)
	Centropages typicus	Skagerrak, North Sea	0.15–0.32	Peterson et al. (1991)
		Inland Sea, Japan	0.19–0.70	Liang et al. (1994)
		Alaska coast, USA	0.07	Slater and Hopcroft (2005)
	Eurytemora affinis	San Francisco Estuary, USA	0.04–0.05	Kimmerer et al. (2014)
	Limnoithona tetraspina	San Francisco Estuary, USA	0.16	Gould and Kimmerer (2010)
	Metridia okhotensis		0.10	Liu and Hopcroft (2006a), Hopcroft et al. (2005)
	Metridia pacifica		0.11	Hopcroft et al. (2005)
	Oithona davisae	Inland Sea, Japan	0.07–0.49	Uye and Sano (1995)
	Oithona similis	Kattegat, Denmark	0.10	Sabatini and Kiørboe (1994)
	Paracalanus parvus	Skagerrak, North Sea	0.04–0.23	Peterson et al. (1991)
	Pseudocalanus acuspes	Chukchi Sea	0.06–0.09	Ershova et al. (2017)
	Pseudocalanus elongatus	Southern North Sea	0.05–0.13	Renz et al. (2008)
	Pseudocalanus minutus	Alaska coast, USA	~0.06	Liu and Hopcroft (2008)
	Pseudocalanus newmani		0.06–0.09	Liu and Hopcroft (2008)
		Chukchi Sea	0.03–0.07	Ershova et al. (2017)
	Pseudodiaptomus forbesi	San Francisco Estuary, USA	0.02–0.03	Kimmerer et al. (2014)
	Pseudodiaptomus marinus	Inland Sea, Japan	0.03–0.27	Liang and Uye (1997)
	Sinocalanus tenellus	Brackish-water, Japan	0.07–0.41	Kimoto et al. (1986)
	Temora longicornis	Skagerrak, North Sea	0.01–0.05	Peterson et al. (1991)
		Barents Sea	0.01–0.22	Dvoretsky and Dvoretsky (2014)
		North Sea	0.02–0.08	Halsband-Lenk et al. (2002)
	Temora stylifera	Mediterranean Sea	0.21	Halsband-Lenk et al. (2001)
		Mediterranean Sea	0.02	Halsband-Lenk et al. (2004)
		North Sea	0.07	Halsband-Lenk et al. (2002)

material requirements from among the experimental approaches. Among the contemporary methods, the materials produced over time are visible only for the EP method. The major disadvantage of the EP method is that its application is only for reproducing adult females. Berggreen et al. (1988) suggested that growth rates estimated with the EP method was applicable to juveniles, however, many scientists have pointed out that egg production is frequently not equivalent to the juvenile somatic growth (McLaren and Leonard, 1995; Hopcroft and Roff, 1998b; Hirst and McKinnon, 2001), particularly when food becomes limiting.

5.3. Procedures

5.3.1. Field collection of target adult females

The EP method is an incubation method in which target adult females are collected with a plankton net at slow towing speeds and are then gently transferred into a plastic container. Following microscopic identification of healthy (i.e., actively swimming with non-damaged appendages and antennae) adult females, individuals or batches of adult females are transferred into seawater-filled incubation chambers.

5.3.2. Incubation

Incubation chambers containing target adult females are placed in a temperature-controlled incubator. The incubation period is always 24 h due to diel patterns of egg production (e.g., Marcus, 1985; Runge, 1985; Laabir et al., 1995). Since some fractions of females are unproductive, individual incubations are recommended (Kimmerer et al., 2005). For egg-carrying spawners, random selection would result in a large proportion of the females already having egg sacs, in which case the connection between egg laying and incubation time is broken. Thereby most researchers use some modifications of the egg ratio method originally described by Edmondson et al (1962). The number of eggs released in the chamber for broadcast-spawning females or the number of eggs in a clutch for egg-carrying females are counted using the dissecting microscope, and then the masses of eggs are measured using microbalance. In case of difficulty weighing eggs, it may be possible to measure egg volume and use an approximate cytoplasm density for estimating egg mass (i.e., 0.14 pg C m^{-3}, Sabatini and Kiørboe, 1994).

5.4. Calculation

Mass-specific growth rate (g_{EP}: day^{-1}) is calculated for broadcast-spawning females using the following equation.

$$g_{EP} = (N_E \times W_E)/W_F/t \quad (7)$$

where, N_E is the clutch size (number of eggs), W_E is the egg mass (e.g., μg C egg^{-1}), W_F is the adult female body mass (e.g., μg C female^{-1}) and t is the incubation period (days). Mass-specific growth rate (g_{EP}: day^{-1}) is calculated for egg-carrying females as follows:

$$g_{EP} = (N_C \times F \times W_E)/W_F/t \quad (8)$$

where, N_C is the number of eggs per clutch and F is the frequency of clutch formation during the incubation period (t). This equation can be transformed into the following equation (Nielsen and Sabatini, 1996).

$$g_{EP} = (N_C/N_F) \times HR \times (W_E/W_F) \quad (9)$$

where, N_F is the number of females incubated and HR is the hatching

rate (day^{-1}). The hatching rate can be expressed as the reciprocal of egg-hatching duration (days) (McKinnon and Klumpp, 1998).

5.5. Notes and comments

For broadcasting females, released eggs should be separated from the incubated females using a mesh false bottom placed above the bottom of the incubation chamber in order to avoid potential egg cannibalism (Dagg, 1978) or damage to fragile eggs (Hopcroft et al., 2005). As mentioned above, one major requirement for this method is that the body mass of incubated adult females is in steady-state. However, there is an increasing awareness that this assumption is not reasonable since accumulated lipids are sometimes metabolized for gonad maturation (e.g., Hirche and Niehoff, 1996; Calbet and Irigoien, 1997) and egg production (e.g., Tande and Hopkins, 1981; Hagen and Schnack-Schiel, 1996). Based on a literature review of the EP method (Hirst and McKinnon, 2001), potential errors (both under- and over-estimation) affect rate estimates with the EP method: steady-state assumption about female mass, in particular for metazooplankton accumulating lipids. We have no practical solution for this problem, however, the EP method is still useful for evaluating patterns in growth relationships to various environmental drivers, and due to its practicality for routine measurement. It is also more rapidly responsive to changes in food concentration than other measurements of growth. It is generally not recognized that this method provides a standardized estimate of daily production that is not identical to the instantaneous mass-specific methods, with the two related as follows: $G = \exp(g) - 1$. At low values, the relative difference between the two is small, but they diverge rapidly as values increase.

6. Empirical models

6.1. Principle

Empirical models have been applied for various taxonomic groups in metazooplankton communities in different regions of the ocean. Currently, several empirical models are available. These models require input information on target animals and their environments, and assume that growth rates are determined by ambient conditions interacting with the biological processes of the target organisms.

6.2. Advantages and disadvantages

No routine sampling or incubations are required, since these models compute growth rates from some measured variables. The models have a wide applicability to various groups from specific stages or species (i.e., population) to community guilds and to any environments, even when information on the target animals is limited. Among the disadvantages, the growth estimates involve uncertainty subjected to the model structures, and their initial parameterization. Therefore, the predicted rates usually differ from direct field measurements (typically based on incubations). Applicability is dependent on the data sets used in the development of each model. Since many models rely on data sets derived from coastal sites and laboratory experiments, applications of the models to offshore waters are relatively few compared to coastal sites (Tables 5–8). In the last three decades, growth rate estimates with these models have been employed for various populations, taxonomic groups and zooplankton-community guilds.

6.3. Annual P/B ratio model

A ratio of production to mean biomass in a year (annual P/B ratio) represents the turnover rate of annual biomass subtracting any losses like mortality and advection. Based on a literature review of annual production and biomass of a wide range of aquatic invertebrates, Banse and Mosher (1980) proposed a general model of annual P/B ratio.

$$g_{PB} = 0.65 \times W_s^{-0.37} \quad (10)$$

where g_{PB} is an annual P/B ratio and W_S is individual body mass at maturity of the target animals (kcal individual^{-1}).

The most obvious advantage of the Banse-Mosher model is that it requires only adult body mass, which is easily measurable. Due to the wide coverage of aquatic invertebrates in the data sets, the Banse-Mosher model is applicable to various taxonomic groups with no other ecological information than adult biomass. This model can also generate snap-shot production estimates for remote sites and allows for retrospective analysis of long-term data sets. Relative to other empirical models, a disadvantage of this model is that it is applicable only to population-based studies. Also, since the Banse-Mosher model outputs have an annual basis and are estimated from only the mature body masses, the estimates do not capture temporal or spatial variability of growth during short periods (days to weeks), or allow for any influence of temperature or food concentration. Indeed, the outcomes of this model are inconsistent with the growth rates directly measured by the AC method (e.g., Liu and Hopcroft, 2006a,b). Therefore, g_{PB} is not comparable to those estimated with the other methods. Despite the limitations and disadvantages, the Banse-Mosher model has been applied for several species of copepods and chaetognaths in subpolar waters for the last three decades (Table 7).

6.4. Temperature dependent model

Based on a literature review of field studies on copepods, Huntley and Lopez (1992) proposed a temperature dependent model of growth rate:

$$g_T = 0.0445 \times e^{0.111 \times T} \quad (11)$$

where g_T is the estimated growth rate (day^{-1}) and T is the field temperature (°C).

Ambient temperatures falling within a −1.7 to 30.7 °C range are the only input required for this model, even for various copepod populations. The most obvious advantage of the Huntley-Lopez model is that it can be used for estimating growth rates of snap-shot and long-term data sets, if ambient temperature is available by computing mean temperature in the sampling layer or mixed layer. In terms of disadvantage, the Huntley-Lopez model assumes no food limitation of mass-specific growth rate in nature, even though there is evidence for food limitation (Huntley and Boyd, 1984; Hirst and Bunker, 2003; Liu and Hopcroft, 2006a,b, 2007, 2008). Indeed, the Huntley-Lopez model growth rate estimates are typically higher than direct measurements in nature (e.g., Peterson et al., 2002; Kobari et al., 2003). Therefore, this model might be applicable for coastal copepods inhabiting the limited waters where their growths are not limited under high food availability. In the last two decades, the Huntley-Lopez model has been applied to single and mixed copepod species as well as to metazooplankton guilds from polar to tropical waters (Table 5).

6.5. Temperature and body mass dependent models

In 1997, Hirst and Sheader (1997) proposed a model that relies on field temperature and individual body mass.

$$\log(g_{TW-HS}) = 0.0246 \times T - 0.2962 \times \log(W_C) - 1.1355 \quad (12)$$

where $g_{TW\text{-}HS}$ is the instantaneous growth rate estimated from the Hirst-Sheader model, T is the ambient temperature (°C), and W_C is the individual carbon-based mass of the target animals (μg C individual^{-1}). The Hirst and Lampitt (1998) synthesized a more extensive data set than previous studies and demonstrated model fits for growth rates of broadcast and egg-carrying spawners (Hirst-Lampitt model).

$$\log(g_{TW-HL}) = 0.0087 \times T - 0.4902 \times \log(W_C) - 0.7568 \quad \text{for broadcast spawners} \quad (13)$$

Table 5
Application of temperature dependent model for estimating growth rate (g_T) of zooplankton population or community. Equation to measure growth rate is indicated in text. Asterisks indicate that growth rates are not available but production rates were estimated.

Taxon	Target groups	Location	g_T (day^{-1})	Source
Copepods				
	Acartia lillijeborgi	Cananéia Lagoon estuarine, Brazil	*	Ara (2001b)
	Acartia longiremis	Coastal Barents Sea	*	Dvoretsky and Dvoretsky (2012)
	Bradyidius armatus		*	
	Calanus finmarchicus		*	
	Calanus marshallae	Oregon coast, USA	0.01–0.22	Peterson et al. (2002)
	Centropages hamatus	Coastal Barents Sea	*	Dvoretsky and Dvoretsky (2012)
	Centropages typicus		*	
	Euterpina acutifrons	Cananéia Lagoon estuarine	*	Ara (2001a)
	Metridia longa		*	
	Metridia lucens		*	
	Microcalanus pygmaeus		*	
	Microsetella norvegica		*	
		Coastal Barents Sea	*	Dvoretsky and Dvoretsky (2012)
	Neocalanus cristatus	Oyashio, Western North Pacific	0.05–0.15	Kobari et al. (2003)
	Neocalanus flemingeri		0.04–0.13	
	Neocalanus plumchrus		0.04–0.19	
	Oithona atlantica	Coastal Barents Sea	*	Dvoretsky and Dvoretsky (2012)
	Oithona similis		*	
	Pareuchaeta spp.		*	
	Pseudocalanus spp.		*	
	Temora longicornis		*	
	Tisbe furcata		*	
	Triconia borealis		*	
	Mixed copepod guild	Mondego estuary, Portugal	*	Gonçalves et al. (2015)
		Ria de Aveiro, Portugal	*	Leandro et al. (2007)
		Southeastern Bering Sea	*	Kimmel et al. (2018)
Mixed zooplankton guild				
		Amundsen Gulf, Arctic Ocean	*	Forest et al. (2011)
		Arabian Sea	0.41–1.24	Roman et al. (2000)
		Arctic Sea	*	Sastri et al. (2012)
		Patos Lagoon estuary, Brazil	*	Avila et al. (2012)
		Subtropical front, New Zealand	*	McClatchie et al. (2004)

$$\log(g_{TW-HL}) = 0.0464 \times T - 1.7255 \quad \text{for egg} - \text{carrying spawners} \tag{14}$$

While the Huntley-Lopez model assumes no food limitation on copepod growth, the model for broadcast spawners (also the other empirical and physiological model) suggests that their growth rates are indirectly limited with food availability through their individual body mass. To clarify the effect of food limitation on growth, Hirst and Bunker (2003) proposed another global model of growth rates dependent on field temperature, individual body mass and food availability as follows.

$$\log(g_{TW-HB}) = 0.0186 \times T - 0.288 \times \log(W_C) + 0.417 \times \log(C_A) - 1.209 \tag{15}$$

where C_A is the *in situ* biomass of phytoplankton (chlorophyll *a* concentration: μg l^{-1}).

The major advantage of the Hirst and Bunker (2003) model (generic model based on temperature and individual body mass) is that potential food limited growth is covered and all variables in this model are easily measurable. Both T and C_A are sometimes represented by mean temperature and chlorophyll *a* in the sampling layer or mixed layer, respectively. Individual mass (W_C) can be often estimated with standing stocks of target population or mixed guild divided by their abundance. Similar to the Huntley-Lopez model, these equations are applicable to various copepod populations and the overall copepod community. They can be used to convert biomass data to "production snap-shots" and applied in retrospective analysis of previous biomass data sets. In the last two decades, these models have been the most popular for estimating growth rates of various copepod species, copepod guild and mixed metazooplankton taxa from polar to tropical waters (Table 6). As a disadvantage, however, the model predictions do not consistently align with direct measurements of copepod growth rates in the field, which may not be surprising since the coefficients of determination (r^2) ranged from 0.29 to 0.64 for these temperature and body mass dependent equations. Secondarily, Hirst and Bunker (2003) fit chlorophyll in the above relationship to a simple log-log relationship when their own literature review and bivariate equations showed that the form of that relationship to be Michaelis-Menten equation. Indeed, the models tend to under- or overestimate growth compared with the field-measured rates (e.g., Peterson et al., 2002; Kobari et al., 2003; Yebra et al., 2005; Liu and Hopcroft, 2006a,b, 2007, 2008). These disagreements might result from a wide spectrum of feeding habits of copepods (i.e., omnivore or particle feeding), but this has not been fully approached in the literature. Given the synergistic effects of temperature, food condition, and body size on growth of copepods, a composite nonlinear model developed by Liu and Hopcroft (2006a), exhibits a great promise for describing the growth rates of dominant copepods in the northern Gulf of Alaska (Liu and Hopcroft, 2008).

6.6. Physiological model

Individual net production can be approximated from organismal physiology as follows (Omori and Ikeda, 1984)

$$W_C \times g_P = (K_1 \times R_C)/(A - K_1) \tag{16}$$

where W_C is individual carbon mass (mg C individual^{-1}), g_P is growth rate, K_1 is gross growth coefficient, A is assimilation efficiency and R_C means individual respiration rate (mg C individual^{-1} day^{-1}). Assuming 0.3 for K_1 and 0.7 for A (Ikeda and Motoda, 1978), the above equation can be transformed to

$$g_P = 0.75 \times R_C/W_C \tag{17}$$

Based on numerous experiments measuring respiration rates on various taxonomic groups throughout the oceans, Ikeda (1985)

Table 6
Application of temperature body mass dependent model for estimating growth rate (g_{TW}) of zooplankton population or community. Equations to measure growth rate are indicated in text. Asterisks show that growth rates are not available but production rates were estimated.

Taxon	Target groups	Location	g_{TW} (day^{-1})	Source
Copepods				
	Acartia lillijeborgi	Cananéia Lagoon estuarine, Brazil	*	Ara (2001b)
			*	Ara (2004)
	Acartia longiremis	Coastal Barents Sea	*	Dvoretsky and Dvoretsky (2012)
	Acartia tonsa	Cananéia Lagoon estuarine, Brazil	*	Ara (2004)
	Acartia tonsa	Patos Lagoon estuary, Brazil	*	Muxagata et al. (2012)
	Acartia spp.	Gulf of Alaska shelf	*	Coyle and Pinchuk (2003)
		Southeastern Bering Sea	*	Kimmel et al. (2018)
	Aetideidae spp.	Gulf of Alaska shelf	*	Coyle and Pinchuk (2003)
	Bradyidius armatus	Coastal Barents Sea	*	Dvoretsky and Dvoretsky (2012)
	Calanus chilensis	Mejillones Peninsula, Chile	0.04–0.11	Escribano et al. (2001)
	Calanus finmarchicus		*	
	Calanus helgolandicus	English Channel	0.08–0.18	Yebra et al. (2005)
	Calanus marshallae	Gulf of Alaska shelf	*	Coyle and Pinchuk (2003)
		Oregon coast, USA	0.01–0.22	Peterson et al. (2002)
	Calanus pacificus	Gulf of Alaska shelf	*	Coyle and Pinchuk (2003)
	Calanus spp.	Southeastern Bering Sea	*	Kimmel et al. (2018)
	Candacia columbiae	Gulf of Alaska shelf	*	Coyle and Pinchuk (2003)
	Centropages abdominalis		*	
	Centropages hamatus	Coastal Barents Sea	*	Dvoretsky and Dvoretsky (2012)
	Centropages typicus		*	
	Clausocalanus furcatus	Santos estuarine, Brazil	0.15–0.18	Miyashita et al. (2009)
	Clausocalanus spp.	Gulf of Alaska shelf	*	Coyle and Pinchuk (2003)
	Corycaeus spp.	Santos estuarine, Brazil	0.26–0.29	Miyashita et al. (2009)
	Ctenocalanus spp.		0.14–0.16	
	Epilabidocera amphitrites	Gulf of Alaska shelf	*	Coyle and Pinchuk (2003)
	Eucalanus bungii	Gulf of Alaska shelf	*	Coyle and Pinchuk (2003)
	Euchaeta elongata		*	
	Euchaeta marina	Santos estuarine, Brazil	0.09	Miyashita et al. (2009)
	Eurytemora spp.	Gulf of Alaska shelf	*	Coyle and Pinchuk (2003)
	Euterpina acutifrons	Cananéia Lagoon estuarine, Brazil	*	Ara (2001a)
			*	Ara (2004)
	Heterorhabdus spp.	Gulf of Alaska shelf	*	Coyle and Pinchuk (2003)
	Heterostylites spp.		*	
	Lucicutia spp.		*	
	Mesocalanus tenuicornis		*	
	Metridia longa	Coastal Barents Sea	*	Dvoretsky and Dvoretsky (2012)
	Metridia lucens		*	
	Metridia okhotensis	Gulf of Alaska shelf	*	Coyle and Pinchuk (2003)
	Metridia pacifica		*	
	Metridia pacifica	Southeastern Bering Sea	*	Kimmel et al. (2018)
	Microcalanus pygmaeus	Coastal Barents Sea	*	Dvoretsky and Dvoretsky (2012)
	Microcalanus spp.	Gulf of Alaska shelf	*	Coyle and Pinchuk (2003)
	Microsetella norvegica	Coastal Barents Sea	*	Dvoretsky and Dvoretsky (2012)
	Microsetella spp.	Santos estuarine, Brazil	0.53–0.58	Miyashita et al. (2009)
	Monothula subtilis		0.29–0.31	
	Neocalanus cristatus	Gulf of Alaska shelf	*	Coyle and Pinchuk (2003)
		Oyashio, Western North Pacific	0.01–0.10	Kobari et al. (2003)
	Neocalanus flemingeri		0.01–0.11	
	Neocalanus plumchrus		0.02–0.13	
	Neocalanus plumchrus-flemingeri	Gulf of Alaska shelf	*	Coyle and Pinchuk (2003)
Copepods				
	Oithona atlantica	Coastal Barents Sea	*	Dvoretsky and Dvoretsky (2012)
	Oithona hebes	Cananéia Lagoon estuarine, Brazil	*	Ara (2004)
	Oithona nana	Santos estuarine, Brazil	0.37–0.41	Miyashita et al. (2009)
	Oithona oswaidocruzi	Cananéia Lagoon estuarine, Brazil	*	Ara (2004)
	Oithona plumifera		0.24–0.25	
	Oithona similis	Coastal Barents Sea	*	Dvoretsky and Dvoretsky (2012)
	Oithona spp.	Gulf of Alaska shelf	*	Coyle and Pinchuk (2003)
		Santos estuarine, Brazil	0.54–0.56	Miyashita et al. (2009)
		Southeastern Bering Sea	*	Kimmel et al. (2018)
	Oncaea venusta	Santos estuarine, Brazil	0.18–0.20	Miyashita et al. (2009)
	Oncaea waldemari		0.25–0.26	
	Oncaea spp.	Gulf of Alaska shelf	*	Coyle and Pinchuk (2003)
		Santos estuarine, Brazil	0.34–0.37	Miyashita et al. (2009)
	Paracalanus spp.	Gulf of Alaska shelf	*	Coyle and Pinchuk (2003)
	Pareuchaeta spp.	Coastal Barents Sea	*	Dvoretsky and Dvoretsky (2012)
	Parvocalanus crassirostris	Cananéia Lagoon estuarine, Brazil	*	Ara (2004)
	Pleuromamma spp.	Gulf of Alaska shelf	*	Coyle and Pinchuk (2003)
	Pseudocalanus spp.	Coastal Barents Sea	*	Dvoretsky and Dvoretsky (2012)
		Gulf of Alaska shelf	*	Coyle and Pinchuk (2003)
		Southeastern Bering Sea	*	Kimmel et al. (2018)
	Pseudodiaptomus acutus	Cananéia Lagoon estuarine, Brazil	*	Ara (2004)

(*continued on next page*)

Table 6 (*continued*)

Taxon	Target groups	Location	g_{TW} (day^{-1})	Source
	Racovitzanus antarcticus	Gulf of Alaska shelf	*	Coyle and Pinchuk (2003)
	Scolecithricella spp.	Gulf of Alaska shelf	*	Coyle and Pinchuk (2003)
	Subeucalanus pileatu	Santos estuarine, Brazil	0.08–0.09	Miyashita et al. (2009)
	Tortanus discaudata	Gulf of Alaska shelf	*	Coyle and Pinchuk (2003)
	Temora longicornis	Coastal Barents Sea	*	Dvoretsky and Dvoretsky (2012)
	Temora stylifera	Santos estuarine, Brazil	0.14–0.17	Miyashita et al. (2009)
	Temora turbinata		0.15–0.16	
		Cananéia Lagoon estuarine, Brazil	*	Ara (2002)
			*	Ara (2004)
	Tisbe furcata	Coastal Barents Sea	*	Dvoretsky and Dvoretsky (2012)
	Triconia borealis		*	
	Mixed coeppod guild	Amazon estuary, Brazil	*	Magalhães et al. (2011)
		Amundsen Gulf, Arctic Ocean	*	Forest et al. (2011)
		Cananéia Lagoon estuarine, Brazil	*	Ara (2004)
		Ria de Aveiro, Portugal	*	Leandro et al. (2007)
		Santos estuarine, Brazil	0.22–0.50	Miyashita et al. (2009)
		Sargasso Sea	*	Andersen et al. (2011)
		Southern Benguela	0.04–0.10	Huggett et al. (2009)
		Southeastern Bering Sea	*	Coyle and Pinchuk (2002)
		Strait of Georgia, Canada	*	Sastri and Dower (2009)
		Tropical estuaries, Brazil	*	Araujo et al. (2017)
Mixed zooplankton guild				
		ALOHA, subtropical North Pacific	*	Valencia et al. (2018)
		ALOHA, subtropical North Pacific	0.02–0.17	Roman et al. (2002a)
		Arabian Sea	0.05–0.64	Roman et al. (2000)
		Arctic fjord, Svalbard	*	Trudnowska et al. (2014)
		Arctic Sea	*	Sastri et al. (2012)
		Barents Sea	*	Basedow et al. (2014)
		BATS, subtropical North Atlantic	0.02–0.15	Roman et al. (2002a)
		Bay of Bengal	*	Fernandes and Ramaiah (2017)
		Canary Islands, Eastern North Atlantic	*	Garijo and Hernández-León (2014)
		Coral reef, Japan	*	Nakajima et al. (2017)
		Coral reef, Malaysia	*	Nakajima et al. (2014)
		Equatorial Pacific	*	Roman et al. (2002b)
		Patos Lagoon estuary, Brazil	*	Avila et al. (2012)
		Strait of Georgia, Canada	*	Sastri and Dower (2009)
		Yatsushiro Bay, Japan	*	Hayashi and Uye (2008)

developed a global model of metazooplankton oxygen consumption rates (R_O: µl O_2 individual^{-1} h^{-1}).

$$R_O = e^{0.525+0.835\times\ln(W_C)+0.060\times T} \quad (18)$$

where W_C is the individual carbon-based mass of the target animals (mg C individual^{-1}) and T is the ambient temperature (°C). Therefore, growth rate (g_P: day^{-1}) can be estimated using physiological equations as follows.

$$g_P = 0.75 \times R_O \times 10^{-3} \times RQ \times F \times 24/W_C \quad (19)$$

Table 7
Application of annual P:B ratio model for estimating growth rate (g_{PB}) of zooplankton population or community. Equation to measure growth rate is indicated in text. Asterisks show that growth rates are not available but production rates were estimated.

Taxon	Target groups	Location	g_{PB} (day^{-1})	Source
Copepods				
	Calanus finmarchicus	Scotian Shelf, Canada	*	Tremblay and Roff (1983)
	Calanus glacialis		*	
	Calanus hyperboreus		*	
	Candacia armata		*	
	Centropages typicus		*	
	Clausocalanus sp.		*	
	Eucalanus bungii	Oyashio, Western North Pacific	0.02	Ikeda et al. (2008)
	Heterorhabdus tanneri		0.02	
	Metridia lucens	Scotian Shelf, Canada	*	Tremblay and Roff (1983)
	Metridia okhotensis	Oyashio, Western North Pacific	0.02	Ikeda et al. (2008)
	Oithona similis	Scotian Shelf, Canada	*	Tremblay and Roff (1983)
	Paracalanus parvus		*	
	Paraeuchaeta birostrata	Oyashio, Western North Pacific	0.01	Ikeda et al. (2008)
	Paraeuchaeta elongata		0.01	
	Paraeuchaeta rubra		0.01	
	Pleuromamma scutullata		0.02	
	Pseudocalanus minutus	Scotian Shelf, Canada	*	Tremblay and Roff (1983)
Chaetognaths				
	Eukrohnia bathypelagica	Oyashio, Western North Pacific	0.01	Ikeda et al. (2008)
	Eukrohnia hamata		0.01	
	Sagitta elegans		0.01	

Table 8
Application of physiological model for estimating growth rate (g_P) of zooplankton population or community. Equation to measure growth rate is indicated in text. Asterisks show that growth rates are not available but production rates were estimated.

Taxon	Target groups	Location	g_P (day^{-1})	Source
Copepods				
	Acartia lilljeborgi	Cananéia Lagoon, Brazil	*	Ara (2001b)
	Euterpina acutifrons		*	Ara (2001a)
	Neocalanus cristatus	Oyashio, Western North Pacific	0.01–0.07	Kobari et al. (2003)
	Neocalanus flemingeri		0.01–0.07	
	Neocalanus plumchrus		0.02–0.08	
	Mixed coeppod guild	Inland Sea of Japan	*	Uye et al. (1987)
		Cananéia Lagoon, Brazil	*	Ara (2004)
Mysids				
	Anisomysis pelewensis	Great Barrier Reef, Australia	*	Carleton and McKinnon (2007)
	Anisomysis lamellicauda		*	
	Anisomysis laticauda		*	
	Anisomysis pelewensis		*	
	Doxomysis littoralis		*	
	Erythrops nana		*	
	Gastrosaccus indicus		*	
	Prionomysis stenolepis		*	
Mixed zooplankton guild				
		Kuroshio, East China Sea	*	Ikeda and Motoda (1978)
		Funka Bay, Japan	*	Odate and Maita (1988)
		Inland Sea of Japan	*	Uye and Shimazu (1997)
		Dokai Inlet, Japan	*	Uye et al. (1998)
		Ise Bay, Japan	*	Uye et al. (2000)
		North Western Mediterranean	*	Gaudy et al. (2003)
		Equatorial Pacific	*	Gaudy and Champalbert (2003)
		Lake Nakaumi, Japan	*	Uye et al. (2004)
		Western North Pacific	*	Yokoi et al. (2008)
		Yellow Sea	*	Huo et al. (2012)
		Coral reaf, Malaysia	*	Nakajima et al. (2014)
		Australian coast	*	McKinnon et al. (2015)
		Western North Pacific	*	Yamaguchi et al. (2017)
		Kuroshio, East China Sea	0.15–0.29	Kobari et al. (2018)

where RQ is respiratory quotient and F is the conversion factor for oxygen to carbon (i.e., 12/22.4). The respiration quotient is assumed to be 1 for carbohydrates as a metabolic substrate, 0.8 for proteins and 0.7 for lipids (Omori and Ikeda, 1984).

Due to wide coverage of taxonomic groups in the data sets, the Ikeda-Motoda model is applicable to a wide range of target animals such as specific stages, populations and mixed taxonomic groups and requires even little knowledge on their biology and ecology. Due to the global coverage of the respiration rates of epipelagic metazooplankton data sets, the Ikeda-Motoda model can provide snap-shot estimates for remote sites and allows retrospective analysis of long-term data sets. Contrary to the other empirical models which are basically applicable to either copepods or specific populations, community-based growth rates can be estimated with this model. Alternative respiratory models are also available for specific taxonomic groups (e.g., Ikeda, 2014a,c; Ikeda et al., 2001) or pelagic to bathypelagic metazoans (e.g., Ikeda et al., 2007; Ikeda, 2013a,b, 2014b). As disadvantages, some assumptions are required for the Ikeda-Motoda model. Gross growth coefficient (K_1), assimilation efficiency (A) and respiration quotient (RQ) are assumed to be constants, even though there is a large variability among the seasons, sites and taxonomic groups (e.g., Omori and Ikeda, 1984; Le Borgne, 1982; Straile, 1997). Also, field temperature (T) determines the estimated rates, even though animals are exposed to wide vertical thermal range as consequences of diel and seasonal vertical migrations. Thus, growth rates estimated with the Ikeda-Motoda model contain uncertainty from these steady-state variables as gross growth coefficient, assimilation efficiency and respiration quotient. The Ikeda-Motoda model has been applied for several species of copepods and mysids as well as metazooplankton guilds during the last three decades (Table 8).

7. Concluding remarks

Over recent decades, many methods have become available for estimating the growth rates of metazooplankton individuals, populations and communities. Traditional methods were described in the ICES Zooplankton Methodology Manual (Harris et al., 2000) and, recently, biochemical indices of growth have been reviewed (Yebra et al., 2017). Also, during the past two decades, some researchers have discussed problems and assumptions involving these traditional methodologies and proposed solutions and recommendations to at least partially resolve them (Hirst and McKinnon, 2001; Hirst et al., 2005; Kimmerer et al., 2007). However, there has been no comprehensive review to identify the best traditional method for measuring metazooplankton growth in the variable environments, the given organisms and our limited capacity for rate measurement. This review may help researchers identify the most appropriate approach for their target species, taxa or community guild of metazooplankton among the range of traditional methodologies. Note that many methods are relatively specific to particular target groups and all have advantages and disadvantages.

Based on the advantages and disadvantages specific to each method as described above, Table 9 provides a comparison specifying appropriate target species and suitable situations. While the NC method might seem appropriate for metazooplankton at enclosed sites (due to the possibility for high sampling frequency), identification of cohorts may still be difficult due to mixture of populations under advection of different water masses in non-enclosed systems. The AC method is the most suitable for a wide range of epipelagic target groups and situations and applicable to entire communities, but is in general very labor intensive and would be problematic for slow-growing species. MR and EP methods are specific to certain development stages, and thus are not suitable for entire populations or other stages. Both rely on assumptions that may not hold to be true. The MR method as originally developed is

Table 9
Limited, problematic (*) or unavailable situations (**) for applying the traditional (TM) and biochemical methodologies (BM) to estimate growth or production rates of metazooplankton in nature. NC: Natural Cohort method. AC: Artificial Cohort method. MR: Molting Rate method. EP: Egg Production method. E_{MT}: Empirical model dependent on temperature. EM_{TW}: Empirical model dependent on temperature and body mass. EM_{PB}: Annual P/B ratio model. PM: Physiological model. NA: Nucleic acid ratio CB: Chitobiase activity. AARS: Aminoacyl-tRNA synthetase activity.

Occasions		TM							BM		
		NC	AC	MR	EP	EM_T	EM_{TW}	EM_{PB}	PM	NA	CB	AARS
Organisms propaties	Stage duration		Longer than weeks*	Longer than weeks*								
	Body size		Longer than macro*	Longer than macro*								
	Life stage	Non-molting stage**	Non-molting stage**	Non-molting stage**	Juvenile**	Non-molting stage**	Non-molting stage**	Non-molting stage**			Non-molting stage**	
	Guild	Community**		Population to community**	Population to community**	Copepods	Copepods			Mixed populations*		
Environments	Climate regime	Tropical to subtropical*				Polar**						
	Location Food availability	Large advection*				Coastal Food limitation**	Food limitation*[1]	Food limitation*	Food limitation*			

[1] The Hirst-Bunker model represents food limitation on growth.

logically and mathematically erroneous and thus should be replaced by the MMR method. While empirical models are applicable to wide groups and various situations, careful explanation and consideration of the methods and assumptions are necessary due to their global point of view and thus less predictability. Note that empirical models dependent on temperature and/or body mass might be useful for copepods, in particular for coastal copepods in the absence of food limitation.

Due to trade-offs imposed by the advantages, disadvantages and resource limitations, it is important to compare and validate the growth rate estimates using several methods (Yebra et al., 2017). For example, *in situ* metazooplankton productivity can be evaluated by comparisons of production rates estimated with the physiological model with physiological rates measured with the biochemical approaches (e.g., Nakata et al., 1995; Kobari et al., 2018) or growth rates by direct measurements with estimates from a theoretical model (e.g., Peterson et al., 2002; Lin et al., 2013). However, the direct comparisons of growth rate estimates among the traditional methods are quite limited (e.g., Peterson et al., 1991; Yebra et al., 2005). Nowadays, a validation of growth estimates (with measures of estimated precision and accuracy) using cultured or field populations is needed. Such information would contribute to regional and global mapping of metazooplankton productivity as potential indices of the complex responses of marine ecosystems to global warming and ocean acidification.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.pocean.2019.102137.

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