ISBN 978-1-927797-46-4
ISSN 1198-273X

PICES SCIENTIFIC REPORT
No. 63, 2022

Report of Working Group 37 on Zooplankton Production Methodologies, Applications and Measurements in PICES Regions

NORTH PACIFIC MARINE SCIENCE ORGANIZATION

PICES

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Report of Working Group 37 on Zooplankton Production Methodologies, Applications and Measurements in PICES Regions

edited by
Toru Kobari, Akash Sastri and Lidia Yebra

September 2022

North Pacific Marine Science Organization (PICES)
P.O. Box 6000, Sidney, BC, V8L 4B2, Canada
www.pices.int

PICES Scientific Reports

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This report was developed under the guidance of the PICES Science Board and its Biological Oceanography Committee. The views expressed in this report are those of participating scientists under their responsibilities.

Front cover:
Participants of WG 37's Phase 1 Practical Workshop on "Production methodologies and measurements for *in situ* zooplankton" held in 2018 in Manazuru, Japan (top) and Phase 2 Practical Workshop on "Production methodologies and measurements for *in situ* zooplankton" held in 2019 on Quadra Island, Canada (bottom).

This document should be cited as follows:

Kobari, T., Sastri, A. and Yebra, L. (Eds.) 2022. Report of Working Group 37 on Zooplankton Production Methodologies, Applications and Measurements in PICES Regions. PICES Sci. Rep. No. 63, North Pacific Marine Science Organization, Sidney, BC, Canada, 164 pp.

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Acknowledgements

We thank Drs. William T. Peterson, Charles B. Miller and Michael J. Dagg for encouraging the formation of a working group on zooplankton production between PICES and ICES colleagues and for providing valuable comments and suggestions to the working group activities. We also appreciate valuable and helpful comments on the review papers on the biochemical approaches to Dr. David McKinnon and on the traditional methodologies to Drs. Wim Kimmerer and Andrew Hirst. We also thank ICES WGZE and MedZoo members for collaborating on the compilation of Laboratories Working on Zooplankton Production. Thanks are extended to the Secretariat of the North Pacific Marine Science Organization (PICES) for kind support to Working Group 37. Business meetings, workshops and practical workshops organized by WG 37 were supported by PICES, the Manazuru Marine Center for Environmental Research and Education, the Hakai Institute and Faculty of Fisheries, Kagoshima University. Some activities of WG 37 were partially supported by grants from the Japan Society for the Promotion of Science (25340011, 17K00522, 18H04920) and Kagoshima University to TK, and from the Andalusian Government through project MOLDIALB (P11-RMN-7354) and the Spanish Institute of Oceanography (IEO, CSIC) to LY. This scientific report is one of the products of WG 37, in collaboration with the ICES Working Group on Zooplankton Ecology (WGZE).

Toru Kobari, Akash Sastri and Lidia Yebra

In Memoriam

William Thornton Peterson
Hatfield Marine Science Center, National Oceanic and Atmospheric Administration, Newport, Oregon, USA

Dr. William Thornton Peterson passed away on August 12, 2017. He dedicated his life to ocean science and to his family and friends.

Bill obtained a B.Sc. in biology and chemistry at Pacific Lutheran University, and an M.Sc. in oceanography from the University of Hawaii in 1969. After taking a staff position at Oregon State University, he earned a Ph.D. describing the life history and ecology of the copepod *Calanus marshallae* in the Oregon coastal upwelling zone.

Bill was passionate about science, from zooplankton to fish production associated with climate change. Through his publications, he always tried to provide simple explanations for complex processes and interactions in the marine ecosystem. These publications were a result of his broad perspective, effective and hardworking style and friendly personality. Bill organized many international conferences, including sessions and workshops in PICES Annual Meetings, ASLO Meetings and Zooplankton Production Symposia co-sponsored by PICES and ICES. He particularly enjoyed talking with students and early career scientists at these conferences and provided helpful and valuable comments and suggestions. His contributions to ocean science went beyond just publications and conferences. Bill also encouraged the development of many planktonologists.

During the PICES 2012 Annual Meeting in Hiroshima, Japan, Bill organized a workshop on "*Secondary production: Measurement methodology and its application on natural zooplankton community*". At that time, he stimulated discussion among participants on the current problems and prospective activities to advance zooplankton production methodology and measurements. After this workshop, he encouraged his colleagues to establish a working group on zooplankton production methodologies and measurements in international scientific organizations like SCOR, ICES and PICES. Eventually, Bill and his colleagues established the PICES Working Group 37 on *Zooplankton Production Methodologies, Applications and Measurements in PICES Regions* in 2016. Unfortunately, Bill could not attend the workshops and business meetings of this working group, but his encouragements were very helpful and valuable for this working group.

The scientific community is proud of Bill and his many contributions to zooplankton production ecology. Bill, in turn, was blessed by true passion and interests throughout his long and productive life. His scientific legacy and influence will live on for many years. He will be sorely missed by his many friends and colleagues in the PICES community.

William Thornton Peterson

1942–2017

Executive summary

The Working Group on *Zooplankton Production Methodologies, Applications and Measurements in PICES Regions* (WG 37) was established in November 2016 at the PICES 2016 Annual Meeting in San Diego, USA. The objectives of WG 37 were to: 1) summarize assumptions, limitations and recent progress of existing methodologies to measure zooplankton production and 2) identify the methods which were routinely applicable to natural zooplankton populations and communities across a wide range of phyla and trophic levels. The final goal was to provide zooplankton production measurements useful for the quantitative assessment of marine ecosystem function. To achieve this goal, the WG implemented the following terms of references:

1. Summarize assumptions, recent advances and limitations of both traditional and biochemical methodologies for measuring zooplankton production of natural populations and communities.
2. Produce recommendations and procedures for both traditional and biochemical zooplankton production rate measurement methodologies and make them available on a website for worldwide access.
3. Apply practical models for estimating zooplankton production from time-series observations.
4. Develop an interactive website for exchange of information on zooplankton production measurements for regional and/or global mapping.
5. Build a network of scientists and laboratories measuring zooplankton production among PICES member nations.
6. Promote international collaborations among zooplankton production researchers with other international organizations or programs.

With respect to the first and second terms of reference (ToR), the WG published two review papers summarizing assumptions, recent advances and limitations of traditional and biochemical methodologies, providing recommendations and detailing each procedure. For the third ToR, the WG suggested that the physiological model was a widely applicable method for estimating zooplankton production rates using zooplankton biomass time-series and provided several regional examples. To achieve the fourth ToR, we worked on data sets to exchange zooplankton production measurements on the PICES website. As an alternative approach, data sets for zooplankton production estimates used in this final report were uploaded at figshare (https://figshare.com/). In terms of the fifth and sixth ToRs, the WG organized four workshops, one session and two practical workshops, each of which contributed toward building collaborations among and a network of zooplankton production researchers, in particular for early career scientists including students.

Finally, this report provides recommendations for measuring zooplankton production rates; an outline of the advantages/disadvantages and limitations among the various methodologies; criteria with which to choose the method most suited to specific study objectives and goals; and finally, to stimulate a greater number of production rate measurements which will expand the current taxonomic and spatio-temporal coverage.

In terms of future perspectives, WG 37 arrived at several suggestions:

1) Improve sensitivity analysis by establishing regional-scale empirical models based on both environmental and zooplankton parameters;

2) Further investigate application of the physiological model, which is the only applicable method across crustacean and non-crustacean taxonomic groups and retrospectively applicable to long-term zooplankton time-series and data sets; and

3) Compare and inter-calibrate production rate estimates among methods.

1 Introduction

Toru Kobari[1] and Akash Sastri[2]

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[2] Fisheries and Oceans Canada, Institute of Ocean Sciences, Sidney, Canada

1.1 Background

Zooplankton communities occupy a central position in the flow of matter and energy passing from primary producers to higher trophic levels in marine ecosystems (Lalli and Parsons, 1993). Over the past two decades, an increasing emphasis on quantitative assessments of marine ecosystem function has been focused on improving our understanding of how marine ecosystems respond to global climate change (*e.g.*, Walther *et al.*, 2002; Edwards and Richardson, 2004; Boyce *et al.*, 2010). Zooplankton production represents a quantitative proxy for the functional response of marine ecosystems since it corresponds to the biomass yield associated with grazing at the base of marine food webs.

Zooplankton production has long been estimated using a variety of methods that either: 1) follow the development of zooplankton populations/communities over the course of several weeks or months (*e.g.*, Hirche *et al.*, 2001; Ohman and Hirche, 2001); or 2) employ *ex situ* fixed-period incubations (*e.g.*, Burkill and Kendal, 1982; Kimmerer and McKinnon, 1987; Berggreen *et al.*, 1988; Peterson *et al.*, 1991). Incubation-based techniques with simultaneous sampling of natural communities are the most widely used methods in the field. In 2000, Runge and Roff (2000) reviewed the field application of the contemporary methods in a chapter of the ICES Zooplankton Methodology Manual (Harris *et al.*, 2000). However, shortly after its publication, a number of significant issues associated with incubation-based methods emerged. These issues have demanded revision of the application and interpretation of these approaches and their derived production estimates (Hirst and McKinnon, 2001; Hirst *et al.*, 2005; Kimmerer *et al.*, 2007). Meanwhile, advances in biochemical tools for measuring zooplankton growth and production rates, not covered by Runge and Roff (2000), were also developed (Oosterhuis *et al.*, 2000; Sastri and Roff, 2000; Wagner *et al.*, 2001; Yebra and Hernández-León, 2004) and have since been applied across a wide range of organisms and habitats (*e.g.*, Yebra *et al.*, 2004, 2009; Sastri *et al.*, 2012).

Over the past half century, phytoplankton production rates have been measured using radio-isotope (Steeman-Nielsen, 1952) and stable isotope-based approaches (Hama *et al.*, 1983). In the early 1980s, similar measurement approaches were also developed for bacterial production rates (Fuhrman and Azam, 1980). A major consequence of the long-term use of routinely applicable *in situ* methods for phytoplankton productivity is that we can now generate their spatio-temporal patterns at relatively high resolution using satellite imagery. Although efforts for standardizing methodologies for zooplankton have proven successful *i.e.*, SCOR-sponsored working groups covering related topics including harmonization of zooplankton sampling techniques (WG 3 and WG 13), biomass measurement (WG 23) and global comparisons of zooplankton time series (WG 125), the routine and universal application of a single zooplankton growth and production method has not happened because existing methods are only applicable under specified conditions and are not readily compared. Moreover, it is difficult to compare the existing production estimates because zooplankton communities span a wide range of phyla and trophic levels.

In 2012 and 2016, a workshop at the PICES Annual Meeting (Hiroshima, Japan, 2012) and a PICES-sponsored workshop at the ICES/PICES Zooplankton Production Symposium (Bergen, Norway, 2016) were convened to discuss issues surrounding the application of current methods for estimating zooplankton production. The motivation for these workshops was the recognition that there is still limited knowledge of, or confidence in, existing zooplankton production measurement methodologies relative to methods used for estimating primary and bacterial productivity. The two major conclusions emerged from the workshops:

- A need to summarize assumptions, limitations and recent progress of existing methodologies which purport to measure zooplankton production.
- A need to identify methods which are routinely applicable to natural zooplankton populations and communities across a wide range of phyla and trophic levels.

In order to resolve these significant requirements, a working group on zooplankton production methodologies and measurements was proposed during both workshops.

1.2 Rationale

Toru Kobari and Akash Sastri

It was particularly timely to focus on zooplankton production because assumptions and limitations underlying the most commonly applied methods have been reconsidered and other approaches have also been developed since the publication of the ICES Zooplankton Methodology Manual in 2000. A major consequence of these recent developments has been a general confusion about how these methods should be applied for natural zooplankton populations and communities, and how the various estimates could be compared. The IPCC report (IPCC, 2013) had reaffirmed that global warming exerts widespread impacts on natural systems; a quantitative evaluation of secondary productivity was therefore both timely and critical for understanding how marine ecosystems adapt to continued global climate change. However, there was still little information on zooplankton production as a proxy for the integrated biological response of lower trophic levels in marine food webs. Indeed, the generation of global maps of primary productivity was routine, but the ability to make similar spatial comparisons was lacking for zooplankton productivity. At that stage, a comprehensive review of zooplankton production methodologies (in the context of recent advances) would allow us to:

- Elaborate on recommendations for the standardized application of traditional and biochemical zooplankton production measurement methodologies for worldwide users and
- Develop and apply practical methods for estimating zooplankton production to existing time-series.

It was reasonable that the working group activities would be sponsored by an international scientific organization such as PICES, since similar terms of reference had been ongoing for the ICES Working

Group on Zooplankton Ecology (WGZE). A PICES Biological Oceanography Committee (BIO)-sponsored working group could promote information exchange and collaborations not only between PICES and ICES through WGZE but also among previous (*e.g.*, SCOR WG 125) and ongoing projects (*e.g.*, IGMETS and IMBeR). Also, the working group would provide opportunities for training in countries bordering the North Pacific Ocean (*e.g.*, Chinese Taipei and Mexico). For this purpose, the proposed working group would have the assembled scientific expertise from PICES member countries with support from members from ICES nations and experts from several other countries in order to fully represent the worldwide community of zooplankton researchers as well as to foster a global exchange of scientific information and discussion.

1.3 Working Group timeline

Toru Kobari and Akash Sastri

During the PICES 2012 Annual Meeting in Hiroshima, Japan, Drs. Bill Peterson and Toru Kobari convened a BIO workshop on "*Secondary production: Measurement methodology and its application on natural zooplankton community*". Participants discussed and shared the contemporary problems and future prospects on zooplankton production. Concurrently, Drs. Lidia Yebra and Kobari explored the possibility of an international collaboration focused on zooplankton production methodologies and their applications during the ICES Working Group on Zooplankton Ecology (WGZE) meetings held at Málaga, Spain in 2012 and at Reykjavik, Iceland in 2014. Through these workshop and meetings, Drs. Yebra and Kobari submitted proposals for international working groups on "Zooplankton Production Measurement Methodologies and Their Application" in 2013 and "Towards a Global Comparison of Zooplankton Production: Measurement, Methodologies and Applications" in 2015 to the Scientific Committee on Oceanic Research (SCOR). These proposals were not approved.

During the ICES/PICES 2016 Zooplankton Production Symposium in Bergen, Norway, Drs. Yebra and Kobari convened the workshop on "*ICES/PICES cooperative research initiative – Towards a global measurement of zooplankton production*". Participants discussed opportunities to foster cooperative research activities and working groups on zooplankton production among members of the PICES and ICES communities.

Following the Zooplankton Production Symposium, Drs. Akash Sastri and Kobari called on colleagues with expertise in zooplankton ecology from PICES member countries, and submitted a proposal for a Working Group on "Zooplankton Production Methodologies, Applications and Measurements in PICES Regions" to the Biological Oceanography Committee. BIO supported the proposal and recommended it to Science Board for endorsement. It was subsequently approved by Governing Council during PICES-2016.

PICES Working Group (WG 37) on *Zooplankton Production Methodologies, Applications and Measurements in PICES Regions* started its term in November 2016. The WG Co-chairs, Drs. Sastri and Kobari, convened a workshop on "*Advantages and limitations of traditional and biochemical methods of measuring zooplankton production*" during the PICES 2017 Annual Meeting held in Vladivostok, Russia. The first WG meeting was also held just after the workshop, and members discussed the terms of reference, prospective issues and a time-line for WG activities.

During the 2018 Ocean Sciences Meeting in Portland, USA, the WG Co-chairs convened a session entitled, "*Zooplankton productivity as a function of trophodynamics in marine ecosystems*". As one of the outreach activities for students and early career scientists, a Practical Workshop on "*Production methodologies and measurements for in situ zooplankton: Phase 1*" was organized by the WG Co-chairs, Drs. Koichi Ara (Nihon University) and Shinji Shimode (Yokohama National University) at the Manazuru Marine Center for Environmental Research and Education in Manazuru (Japan) prior to the PICES 2018 Annual Meeting. During the Annual Meeting, in Yokohama, Japan, the WG 37 Co-chairs convened a workshop on "*Regional evaluation of secondary production observations and application of methodology in the North Pacific*". A second WG meeting was held after the workshop and members discussed the current status on terms of references and a draft plan of WG final report.

Following the success of the Practical Workshop outreach activity, a Practical Workshop on "*Production methodologies and measurements for in situ zooplankton: Phase 2*" was convened by the WG 37 Co-chairs and members, Drs. Yebra and Karyn Suchy, and by Dr. Jennifer Jackson (Hakai Institute/POC Committee) at the Hakai Institute on Quadra Island, Canada, just before the PICES 2019 Annual Meeting. During the Annual Meeting, in Victoria, Canada, the WG Co-chairs and Dr. Yebra convened a workshop on "*PICES/ICES collaborative research initiative: Toward regional to global measurements and comparisons of zooplankton production using existing data sets*". A third WG business meeting was held after the workshop and members discussed the current status on terms of references and the WG final report.

WG 37 also supported another outreach activity, a PICES 2020 Spring School on Coastal Ocean Observatory Science with the theme "*What is the Deep Scattering Layer (DSL) in the coastal region*". This Spring School was organized and was to be convened by Drs. Naoki Yoshie (AP-NPCOOS), Toru Kobari (Co-chair of WG 37) and Gen Kume (Kagoshima University) at the Kagoshima University in southern Kyushu, Japan, in March 2020. Unfortunately, under the severe situations due to the worldwide COVID-19 pandemic, this Spring School was cancelled just two weeks before the planned start date. A fourth WG meeting was convened on-line October 1, 2020, since all PICES 2020 Annual Meeting activities were virtual. The members discussed the achievements and status of each term of reference, the WG final report, and submitted a request for an extension of WG 37 until 2021, due to disruptions caused by the pandemic. After submitting this final report, a workshop on "*Can we link zooplankton production to fisheries recruitment?*" was convened by Drs. Hui Liu (Texas A&M University), Karyn Suchy (University of British Columbia), Russ R. Hopcroft (University of Alaska) and Toru Kobari at the PICES 2021 Annual Meeting, and a final WG wrap-up meeting was convened by the Co-chairs.

WG 37 reports from the Annual Meetings and workshops noted above are provided in Appendix 5. Terms of reference are given in Appendix 1 and WG 37 members are noted in Appendix 2. Laboratories that are working on zooplankton production throughout the world are listed in Appendix 3. A comprehensive bibliography of zooplankton production in the PICES region is given in Appendix 4 and journal and PICES Press publications by WG 37 are presented in Appendix 6.

2 Principle, Assumptions and Advantages/Disadvantages

Toru Kobari[1], Akash Sastri[2], Lidia Yebra[3], Karyn Suchy[4], Russ R. Hopcroft[5] and Hui Liu[6]

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2.1 Introduction

Toru Kobari

As discussed in section 1.1, there is still limited confidence and consensus on the assumptions and advantages/disadvantages for existing zooplankton production measurement methodologies due to the recent revisions of some traditional methods, newly proposed biochemical approaches and very few comparisons of production rates estimated among methodologies. Here, we summarize principles, assumptions and advantages/disadvantages (or limitations) of the six traditional methodologies and the three most widely applied biochemical approaches.

2.2 Traditional methodologies

Toru Kobari

Kobari *et al*. (2019a) reviewed the traditional methodologies for measuring and estimating zooplankton growth rates and this review was part of our WG activities.

2.2.1 Natural cohort

Toru Kobari

The basic approach for estimating weight-specific growth rate is to identify a group of individuals belonging to the same population characterized with a clear stage structure (*i.e*., natural cohort) and to measure the weight increment over a defined period of time. The natural cohort method was first employed on copepods (Heinle, 1966). It relies on three major assumptions/requirements: 1) intermittent recruitment of traceable cohorts, 2) securing time-series samples of the target population; and 3) short sampling intervals relative to their generation times. Cohorts can be identified by temporal changes in developmental stage composition or of size distributions of body length and weight through time. Growth rates are represented by variations in biomass for the cohort observed between sampling intervals. Growth measurements by the natural cohort method are the most common among the traditional methodologies, and they have been applied to many taxonomic groups over the world oceans (Table 2.1).

Table 2.1 Application of natural cohort and modified natural cohort methods for estimating growth rate (g_{NC}) of zooplankton populations and communities. Modified from Kobari *et al*. (2019a).

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)
	Acartia omori	Fukuyama Bay, Japan	N: 0.11–0.38	Liang and Uye (1996a)
			C: 0.11–0.39	
	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 Tande (1990)
	Calanus marshallae	Bering Sea	0.10	Vidal and Smith (1986)
	Centropages abdominalis	Fukuyama Bay, Japan	N: 0.12–0.30	Liang *et al*. (1996)
			C: 0.16–0.41	
	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)
	Microsettela norvegica	Fukuyama Bay, Japan	N: 0.00–0.39	Uye *et al*. (2002)
			C: 0.02–0.18	
	Neocalanus cristatus	Bering Sea	0.05–0.06	Vidal and Smith (1986)
		Oyashio, western N 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	Uye and Sano (1998)
			C: 0.06–0.45	
	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)

Table 2.1 Continued.

Taxon	Target groups	Location	g_{NC} (day^{-1})	Source
Copepods				
	Paracalanus sp.	Kaneohe Bay, USA	0.92	Newbury and Bartholomew (1976)
		Fukuyama Bay, Japan	N: 0.06–0.19	Liang and Uye (1996b)
			C: 0.10–0.36	
	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 of Japan	0.24	Uye *et al*. (1983)
		Fukuyama Bay, Japan	N: 0.05–0.50	Liang and Uye (1996c)
			C: 0.02–0.41	
	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)
Appendicularians				
	Oikopleura dioica	Inland Sea of Japan	0.26–3.00	Uye and Ichino (1995)

C: copepodite stage. N: nauplius stage.

The most obvious advantage is, at least theoretically, a wide applicability to any group, such as particular developmental stages, populations, or entire communities. Disadvantages of the natural cohort approach include requisite identification of cohort growth progress, which is laborious and difficult (sometimes impossible), in particular for those taxonomic groups with continuous recruitment and short generation times, such as small coastal or subtropical species. It is difficult to follow developmental progress at remote oceanic sites and even for coastal sites with extensive mixing or strong advection of different water masses, even when a clear cohort structure is apparent. Also, microscopic identification is time-consuming and requires extensive expertise.

Despite the disadvantages mentioned above, the natural cohort method has been successfully applied to small species with short generation times (*e.g*., Landry, 1978; Liang *et al*., 1996; Liang and Uye 1996a, b, 1997; Uye *et al*., 2002) or continuous recruitment (*e.g*., Jerling and Wooldridge 1991; Webber and Roff, 1995) or even at remote oceanic sites (*e.g*., Miller *et al*., 1984; Hirche *et al*., 2001). Each of these studies overcome challenges identifying clear cohort structure by sampling frequently enough relative to short development or generation times. Another solution for estimating development time is to compare the development or generation times for the cohorts evaluated in the time-series to those derived from laboratory incubations, generating a modified natural cohort method (*e.g*., Uye 1982; McLaren *et al*., 1989; Uye and Sano, 1998). On the other hand, the natural cohort method can be applied at sites affected by the mixing of water masses or by strong advection, by following populations or communities using tracers for the constituent water masses (*e.g*., Kobari *et al*., 2010).

2.2.2 Artificial cohort

Toru Kobari, Russell R. Hopcroft and Hui Liu

The artificial cohort method is applicable to most mesozooplankton taxonomic groups. This method was first employed for *Acartia fancetti* (formerly *Acartia tranteri*) in Westernport Bay, Australia (Kimmerer and McKinnon, 1987). Artificial cohorts are composed of target size ranges (*i.e.*, developmental stages) and are created by selective sieving and then incubating during a defined period of time. Growth rates are estimated by differences in biomass measured between the beginning and the end of the incubation. This method relies on two major underlying assumptions: 1) the artificially created cohort includes only target development stages and; 2) it reflects natural development and mortality rates. The artificial cohort method has been applied to diverse taxonomic groups throughout the world oceans as well as in the laboratory (Table 2.2).

Table 2.2 Application of the artificial cohort method for estimating growth rate (g_{AC}) of zooplankton populations and communities. Modified from Kobari *et al*. (2019a).

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: –0.09–0.31 N: –0.07–0.20	Campbell *et al*. (2001)
		North Atlantic	–0.07–0.22	Yebra *et al*. (2006b)
	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		
	Paracalanus aculeatus			
	Paracalanus parvus	Skagerrak, North Sea	0.16–0.48	Peterson *et al*. (1991)

Table 2.2 Continued.

Taxon	Target groups	Location	g_{AC} (day^{-1})	Source
Copepods				
	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*. (2018)
	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	McKinnon and Duggan (2003)
			N: 0.43	
		Great Barrier Reef, Australia	C: 0.12–0.53	McKinnon *et al*. (2005)
Mixed cyclopoid guild				
		Indian Ocean	C: 0.28	McKinnon and Duggan (2003)
			N: 0.38	
		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	

C: copepodite stage. N: nauplius stage.

The artificial cohort method can be applied to various groups of mesozooplankton, such as specific developmental stages or size groups, populations and communities. Another advantage is that it is applicable to animals with continuous recruitment, short generation times or without metamorphosis. Growth measurements can be estimated for several species or groups at the same time in a common incubation. Disadvantages are the need for incubations, and that identification of target groups among the animals incubated is laborious and difficult, in particular for small individuals. At each of the many procedural steps, special care is required in collection, handling and incubation because growth of target animals incubated should be representative of those in the field.

Despite the complicated procedures and the time-consuming microscopic identifications, the artificial cohort method is the most applied for growth measurements among the incubation techniques. However, without sufficient care with the procedures, critical assumptions may not be met. For example, some animals from outside of the target group may leak into the artificial cohort (Kimmerer *et* *al*., 2007; Kobari, 2010). Despite large numbers (*e.g*., more than 50 individuals: Kimmerer *et al*., 2007) of incubating animals required to secure growth during relative short incubation period, it can be difficult to determine a suitable density of the target animals at the beginning of the incubation. Some crustaceans and gelatinous forms are fragile and inhibited in their development (or die) due to handling damage. The estimated growth of the target animals can fluctuate strongly due to the poor reproducibility of the experiments. Also, as Kimmerer *et al*. (2007) mention, potential errors (both under- and overestimation) can arise from incorrect assumptions about growth connected with the shifts of age-within-stage for the incubated animals. While tradeoffs are often required between optimal measurements and the logistics of obtaining them, some recommendations are provided for the artificial cohort method, including: 1) use direct measurements on biomass for the target animals; 2) choose incubation periods about equal to the anticipated stage duration times; and 3) seek constant growth in the incubation by minimizing food limitation (*e.g*., reduced incubation time and increased volume of the incubation).

2.2.3 Molting rate

Toru Kobari

The molting rate method can be applied for crustaceans, the predominant group in mesozooplankton communities throughout the world oceans. This method was proposed by Burkill and Kendall (1982) who first employed it for the copepod, *Eurytemora affinis*, in the Bristol Channel. They incubated sorted batches *E. affinis*, all at the same developmental stage, during defined periods and measured the fraction (MR) of numbers of newly molted into the next stage to those of individually sorted stages. Since the reciprocal of MR is equivalent to stage duration, growth rate can be determined as the difference of body mass between the two stages divided by MR. This method relies on three major requirements: 1) molting comparable to the habitat (*i.e*., no sampling and bottle effect); 2) steady-state molting and weight 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 molting rate method have been conducted for copepods and euphausiids (Table 2.3).

The main advantage of the molting rate method is its simple experimental design and procedures. Materials required are common and not expensive. The molting rate method is applicable to continuously reproducing populations. As disadvantages, the molting rate method is based on sorted samples of specific stages and applicable only to crustaceans. Microscopic identification of developmental stages for incubating animals might be difficult with ship motion, in particular for small crustaceans. Moreover, identifying and sorting large numbers of animals for incubation is required since growth during relative short incubation period is needed for the sampling variability of proportions molted.

Table 2.3 Application of the molting rate method for estimating growth rate (g_{MR}) of zooplankton populations and communities. Modified from Kobari *et al*. (2019a).

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, S. 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*. (2018)
	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	–0.03–0.13	Shaw *et al*. (2010)
		Gulf of Alaska, Eastern North Pacific	0.00–0.01	Pinchuk and Hopcroft (2007)
	Thysanoessa inermis		–0.00–0.02	
	Thysanoessa spinifera		–0.00–0.03	

C: copepodite stage. N: nauplius stage.

The duration of incubations (t) must be shorter than the stage duration (D) of the target crustaceans (*i.e.*, $t < D$) in order to estimate the proportions molting for MR. While crustacean molting is likely independent of food, molting rate would be overestimated with this method under molting burst during nighttime (Miller *et al*., 1984). For large crustacean swimmers like euphausiids and amphipods, incubation bottles should be enlarged or density of incubating individuals decreased due to bottle effects on molting and to ensure enough food for physiological requirements and growth. As with the artificial cohort method, relatively large numbers of animals are required for incubation due to the sampling variability of age-within-stages. However, this might be a trade-off as food limitation on their growth might be apparent with high incubation densities. Note that Hirst *et al*. (2005, 2014) have suggested potential errors (both under- and overestimation) underlying the molting rate method by steady-state assumptions on stage duration and weight increment between two consecutive stages, as well as a normal distribution of age-within-stage for field collected individuals. Such errors are particularly inflated for some stages when the following stage has a different rate of body mass increment or is not actively molting, such as mature or dormant copepods. These errors can be minimized with the new equations in which body mass and stage duration are corrected with and without mortality (Hirst *et al*., 2005, 2014), while additional measurements and computations are necessary. Direct measurement of body mass at the beginning and end of the incubations also minimizes these errors.

2.2.4 Egg production

Toru Kobari

Some traditional methodologies are not applicable to adult males and females with no or very low increment of somatic growth; however, the egg production method can be applied to adult females producing eggs. It was first employed for *Acartia tonsa* in laboratory experiments (Runge, 1985). Adult females of the target species are incubated, usually for 24 hours, 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 requirements: 1) the body mass of an incubated female is steady-state; and 2) the eggs are produced with the ingested materials (rather than stored lipid). In the last four decades, the egg production method has been the most widely used to measure copepod growth rates (>85% of the copepod growth data compiled by Hirst *et al*. (2003) were from egg production experiments) (Table 2.4).

The obvious advantage of this method is that it measures production of mature life stages for which most growth is focused on reproduction. The egg production method is employed by many researchers due to the simple experimental design, minimal handling and commonly available materials. Since reproductively mature animals are generally the largest among the life stages, they are easier to identify to development stage and/or species at the beginning of the incubation. Among the contemporary methods, the mass produced over time is visible only for the egg production method. The main disadvantage is that is only applicable to reproducing adult females. Also, adult production is not equivalent to the juvenile somatic growth determined by the previous methods (Hirst and McKinnon, 2001).

Table 2.4 Application of the egg production method for estimating growth rate (g_{EP}) of zooplankton populations and communities. Modified from Kobari *et al*. (2019a).

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	–0.13–0.45	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 of Japan	~0.09	Uye and Murase (1997)
	Centropages typicus	Skagerrak, North Sea	0.15–0.32	Peterson *et al*. (1991)
		Inland Sea of 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 of 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 of 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)

For broadcasting females, released eggs should be separated from their mothers using mesh placed above the bottom of the incubation chamber due to potential cannibalism of eggs (Ohman and Hirche, 2001). While body mass of incubated adult females should be steady-state, there has been increasing information in the last two decades that this assumption might be insufficient, since accumulated lipids are 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 on the egg production method (Hirst and McKinnon, 2001), potential errors (both under- and overestimation) affect the estimates with the egg production method: steady-state assumption about female mass, in particular for mesozooplankton accumulating lipids. Whereas we have no practical solution for this problem, growth rate measurements with the egg production method would be still applicable for species in which female mass undergoes minimal change during the adult stage.

2.2.5 Models

Toru Kobari

Empirical models have been developed through synthesis of species- or group-specific field estimates of growth rates. These models are applicable to various mesozooplankton taxonomic groups in different regions of the ocean. There are currently several available empirical models, including the temperature-dependent model (Huntley and Lopez, 1992), temperature and body mass dependent models (Hirst and Sheader, 1997; Hirst and Lampitt, 1998; Hirst and Bunker, 2003), annual P/B ratio model (Banse and Mosher, 1980) and the physiological model (Ikeda and Motoda, 1978). Each model requires some information about the target animals *(i.e.*, individual body size, spawning type, *etc*.) and/or their environments (*i.e.*, temperature, phytoplankton biomass), and therefore assume that growth rates are determined by ambient conditions interacting with the biological processes of the target organisms.

No routine sampling or incubations are required, as these models compute instantaneous growth rates from measured biological and physical variables. The models have a wide applicability to various groups from specific stages or species (*i.e.*, population) to communities, and are applied to environments with little growth information on the target animals. Among the disadvantages, the growth estimates involve uncertainty specific to the models. Therefore, the outcomes estimated with the models are usually different from those directly measured by field observations and those typically based on incubations. Applicability is dependent on the data sets used in the development of the model. Since many models rely on the data sets derived from coastal sites and laboratory experiments, applications of models to pelagic sites are relatively few compared with those to coastal sites (Tables 2.5 to 2.8). In the last three decades, growth measurements by these models have been accumulated for various populations, taxonomic groups and zooplankton-community guilds.

Table 2.5 Application of temperature dependent model for estimating growth rate (g_T) of zooplankton population and community. Modified from Kobari *et al.* (2019a).

Taxon	Target groups	Location	g_T(day^{-1})	Source
Copepods				
	Calanus marshallae	Oregon coast, USA	0.01–0.22	Peterson *et al.* (2002)
	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	
Mixed zooplankton guild				
		Arabian Sea	0.41–1.24	Roman *et al.* (2000)

Table 2.6 Application of the temperature and body mass dependent model for estimating growth rate (g_{TW}) of zooplankton populations and communities. Modified from Kobari *et al.* (2019a).

Taxon	Target groups	Location	g_{TW}(day^{-1})	Source
Copepods				
	Calanus chilensis	Mejillones Peninsula, Chile	0.04–0.11	Escribano *et al.* (2001)
	Calanus helgolandicus	English Channel	0.08–0.18	Yebra *et al.* (2005)
	Calanus marshallae	Oregon coast, USA	0.01–0.22	Peterson *et al.* (2002)
	Clausocalanus furcatus	Santos estuary, Brazil	0.15–0.18	Miyashita *et al.* (2009)
	Corycaeus spp.	Santos estuary, Brazil	0.26–0.29	Miyashita *et al.* (2009)
	Ctenocalanus spp.		0.14–0.16	
	Euchaeta marina	Santos estuary, Brazil	0.09	Miyashita *et al.* (2009)
	Microsetella spp.	Santos estuary, Brazil	0.53–0.58	Miyashita *et al.* (2009)
	Monothula subtilis		0.29–0.31	
	Neocalanus cristatus	Oyashio, Western North Pacific	0.01–0.10	Kobari *et al.* (2003)
	Neocalanus flemingeri		0.01–0.11	
	Neocalanus plumchrus		0.02–0.13	
	Oithona nana	Santos estuary, Brazil	0.37–0.41	Miyashita *et al.* (2009)
	Oithona plumifera	Cananéia Lagoon estuary, Brazil	0.24–0.25	Ara (2004)
	Oithona spp.	Santos estuary, Brazil	0.54–0.56	Miyashita *et al.* (2009)
	Oncaea venusta	Santos estuary, Brazil	0.18–0.20	Miyashita *et al.* (2009)
	Oncaea waldemari		0.25–0.26	
	Oncaea spp.	Santos estuary, Brazil	0.34–0.37	Miyashita *et al.* (2009)
	Subeucalanus pileatu	Santos estuary, Brazil	0.08–0.09	Miyashita *et al.* (2009)
	Temora stylifera	Santos estuary, Brazil	0.14–0.17	Miyashita *et al.* (2009)
	Temora turbinata		0.15–0.16	
	Mixed copepod guild	Santos estuary, Brazil	0.22–0.50	Miyashita *et al.* (2009)
	Mixed copepod guild	Southern Benguela	0.04–0.10	Huggett *et al.* (2009)
Mixed zooplankton guild				
		ALOHA, subtropical North Pacific	0.02–0.17	Roman *et al.* (2002)
		Arabian Sea	0.05–0.64	Roman *et al.* (2000)
		BATS, subtropical North Atlantic	0.02–0.15	Roman *et al.* (2002)

Table 2.7 Application of the annual P:B ratio model for estimating growth rate (g_{PB}) of zooplankton populations and communities. Modified from Kobari *et al*. (2019a).

Taxon	Target groups	Location	g_{PB} (day^{-1})	Source
Copepods				
	Eucalanus bungii	Oyashio, Western North Pacific	0.02	Ikeda *et al*. (2008)
	Heterorhabdus tanneri		0.02	
	Metridia okhotensis	Oyashio, Western North Pacific	0.02	Ikeda *et al*. (2008)
	Paraeuchaeta birostrata	Oyashio, Western North Pacific	0.01	Ikeda *et al*. (2008)
	Paraeuchaeta elongata		0.01	
	Paraeuchaeta rubra		0.01	
	Pleuromamma scutullata		0.02	
Chaetognaths				
	Eukrohnia bathypelagica	Oyashio, Western North Pacific	0.01	Ikeda *et al*. (2008)
	Eukrohnia hamata		0.01	
	Sagitta elegans		0.01	

Table 2.8 Application of the physiological model for estimating growth rate (g_P) of zooplankton populations and communities. Modified from Kobari *et al*. (2019a).

Taxon	Target groups	Location	g_P (day^{-1})	Source
Copepods				
	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 zooplankton guild				
		Kuroshio, East China Sea	0.15–0.29	Kobari *et al*. (2018)

2.3 Biochemical approaches

Toru Kobari, Akash Sastri and Lidia Yebra

Yebra *et al*. (2017) reviewed the biochemical approaches in use to estimate zooplankton growth rates and this review was part of our WG activities.

2.3.1 Nucleic acids

Toru Kobari and Lidia Yebra

Protein synthesis is a complex process involving multiple steps: translation, transcription, aminoacylation, co-translational transport and post-translational modification. The cellular contents of RNA relative to those of DNA or protein vary with cellular activity and/or protein synthesis. Thus, variability of nucleic acids within an individual can be theoretically representative of somatic growth. Several indices of zooplankton growth have been developed using nucleic acids such as concentration of DNA or RNA (*e.g.*, Sutcliffe 1965; Dagg and Littlepage, 1972; Ota and Landry, 1984), and ratios of RNA:DNA and RNA:protein ratios (*e.g.*, Ota and Landry, 1984; McKee and Knowles, 1987; Wagner *et al.*, 2001, among others).

These physiological functions are common to the entire zooplankton community, thus broadly applicable. Also, the assay of nucleic acids is simple and rapid as it does not require incubations, thereby allowing processing of several samples at once even in small organisms (Wagner *et al.*, 1998; Berdalet *et al.*, 2005a, b). However, the nucleic acid concentrations and ratios within an individual are species-specific or even stage-specific and cannot be applied to mixed populations (*e.g.*, Ikeda *et al.*, 2007; Yebra *et al.*, 2011; Kobari *et al.*, 2017).

2.3.2 Chitobiase activity

Akash Sastri and Karyn Suchy

Chitobiase is a chitinolytic enzyme produced by crustaceans (all arthropods) as part of the moult cycle (see Roff *et al.*, 1994). All crustacean zooplankton shed their chitinous exoskeleton on a periodic basis to accommodate growth and/or significant developmental change. Chitobiase in particular, is secreted by epidermal vesicles and catalyzes the breakdown and recycling of chitin from the old to new exoskeleton. The activity of chitobiase in homogenates has been used as an index of moulting rate (Espie and Roff, 1995). Whereas, the activity of the enzyme liberated into the water with shedding of the exoskeleton has been found to vary with body size and the increment of growth for a variety of crustacean zooplankton groups (Vrba and Machacek, 1994; Oosterhuis *et al.*, 2000; Sastri and Roff, 2000; Sastri and Dower, 2009; Sastri *et al.*, 2013). This "liberated" enzyme activity has been used to estimate community-level developmental and biomass production rates by several laboratory and field studies (*e.g.*, Oosterhuis *et al.*, 2000; Sastri and Roff, 2000; Sastri and Dower, 2009; Suchy *et al.*, 2016a). A key advantage of this approach is that it relies on a single, broadly applicable, body-size dependent relationship between chitobiase activity and growth increment for multiple groups (*i.e.*, copepods, decapod larvae, mysids, krill, *etc*.). Thus, estimates of the rate of enzyme production in the water column can be made directly: 1) without the need to "calibrate" for each species/group; 2) does not rely on the contents and variability associated with net casts; and 3) can be used in a manner analogous to radiocarbon uptake approaches for primary production rate and therefore used to directly measure phytoplankton to zooplankton transfer efficiency (see Suchy *et al.*, 2016b).

2.3.3 Aminoacyl tRNA synthetases activity

Lidia Yebra and Toru Kobari

Somatic growth is defined as the increase in biomass, mostly protein content of organisms. As mentioned before, protein synthesis is a complex process in which the first step is the amino acid activation and the aminoacylation of tRNA, *i.e.*, the union of amino acids to the tRNA (Schimmel and Soll, 1979). Aminoacylation is a universal process in cells, from bacteria to humans, that is catalyzed by the enzymes aminoacyl-tRNA synthetases (AARS). AARS activity is related to protein synthesis rates and therefore, their activity has been correlated to growth in several zooplankton taxa including copepods, cladocerans, euphausiids and fish larvae (see Yebra *et al*., 2017).

The AARS method does not require incubations; it is a simple, quick and non-radioactive assay (Yebra and Hernández-Léon, 2004). Contrary to traditional enzymatic assays, substrates are not added, providing an *in situ* approach to growth estimation, rather than the *in vitro* maximum potential activity of the enzymes. Given the universality of aminoacylation, the assay is broadly applicable across the zooplankton spectrum once it is calibrated for the targeted group. Also, as it can be combined with other biochemical analyses, it allows for the assessment of multiple variables from a single sample (*e.g*., Yebra *et al*., 2004) and facilitates the comparison among different methodologies (*e.g*., Yebra *et al*., 2005).

3 Zooplankton Production Measurements in Regional Seas[1]

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3.1 Japanese studies

Toru Kobari

There exist multiple studies that investigate mesozooplankton productivity in Japanese waters (see Table 3.1). Mesozooplankton productivity measurements have been extensively conducted in the coastal waters (*e.g.*, Uye, 1982; Uye *et al.*, 1983; Ara and Hiroumi, 2007), while some reports were found at the open ocean, like the Oyashio (*e.g.*, Kobari *et al.*, 2003; Ikeda *et al.*, 2008), North Pacific (NP) Region 19 (*e.g.*, Iguchi and Ikeda 1999; Ikeda *et al.*, 2002) and the Kuroshio (*e.g.*, Nakata, 1990; Kobari *et al.*, 2018). The extensive number of measurements at coastal sites arises from easy accessibility and opportunity for high sampling frequency.

Productivity measurements were mostly performed on copepod populations (*e.g.*, Huang *et al.*, 1993; Liang *et al.*, 1994) and community guilds (*e.g.*, Uye and Shimazu, 1997; Uye *et al.*, 1998; Kobari *et al.*, 2018, 2019b), in contrast with other zooplankton groups like appendicularians (*e.g.*, Uye and Ichino, 1995; Tomita *et al.*, 1999) and amphipods (*e.g.*, Ikeda and Shiga, 1999; Yamada and Ikeda, 2006). These measurements were mostly based on the traditional methodologies like the natural cohort method, including the modified natural cohort method (*e.g.*, Liang and Uye, 1996a,b,c, 1997), molting rate method (*e.g.*, Kobari *et al.*, 2010), egg production method (*e.g.*, Uye and Murase 1997; Yamaguchi *et al.*, 2010), physiological model (*e.g.*, Ikeda and Motoda 1978; Yamaguchi *et al.*, 2017; Kobari *et al.*, 2018) and empirical models (*e.g.*, Ara and Hiroumi 2009; Nakajima *et al.*, 2017). In recent years, biochemical approaches like nucleic acid ratios (*e.g.*, Nakata *et al.*, 1994; Ikeda *et al.*, 2007; Kobari *et al.*, 2013, 2017) and minoacyl tRNA synthetases activity (*e.g.*, Kobari *et al.*, 2018, 2019b) have been applied to copepod populations or mesozooplankton guilds.

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[1] The use of numbered biogeographic regions in the PICES Convention Area used in the following sections follows the terminology for numbered areas named in accordance with Decision 2016/s/11(vii) adopted by PICES Governing Council. A map showing the biogeographical regions can be found at https://meetings.pices.int/publications/special-publications/NPESR/2021/index.

For the Inland Sea of Japan, production rate estimates were conducted for predominant copepod species using the modified natural cohort method based on high-frequency sampling in the embayment (*e.g.*, Liang and Uye, 1996a,b,c, 1997). Production rates were estimated by multiplying the stage-specific growth rates measured from laboratory incubations by stage-specific biomass. The production rates were greatly variable among the seasons, measuring 27.8 mgC m^{-3} day^{-1} for egg-broadcasting *Paracalanus* sp. (Liang and Uye, 1996b) and up to 2.5 mgC m^{-3} day^{-1} for egg-carrying *Pseudodiaptomus marinus* (Liang and Uye, 1997), which commonly appeared in the coastal waters, and 10.9 mgC m^{-3} day^{-1} for the numerically abundant copepod, *Oithona davisae* (Uye and Sano, 1998). Such approaches have enabled us to provide a fine temporal resolution for production rates which were variable among seasons.

In the Oyashio region, production rate estimates were conducted for some predominant species by applying empirical models to the monthly collected samples throughout the year at a single station (*e.g.*, Kobari *et al*., 2003; Ikeda *et al*., 2008). Based on the natural cohort method or empirical models, annual production rates were variable among the species: 19.3 gC m^{-2} $year^{-1}$ for *Neocalanus cristatus*, *N. flemingeri* and *N. plumchrus* (Kobari *et al*., 2003), 5.0 gC m^{-2} $year^{-1}$ for the diurnally migrating *Metridia pacifica* and *M. okhotensis* (Ikeda *et al*., 2008) and 2.1 gC m^{-2} $year^{-1}$ for carnivorous *Eukrohnia hamata* (Ikeda *et al*., 2008). These approaches have enabled production rate estimation for mesozooplankton communities in relatively remote sites.

In the Kuroshio waters, production rates were estimated for the mesozooplankton guild by applying the physiological model to samples widely collected from the various sites (*e.g.*, Ikeda and Motoda, 1978; Kobari *et al*., 2018, 2019b). Production rates were estimated by multiplying the community-based growth rates estimated from the physiological model by community biomass. The summertime production rates were not significantly different between the continental shelf waters (1.0 mgC m^{-3} day^{-1}) and the Kuroshio waters (0.7 to 1.1 mgC m^{-3} day^{-1}). Since the Kuroshio area and neighboring waters are nursery grounds for foraging fish larvae (Sassa *et al*., 2008, 2009; Sassa and Tsukamoto, 2010), such production estimates might provide important information regarding larval fish survival and recruitment.

In summary, zooplankton productivity measurements have been made extensively in Japanese waters using a variety of techniques. These measurements were mainly based on the traditional method for copepod populations or the entire mesozooplankton community. In addition, some biochemical approaches have been recently applied as alternative methodologies in order to provide fine temporal and spatial resolution. Major target groups are biased towards metazoan crustaceans (mainly copepods) and thus there is little information on the other taxonomic groups such as protozoans and gelatinous forms. Due to the applicability to wide taxonomic groups and sufficient reproducibility of quick measurements, more applications of the biochemical approaches and their comparisons to the traditional methodologies should be encouraged for integrating information on zooplankton productivity measurements.

Table 3.1 List of previous studies on direct measurements of zooplankton productivity using the traditional methodologies and biochemical approaches in Japanese waters.

Taxon	Target groups or species	Daily rate	Annual rate	Ratio	Location	Methodology used	Reference
Copepod species							
	Acartia clausi	7–66 eggs female^{-1} day^{-1}			Laboratory	Egg production	Uye (1981)
		<0.1–3.2 mgC m^{-3} day^{-1}	163 mgC m^{-3} year^{-1}		Inland Sea of Japan	Modified natural cohort	Uye (1982)
		6–32 eggs female^{-1} day^{-1}				Egg production	
	Acartica erythraea	13 eggs female^{-1} day^{-1}			Inland Sea of Japan	Egg production	Checkley *et al.* (1992)
	Acrtia omorii	~36.8 mgC m^{-3} day^{-1}				Modified natural cohort	Liang and Uye (1996b)
	Acartica pacifia	9 eggs female^{-1} day^{-1}			Inland Sea of Japan	Egg production	Checkley *et al.* (1992)
	Acartica steueri	2–55 eggs female^{-1} day^{-1}			Laboratory	Egg production	Uye (1981)
	Calanus sinicus	0.1–1.3 day^{-1}			Laboratory	Incubation	Uye (1988)
		~4.2 mgC m^{-3} day^{-1}	31–358 mgC m^{-3} year^{-1}		Inland Sea of Japan	Natural cohort	Huang *et al.* (1993)
		1–72 eggs female^{-1} day^{-1}				Egg production	Uye and Murase (1997)
		<0.01–0.14 day^{-1}					
	Centropages abdominalis	1–142 eggs female^{-1} day^{-1}				Egg production	Liang *et al.* (1994)
		0.2–0.7 day^{-1}				Egg production	Liang *et al.* (1994)
		~12.4 mgC m^{-3} day^{-1}				Modified natural cohort	Liang and Uye (1996a)
	Eucalanus bungii	0.04 day^{-1}			Oyashio	Molting rate	Kobari *et al.* (2010)
		0–47 eggs female^{-1} day^{-1}				Egg Production, Starvation tolerance	Takahashi and Ide (2011)
				0.8–9.2		Nucleic acid ratio (RNA:DNA)	Kobari *et al.* (2013)
	Metridia pacifica	<0.01–0.02 mgC m^{-3} day^{-1}	0.97 mgC m^{-3} year^{-1}		Toyama Bay	Natural cohort	Ikeda *et al.* (2002)
	Microsetella norvegica	0–4.9 mgC m^{-3} day^{-1}			Inland Sea of Japan	Modified natural cohort	Uye *et al.* (2002)
	Neocalanus cristatus	0.2–203.0 mgC m^{-2} day^{-1}	12 gC m^{-2} year^{-1}		Oyashio	Natural cohort	Kobari *et al.* (2003)
				1.3–2.6		Nucleic acid ratio (RNA:DNA)	Ikeda *et al.* (2007)
		0.06 day^{-1}				Molting rate	Kobari *et al.* (2010)
				0.4–6.8		Nucleic acid ratio (RNA:DNA)	Kobari *et al.* (2013)

Table 3.1 Continued.

Taxon	Target groups or species	Daily rate	Annual rate	Ratio	Location	Methodology used	Reference
Copepod species							
	Neocalanus plumchrus	0–139.6 mgC m^{-2} day^{-1}	6 gC m^{-2} $year^{-1}$			Natural cohort	Kobari *et al.* (2003)
				1.3–4.0		Nucleic acid ratio (RNA:DNA)	Ikeda *et al.* (2007)
		0.03–0.10 day^{-1}				Molting rate	Kobari *et al.* (2010)
	Neocalanus flemingeri	0–28.2 mgC m^{-2} day^{-1}	2 gC m^{-2} $year^{-1}$			Natural cohort	Kobari *et al.* (2003)
				1.2–4.6		Nucleic acid ratio (RNA:DNA)	Ikeda *et al.* (2007)
		0.02–0.03 day^{-1}				Molting rate	Kobari *et al.* (2010)
				0.8–11.9		Nucleic acid ratio (RNA:DNA)	Kobari *et al.* (2013)
	Oithona davisae	<1–10 eggs $female^{-1}$ day^{-1}			Inland Sea of Japan	Egg production	Uye and Sano (1995)
		<0.1–0.5 day^{-1}				Egg production	
		~10.9 mgC m^{-3} day^{-1}	650 mgC m^{-3} $year^{-1}$			Modified natural cohort	Uye and Sano (1998)
	Paracalanus sp.			0.5–3.8	Kuroshio	Nucleic acid ratio	Nakata (1990)
		4–67 eggs $female^{-1}$ day^{-1}			Inland Sea of Japan	Egg production	Uye and Shibuno (1992)
		<0.1–0.5 day^{-1}					
		1–7 eggs $female^{-1}$ day^{-1}		3.9–7.3	Kuroshio	Nucleic acid ratio (RNA:DNA)	Nakata *et al.* (1994)
		~27.8 mgC m^{-3} day^{-1}	734 mgC m^{-3} $year^{-1}$		Inland Sea of Japan	Modified natural cohort	Liang and Uye (1996b)
	Pseudodiaptomus marinus	<0.1–0.5 mgC m^{-3} day^{-1}	21 mgC m^{-3} $year^{-1}$			Modified natural cohort	Uye *et al.* (1983)
		~2.5 mgC m^{-3} day^{-1}	51 mgC m^{-3} $year^{-1}$			Modified natural cohort	Liang and Uye (1997)
		2–14 eggs $female^{-1}$ day^{-1}				Egg production	Liang and Uye (1997)
		<0.1–0.2 day^{-1}				Egg production	
	Sinocalanus tenellus	0.1–1.1 day^{-1}			Laboratory	Incubation	Kimoto *et al.* (1986)

Table 3.1 Continued.

Taxon	Target groups or species	Daily rate	Annual rate	Ratio	Location	Methodology used	Reference
Other mesozooplankton							
	Aurelia aurita	0.05–0.08 day^{-1}			Inland Sea of Japan	Natural cohort	Uye and Shimauchi (2005)
	Boreomysis californica	141 mgDM m^{-2} year^{-1}			Oyashio	Natural cohort	Chikugo *et al.* (2013)
	Cyphocaris challengeri	<0.1–1.3 mgC m^{-2} day^{-1}	164 mgC m^{-2} year^{-1}			Natural cohort	Yamada and Ikeda (2006)
	Eucopia australis		192 mgDM m^{-2} year^{-1}			Natural cohort	Chikugo *et al.* (2013)
	Euphausia pacifica	0–0.17 mgC m^{-3} day^{-1}	8.2 mgC m^{-3} year^{-1}		Toyama Bay	Natural cohort	Iguchi and Ikeda (1999)
	Hymenodora frontalis	124 mgDM m^{-2} year^{-1}			Oyashio	Natural cohort	Chikugo *et al.* (2013)
	Meterythrops microphtalma	17 mgDM m^{-2} year^{-1}				Natural cohort	
	Oikopleura dioica	<0.1–22.1 mgC m^{-3} day^{-1}	953 mgC m^{-3} year^{-1}		Inland Sea of Japan	Modified natural cohort	Uye and Ichino (1995)
	Oikopleura longicauda	<0.1–103 mgC m^{-2} day^{-1}	4.5 gC m^{-2} year^{-1}			Natural cohort	Tomita *et al.* (1999)
	Oikopleura longicauda house	0.1–266 mgC m^{-2} day^{-1}	11.3 gC m^{-2} year^{-1}			Natural cohort	
	Parasagitta elegans	0.03–0.29 mm day^{-1}			Oyashio	Natural cohort	Kotori (1999)
	Primno abyssalis	<0.1–0.2 mgC m^{-2} day^{-1}	37 mgC m^{-2} year^{-1}			Natural cohort	Yamada and Ikeda (2006)
	Themisto japonica	<0.01–0.03 mgC m^{-3} day^{-1}	0.97 mgC m^{-3} year^{-1}		Toyama Bay	Natural cohort	Ikeda and Shiga (1999)
		0–2.6 mgC m^{-2} day^{-1}	228 mgC m^{-2} year^{-1}		Oyashio	Natural cohort	Yamada and Ikeda (2006)
	Themisto pacifica	<0.1–3.7 mgC m^{-2} day^{-1}	284 mgC m^{-2} year^{-1}			Natural cohort	

Table 3.1 Continued.

Taxon	Target groups or species	Daily rate	Annual rate	Ratio	Location	Methodology used	Reference
Taxon guild							
	Heterotrophic nano-flagellates	0.4–56.6 μgC L^{-1} day^{-1}			Sagami Bay	Empirical models	Ara and Hiroumi (2009)
	Microzooplankton guild	5.5–25.6 μgC L^{-1} day^{-1}			Dokai Inlet	Empirical models	Uye *et al.* (1998)
		0.18–1.75 μgC L^{-1} day^{-1}			Ise Bay	Physiological models	Uye *et al.* (2000)
		2.6–30.3 mgC m^{-3} day^{-1}			Oyashio	Empirical models	Shinada *et al.* (2001)
		1.1–84.6 μgC L^{-1} day^{-1}			Sagami Bay	Empirical models	Ara and Hiroumi (2009)
Copepods		0.6–4.9 mgC m^{-3} day^{-1}	34 gC m^{-2} year^{-1}		Inland Sea of Japan	Physiological models	Uye *et al.* (1986)
		0.3–45.2 mgC m^{-3} day^{-1}	2.5 gC m^{-3} year^{-1}				
		2–52 mgC m^{-3} day^{-1}	7.7–17.6 mgC m^{-3} year^{-1}		Inland Sea of Japan	Physiological models	Uye *et al.* (1986)
					Inland Sea of Japan	Modified natural cohort	Uye and Liang (1998)
		0.1–1.8 μgC L^{-1} day^{-1}			Japanese coast of NP Region 19	Natural cohort	Uye *et al.* (2004)
Particle-feeding copepods		<0.1–7.4 mgC m^{-3} day^{-1}					
Carnivorous copepods		<0.1 μgC L^{-1} day^{-1}					
Particle-feeding mesozooplankton guild		~49.9 μgC L^{-1} day^{-1}			Inland Sea of Japan	Empirical models	Uye and Shimizu (1997)
		13.9–56.5 µgC L^{-1} day^{-1}			Dokai Inlet	Empirical models	Uye *et al.* (1998)
		0.27–3.21 μgC L^{-1} day^{-1}			Ise Bay	Physiological models	Uye *et al.* (2000)
		0.7–16.4 μgC L^{-1} day^{-1}			Yatsushiro Bay	Empirical models	Hayashi and Uye (2008)
			35.4 gC m^{-2} year^{-1}		Oyashio	Natural cohort, Empirical models	Ikeda *et al.* (2008)
		26–250 μgC L^{-1} day^{-1}			North Pacific	Physiological models	Yamaguchi *et al.* (2017)

Table 3.1 Continued.

Taxon	Target groups or species	Daily rate	Annual rate	Ratio	Location	Methodology used	Reference
	Carnivorous mesozooplankton guild	~13.4 mgC m^{-2} day^{-1}			North Pacific	Physiological models	Yamaguchi *et al*. (2017)
		0.5–7.3 mgC m^{-3} day^{-1}			Inland Sea of Japan	Empirical models	Uye and Shimizu (1997)
		0.09–1.79 mgC m^{-3} day^{-1}			Dokai Inlet	Empirical models	Uye *et al*. (1998)
		0.1–4.9 mgC m^{-3} day^{-1}			Ise Bay	Physiological models	Uye *et al*. (2000)
			5.7gC m^{-2} $year^{-1}$		Oyashio	Natural cohort, Empirical models	Ikeda *et al*. (2008)
	Mesozooplankton guild	10–60 mgC m^{-2} day^{-1}			Kuroshio	Physiological models	Ikeda and Motoda (1978)
		0.3–7.3 mgC m^{-3} day^{-1}			Oyashio	Empirical models	Shinada *et al*. (2001)
		0.7–1.1 mgC m^{-3} day^{-1}			Kuroshio	Physiological models	Kobari *et al*. (2018)
		0.9–2.1 μmolPPi $mgProt^{-1}$ $hour^{-1}$				AARS	
		0.1–11.4 mgC m^{-3} day^{-1}				Physiological models	Kobari *et al*. (2019b)
		0.5–11.7 μmolPPi $mgProt^{-1}$ $hour^{-1}$				AARS	

AARS: aminoacyl-tRNA synthetases

3.2 Korean studies

Hyung-Ku Kang, Min-Chul Jang, Jung-Hoon Kang and Se-Jong Ju

3.2.1 Introduction

There is limited information on secondary production of mesozooplankton, in particular copepods, in Korean waters including the southern waters of Korea, and those bordering the northern East China Sea, the Yellow Sea and NP Region 19. Secondary production of the copepods *Acartia steueri* and *Acartia omorii* in Ilkwang Bay, southeastern coast of Korea, was likely the first study in Korean waters (Kang and Kang, 2005; Kang *et al*., 2007). Recently, production of *Euchaeta plana* and *Paraeuchaeta russelli* in the southeastern sea of Korea was reported by Kim *et al*. (2018) and production of *Calanus sinicus* in the southern waters of Korea and the northern East China Sea in spring was estimated by Kang and Kim (2021). Egg production rate (EPR) was also measured or estimated in addition to secondary production estimates. EPRs were measured for *A. steueri* in Ilkwang Bay by Jung *et al*. (2004), *Acartia hongi* in the Kyeonggi Bay, Yellow Sea, by Youn and Choi (2007), *C. sinicus* on the Korean coast of the Yellow Sea during spring by Kang *et al*. (2011) and *Paracalanus parvus* on the eastern coast of the southern waters of Korea by Jang *et al*. (2013). Here, we review the published information on secondary production and, in some selected papers, on egg production of copepods in Korean waters.

3.2.2 Methods

Total production of copepods can be calculated as the sum of the EPR of adult females and somatic production of juveniles, including nauplii and copepodites, and excluding adult males (Runge and Roff, 2000). Total production rate of the copepod population was calculated as:

$$P = \Sigma\,(B_i \times g_i) + B_f \times g_f \tag{1}$$

where B_i and B_f are the biomass of juveniles and adult females, respectively; g_i is the growth rate of juveniles; and g_f is the weight-specific egg production rate (WSEPR) of adult females. For somatic production, nauplii 2 to copepodite 5 for *A. steueri* and *A. omorii* by Kang and Kang (2005) and Kang *et al*. (2007), respectively, copepodite 1 to copepodite 5 for *C. sinicus* by Kang and Kim (2021) and copepodite 4 to copepodite 5 for *E. plana* and *P. russelli* by Kim *et al*. (2018) were considered (Table 3.3).

To calculate the somatic production of copepods, it is necessary to know the growth rate of juveniles. Kang and Kang (1998b) reared *A. steueri* juveniles in the laboratory with excessive food to determine the development time of each juvenile and then calculated the stage duration of each juvenile at a given temperature. Kang and Kang (2005) measured the body weight of juveniles collected in the field and calculated the growth rate of each juvenile using the stage duration data from Kang and Kang (1998b). In addition, Kang *et al*. (2007) measured the body weight of *A. omorii* juveniles in the field using juvenile development time equations developed by Uye (1980) to calculate the stage duration of each juvenile.

Empirical growth rate equations reported in the literature have also been used to estimate production from growth rates. Kim *et al*. (2018) applied an empirical equation to estimated growth rate for egg-sac spawners *E. plana* and *P. russelli* (Hirst and Bunker, 2003) using water temperature and body weight data (Table 3.3). Kang and Kim (2021) estimated the growth rates of juveniles of *C. sinicus* from an empirical equation for broadcaster spawners (Hirst and Bunker, 2003) using water temperature, chlorophyll a (Chl-*a*) concentration and individual body weight data.

EPR was measured in terms of number of eggs female^{-1} day^{-1} in both species with the broadcast and egg-sac spawners in the field or in the laboratory (Table 3.3). WSEPR, *i.e.*, the weight of eggs day^{-1} unit female body weight^{-1}, can be calculated. In copepods with egg masses (*e.g.*, Euchaetidae), the egg ratio method (Runge and Roff, 2000) can be applied using information on the density of females, density of eggs in the field and the hatching rate of eggs. The hatching rate of eggs can be estimated indirectly using an empirical equation between the hatching rate and temperature (Hirst and Bunker, 2003). Body weight of nauplii and copepodites was estimated using the relationship of body length and weight from either literature or their own equations (*e.g.*, Kang and Kang (2005) for *A. steueri* and Youn (2004) for *A. hongi*; Table 3.3).

Table 3.3 Summary of secondary production and/or egg production rate of copepods from Korean waters with methodology used.

Species	Stage	Body weight (W, μgC)	Instantaneous growth rate of stage i (g_i, d^{-1})	Egg production rate (EPR, eggs female^{-1} d^{-1}) or weight-specific EPR (g_f, d^{-1}) of female	Reference
Acartia steueri	N2–C5	For nauplii Log $W = -4.188 + 1.451 \log TL$ For copepodites Log $W = -8.508 + 3.106 \log PL$ From Kang and Kang (1997)	$g_i = (\ln W_{i+1} - \ln W_i)/D_i$ D_i from equations of Kang and Kang (1998b); rearing experiment in the lab	$g_f = 0.00206(T - 0.5)^{1.33}$ Chl-a/(0.912 + Chl-a) From Kang and Kang (1998a)	Kang and Kang (2005)
Acartia omorii	N2–C5	For nauplii $W = TL^{2.64} \times 10^{-7.12}$ For copepodites $W = PL^{3.08} \times 10^{-8.51}$ From Liang & Uye (1996a); Uye (1982)	$g_i = (\ln W_{i+1} - \ln W_i)/D_i$ D_i from equations of Uye (1980); rearing experiment in the lab	$g_f = 0.00000828(T + 12.0)^{3.25}$ Chl-a/(0.470 + Chl-a) From Uye (1981)	Kang *et al*. (2007)
Calanus sinicus	C1–C5	Log $W = 3.378 \log PL - 9.416$ From Uye (1988)	Log10 $g_i = -0.0143[T] - 0.363[\log_{10} W] + 0.135[\log_{10}$ Chl-a] – 0.105 From Hirst and Bunker (2003)	EPR = $(N_e/N_f) \times (24/t)$ Incubation in lab (Runge and Roff, 2000)	Kang and Kim (2021)
Euchaeta plana and *Paraeuchaeta russelli*	C4–C5	Log $W = 2.45 \log PL - 6.25$ From Uye (1982)	$\log_{10} g_i = 0.0333[T] - 0.163[\log_{10} W] - 1.528$ From Hirst and Bunker (2003)	EPR = $(N_e/N_f) \times$ EH Egg ratio method (Runge and Roff 2000) $\log_e$ EH = –2.433 + 0.0877T EH from Hirst and Bunker (2003)	Kim *et al*. (2018)
Acartia steueri	Female	Log $W = -8.508 + 3.106 \log PL$ From Kang and Kang (1997)	–	EPR = $(N_e/N_f) \times (24/t)$ *In situ* incubation (Runge and Roff, 2000)	Jung *et al*. (2004)
Acartia hongi	Female	Log $DW = 3.539 \log PL - 9.585$ From Youn (2004)	–	$g_f = (W_e/W_f) \times (24/t)$ Incubation in lab (Runge and Roff, 2000)	Youn and Choi (2007)
Calanus sinicus	Female	Log $W = 3.378 \log PL - 9.416$ From Uye (1988)	–	EPR = $(N_e/N_f) \times (24/t)$ Incubation in lab (Runge and Roff, 2000)	Kang *et al*. (2011)
Paracalanus parvus	Female	$W = PL^{3.128} \times 10^{28.451}$ From Liang and Uye (1996b)	–	$g_f = (W_e/W_f) \times (24/t)$ *In situ* incubation (Runge and Roff ,2000)	Jang *et al*. (2013)

DW: dry weight (μg), TL: total length (μm), PL: prosome length (μm), W_i: body weight of stage i, W_{i+1}: body weight of stage $i + 1$, D_i: stage duration of stage i (d), T: temperature (°C), Chl-a: chlorophyll-a concentration (μg L^{-1}), EH: egg hatching rate (d^{-1}), N_e: number of eggs, N_f: number of adult females, W_e: weight of eggs produced (μgC), W_f: weight of an adult female (μgC), t: incubation time (hour), CI – CV: copepodite stage 1– copepodite stage 5

3.2.3 Results

Four studies were done on secondary production of copepods, including *A. steueri*, *A. omorii*, *C. sinicus*, *E. plana* and *P. russelli* in Korean waters (Table 3.4). For EPR, excluding the studies on the secondary production, there were also four studies of free-spawners, including *A. steueri*, *A. hongi*, *C. sinicus* and *P. parvus* (Table 3.4). The secondary production and/or EPR in Korean waters was focused mainly on the coastal waters and inner bay. Recently, production of *C. sinicus* has been studied in the offshore waters or continental shelf.

The small copepods *A. steueri* and *A. omorii*, which have a body length of ~1 mm and appear mainly in the coastal waters, showed mean daily secondary production of 69 μgC m^{-3} day^{-1} and 92 μgC m^{-3} day^{-1}, respectively. The larger copepod *C. sinicus*, which has ~2 mm body length, had a mean daily production of 1,160 μgC m^{-3} day^{-1}, which was thus higher than the values of *A. steueri* and *A. omorii*. The carnivorous copepods *E. plana* and *P. russelli* had mean daily production of 5.3 μgC m^{-3} day^{-1} and 17.8 μgC m^{-3} day^{-1}, respectively, and were lower than the production values of *A. steueri* and *A. omorii*, possibly due to lower density of the copepods.

Fecundity of different species of copepods is given in Table 3.4. The daily EPR of *C. sinicus* in the offshore waters in spring (Kang and Kim, 2021) was lower than that in coastal waters (Kang *et al*., 2011), indicating that copepod fecundity can be affected by different environments (*e.g*., food availability and water temperature) given that the same copepod species were present in both regions. The daily EPR of *A. steueri* in Ilkwang Bay estimated from the equation of WSEPR by Kang and Kang (1998a) was similar to the EPR of *A. steueri*, which was incubated in the field, indicating that the laboratory-derived equation of WSEPR might be applied to the same species in the same location. Both the daily EPR of *A. steueri* estimated from the equations or measured *in situ* in Ilkwang Bay was much lower than that of *A. omorii* in Ilkwang Bay, which was estimated from an equation of WSEPR developed by Uye (1981) in Onagawa Bay, Japan. The daily EPR of *A. hongi* in Kyeonggi Bay ranged from 0.8 to 35.0 eggs $female^{-1}$ day^{-1}, which was lower than that of *A. omorii* estimated from the equation of WSEPR by Uye (1981). The daily EPR of *P. parvus* in the coastal waters, which was measured *in situ* incubation, averaged 4 eggs $female^{-1}$ day^{-1}, similar to that of *C. sinicus* in the offshore waters, but lower than that of *Acartia*. Egg-sac spawners *E. plana* and *P. russelli* had a daily EPR ranging from 1.7 to 3.1 eggs $female^{-1}$ day^{-1}, which was the lowest compared to the broadcast spawners, including *Acartia*, *Paracalanus* and *Calanus*.

The WSEPR of *C. sinicus* in spring on the Korean coast of the Yellow Sea (*e.g*., 0.082 day^{-1}) was higher than that of the southern waters of Korea and the northern East China Sea (*e.g*., 0.023 day^{-1}) due to higher food availability in the coastal waters. The WSEPR of *A. steueri* (*e.g*., 0.047 to 0.064 day^{-1}) estimated from the equation using temperature and Chl-*a* concentration was higher than that from *in situ* incubation methods. *A. hongi* had the highest WSEPR with maximum of 0.33 day^{-1}, followed by *P. parvus* with maximum of 0.26 day^{-1}. Egg-sac spawners *E. plana* and *P. russelli* had a mean WSEPR within the range 0.038 to 0.079 day^{-1}. The WSEPR of *P. russelli* was similar to that of *C. sinicus* in the Korean coastal waters of the Yellow Sea.

Table 3.4 Summary of total production, egg production rate (EPR) and weight-specific egg production rate of copepods from Korean waters.

Species	Location	Season	Total production		Egg production rate	Weight-specific EPR	Temperature	Reference
			(mgC m^{-3} yr^{-1})	(μgC m^{-3} d^{-1})	(Eggs female^{-1} d^{-1})	(d^{-1})	(°C)	
Production								
Acartia steueri	Southeastern coast of Korea	One year	(25.1)	10–460 (69)	5.4–12.5	0.028–0.117 (0.064)	10.2–25.4	Kang and Kang (2005); Kang and Kang (1998b)
Acartia omorii	Southeastern coast of Korea	One year	(33.5)	0.03–570 (92)	22–57 (38)		10.2–25.4	Kang *et al.* (2007)
Calanus sinicus	Southern waters of Korea and the northern East China Sea	Apr.–May		20–3,670 (910)	0–14.9 (5.8)	0.003–0.044 (0.023)	13.0–19.1	Kang and Kim (2021)
Euchaeta plana	Southern waters of the Korean coast of NP Region 19	Apr.–Nov.	(1.9)	(5.3)	(1.7)	(0.038)	14.0–23.6	Kim *et al.* (2018)
Paraeuchaeta russelli	Southern waters of the Korean coast of NP Region 19	Apr.–Nov.	(6.5)	(17.8)	(3.1)	(0.079)	14.0–23.6	Kim *et al.* (2018)
EPR								
Acartia steueri	Southeastern coast of Korea	One year			3.8–10.1	0.022–0.071 (0.047)	11.5–25.6	Jung *et al.* (2004)
Acartia hongi	Kyeonggi Bay of the Yellow Sea	Feb.–Dec.			0.8–35.0	0.03–0.33	1.6–26.5	Youn and Choi (2007)
Calanus sinicus	Korean coast of the Yellow Sea	Mar.–Apr.			10.3–34.9 (23.4)	0.038–0.111 (0.082)	6.3–13.3	Kang *et al.* (2011)
Paracalanus parvus	Eastern coast of southern waters of Korea	One year			<1–24 (4)	<0.01–0.26	5.3–26.9	Jang *et al.* (2013)

Parenthesis indicates mean values.

Kang and Kang (2005) showed that there were no significant relationships between the daily production rate of *A. steueri* in Ilkwang Bay and temperature or Chl-*a* concentration, indicating that other unknown factors might be related to the variation of the production rate. Kang *et al*. (2007) reported that the daily production rate of *A. omorii* in Ilkwang Bay was significantly correlated with Chl-*a* concentration, suggesting that standing stocks and/or productivity of phytoplankton were the major influencing factors rather than water temperature for the seasonal variation of production of *A. omorii* in Ilkwang Bay. These results may suggest that different *Acartia* species have different responses to the same environmental condition. It is likely that *A. steueri* is a more offshore species, which is influenced by tidal currents, than *A. omorii*.

Recently, Kang and Kim (2021) reported that production of *C. sinicus* in spring in the northern East China Sea was dominated by somatic production of juveniles, especially by coefficient of variation (CV: 54% of the total production), and that the low EPR contribution to the total production (*e.g*., 3.5%) was likely due to the low fecundity of adult females caused by food limitation. Also, the WSEPR of adult females significantly increased with increasing water temperature at 5 m depth or surface Chl-*a* concentration but decreased with increasing female body weight.

Data on secondary production of Euchaetidae copepods are limited in the world. Recently, Kim *et al*. (2018) tried to estimate the production of egg-sac spawners *E. palana* and *P. russelli* from field samples and suggested that the total production of two Euchaetidae species was positively related to the density of the copepod *Oncaea venusta*, rather than to Chl-*a* concentration, indicating the two copepods might be carnivores.

Considering EPR of copepods, Jung *et al*. (2004) reported that the EPR of *A. steueri* in Ilkwang Bay measured during *in situ* incubation increased with increasing temperature and Chl-*a* concentration. Also, the WSEPR of *A. steueri* decreased with increasing body weight, similar with the generality of adult broadcast spawners (Hirst and Bunker, 2003). Youn and Choi (2007) suggested that phytoplankton biomass was an important factor that affects the EPR of *A. hongi* in Kyeonggi Bay. In addition, during the warm season, the EPR was also influenced by ciliate abundance. Consequently, the egg production of *A. hongi* was generally affected by food availability in Kyeonggi Bay. Kang *et al*. (2011) reported that the WSEPR of *C. sinicus* was negatively correlated with water temperature, but not with Chl-*a* concentration. The ratio of mean EPR to observed mean maximum EPR ranged from 20 to 70% (mean 46%), indicating that ~54% of a female's growth might be limited in the field, thus suggesting that the ratio of observed EPR to mean maximum EPR of the copepod can be applied to understand how the copepod responds to environmental changes. Recently, Jang *et al*. (2013) found that both EPR and WSEPR of *P. parvus* were strongly related to water temperature, but weakly associated with Chl-*a* concentration.

3.2.4 Remarks

Studies on secondary production and/or EPR in Korean waters have focused on copepods. Therefore, other taxa, including appendicularians, chaetognaths, cladocerans and non-calanoid copepods, should be included in future production studies. To measure or estimate the instantaneous growth rate of mesozooplankton is a very difficult task for zooplankton ecologists. Although traditional or biochemical methods have been developed (Yebra *et al*., 2017; Kobari *et al*., 2019a), we need to develop easier and more practical methods. Using the global empirical equation might be a good alternative to roughly estimate the growth rate of copepods (*e.g*., Hirst and Bunker, 2003) if we have abundant data on copepod juveniles in the field.

3.3 Canadian studies

Karyn Suchy and Akash Sastri

Zooplankton productivity measurements in Canadian waters have been fairly sparse and the methods have been inconsistent across the different regions (*e.g.*, East Coast, West Coast [NP Region 11] and Arctic; Table 3.5). Productivity measurements were conducted on the East Coast of Canada between the 1990s and late 2000s. The majority of these studies has focused on measurements of egg production rate for *Calanus finmarchicus* in the St. Lawrence estuary (Plourde and Runge, 1993; Ohman and Runge, 1994; Runge and Plourde, 1996) and the Labrador Sea (Cabal *et al*., 1997; Campbell and Head, 2000; Yebra *et al*., 2009; Head *et al*., 2013). McLaren and Corkett (1981) also measured egg production rates, in addition to somatic production rates (using the “natural cohort” method) of *Eurytemora herdmani* near Halifax, Nova Scotia. Additional studies measuring productivity using the artificial cohort method (Finlay and Roff, 2006) and aminoacyl-tRNA synthetases (AARS) activity (Yebra *et al*., 2009) were carried out in the Bay of Fundy and Labrador Sea, respectively.

In contrast, productivity measurements were not made on the West Coast of Canada (NP Region 11) until more recently, *i.e.*, from the mid-2000s to present, with the implementation of the chitobiase method to obtain community-level crustacean productivity measurements. Chitobiase-based productivity measurements have been conducted in the Strait of Georgia (Sastri and Dower, 2006, 2009) and on the West Coast of Vancouver Island (Sastri *et al*., 2012; Venello *et al*., 2022). In addition, chitobiase-based productivity measurements in Saanich Inlet, British Columbia (Suchy *et al*., 2016b), have been used to directly estimate phytoplankton to zooplankton trophic transfer efficiency and recently were compared to laser optical plankton counter (LOPC)-based productivity measurements using global predictive models (Kwong *et al*., 2020).

In terms of high-latitude-Arctic measurements, only one study has conducted community-level productivity measurements using the chitobiase method in transects within the Bering, Chukchi and Western Beaufort seas (Sastri *et al*., 2012; NP Regions 13, 14, 15 and 24). To date, “community-level” productivity measurements are lacking for the East Coast of Canada with the exception of one study that estimated annual total copepod production on the Scotian Shelf using P/B ratios calculated from adult body mass (Tremblay and Roff, 1983), whereas egg production measurements or *in situ* productivity measurements for single, dominant copepod species are lacking for the West Coast. To our knowledge, the community-level zooplankton productivity measurements in NP Region 11 are the only ongoing productivity measurements being conducted in Canadian waters at this time.

Table 3.5 Summary of somatic and reproductive growth and production rate studies for Canadian waters, identified by region, method, target species/group.

Location	Method	Species	Time period	Sampling	Reference
St. Lawrence Estuary	Egg production	*Calanus finmarchicus*	1991 1991	Single station Multiple stations	Plourde and Runge (1993) Ohman and Runge (1994)
Labrador Sea	Egg production	*Calanus finmarchicus*	1994 2004 1997 1997–2010	Transect Transect Multiple stations Transect	Cabal *et al*. (1997) Yebra *et al*. (2009) Campbell and Head (2000) Head *et al*. (2013)
Nova Scotia	Egg production and cohort method	*Eurytemora herdmani*	1970	Single station	McLaren and Corkett (1981)
Labrador Sea	AARS activity	*Calanus finmarchicus*	2002 and 2004	Transect	Yebra *et al*. (2009)
Bay of Fundy	Artificial cohort method	*Acartia hudsonica*, *Eurytemora herdmani*	2003	Single station	Finlay and Roff (2006)
Scotian Shelf	P/B ratios	Entire copepod community	1979–1980	Multiple stations	Tremblay and Roff (1983)
Strait of Georgia	Chitobiase	Entire crustacean community	2004 2004 and 2005	Single station Single station	Sastri and Dower (2006) Sastri and Dower (2009)
West Coast BC, Bering and Chukchi seas, Western Beaufort Sea	Chitobiase	Entire crustacean community	2008 and 2009	Transect	Sastri *et al*. (2012)
Saanich Inlet	Chitobiase	Entire crustacean community	2010 and 2011	Single station	Suchy *et al*. (2016b)
West Coast Vancouver Island and Gulf of Alaska (Line P)	Chitobiase	Entire crustacean community	2006–present	Multiple stations	Venello *et al*. (2022)

AARS: aminoacyl-tRNA synthetases

4 Application of Physiological Models to Zooplankton Data Sets in the PICES Region

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4.1 Introduction

Toru Kobari and Akash Sastri

Zooplankton time-series have been ongoing over the world oceans for the last century (*e.g.*, Mackas and Beaugrand, 2010). Extensive zooplankton data sets have been amassed and compiled (*e.g.*, World Ocean Database and Coastal and Oceanic Plankton Ecology, Production and Observation Database in National Oceanic and Atmospheric Administration), and used for scientific research and programs (*e.g.*, SCOR Working Group 125). While many approaches are available for us to estimate growth or productivity for natural zooplankton populations and communities (Runge and Roff, 2000; Yebra *et al*., 2017; Kobari *et al*., 2019a), there are few methods applicable to these existing zooplankton data sets due to the limited information such as total abundance and biomass of the zooplankton community. As mentioned in section 2.2.5, empirical and physiological models might be applicable for estimating zooplankton growth or productivity using such zooplankton data sets. Particularly, the physiological model involves the widest applicability from various taxonomic groups to the whole community, given some assumptions. Here, we provide some examples for applications of the physiological model to existing zooplankton data sets in the PICES region.

Production rate of the zooplankton community is estimated with the physiological method of Ikeda and Motoda (1978). Oxygen consumption rates (RO: μL O_2 ind^{-1} h^{-1}) are calculated from the following equation (Ikeda, 1985):

$$\text{Ln } RO_i = -0.2512 + 0.7886 \times \ln DM_i + 0.049 \times T_{WC} \qquad (2)$$

where DM_i is the individual dry mass at size class i (mg), which is the ZB_i (biomass: mg m^{-3}) divided by the ZA_i at size class i (abundance: individuals m^{-3}), and T_{WC} represents the temperature (°C) averaged in the sampling layer. Assuming 0.7 for assimilation efficiency and 0.3 for gross growth efficiency (Ikeda and Motoda, 1978; Omori and Ikeda, 1984), growth rate at size class i (G_i: day^{-1}) is computed using the following equation:

$$G_i = 0.75 \times RO_i \times 10^{-3} \times RQ \times 12/22.4 \times 24/CM_i \qquad (3)$$

where RQ is the respiratory quotient (0.97: Gnaiger, 1983) and CM_i is the individual carbon mass (mgC) which is converted by carbon content to dry mass (0.4: Peters and Downing, 1984). Thus, the zooplankton production rate (ZP_{PM}: mgC m^{-3} day^{-1}) is estimated as follows:

$$ZP_{PM} = \Sigma\,(G_i \times ZB_i \times 0.4). \qquad (4)$$

4.2 NP Regions 18, 19 and 22: Japanese coastal and offshore time-series

Toru Kobari and Deborah K. Steinberg

Japanese waters experience climatological variations from the subtropical to arctic areas and to geographical variations from coastal to pelagic sites. Using the various mesozooplankton data sets from around Japanese waters, including the Oyashio (subarctic and pelagic), the Kuroshio (subtropical and pelagic), Kagoshima Bay (subtropical and coastal) and the Tsushima Strait (temperate and coastal), and compared with those of the Bermuda Atlantic Time Series Study in the North Atlantic Ocean (subtropical and pelagic), community-based growth and production rates were estimated for the mesozooplankton community using physiological models.

Production rates were the lowest for the Bermuda Atlantic Time Series (BATS) and highest at the Tsushima Strait and Kagoshima Bay among the sites (Fig. 4.1). Production rates tended to be higher at such coastal sites compared with those at the pelagic sites. However, some estimates in the Kuroshio were equivalent to those in the coastal sites. Production rates increased with the increase in biomass but exhibited no clear pattern with the community-based growth rates, indicating that the resultant production rates were associated more with biomass rather than growth rates. Community-based growth rates demonstrated two common patterns, a negative correlation to individual body mass and positive to ambient temperature (Fig. 4.2). Community-based growth rates were relatively low to individual body mass in the Oyashio and to ambient temperature at the BATS site, compared with those in the other regions. As shown in Fig. 4.3, production rates were significantly positive to biomass at all sites (Pearson correlation coefficient: $r = 0.921$ to 0.972, $p < 0.01$), while they were insignificantly correlated with the growth rates (Pearson correlation coefficient: $r = -0.128$ to 0.213, $p > 0.01$), except in the Kuroshio (Pearson correlation coefficient: $r = -0.530$, $p < 0.01$).

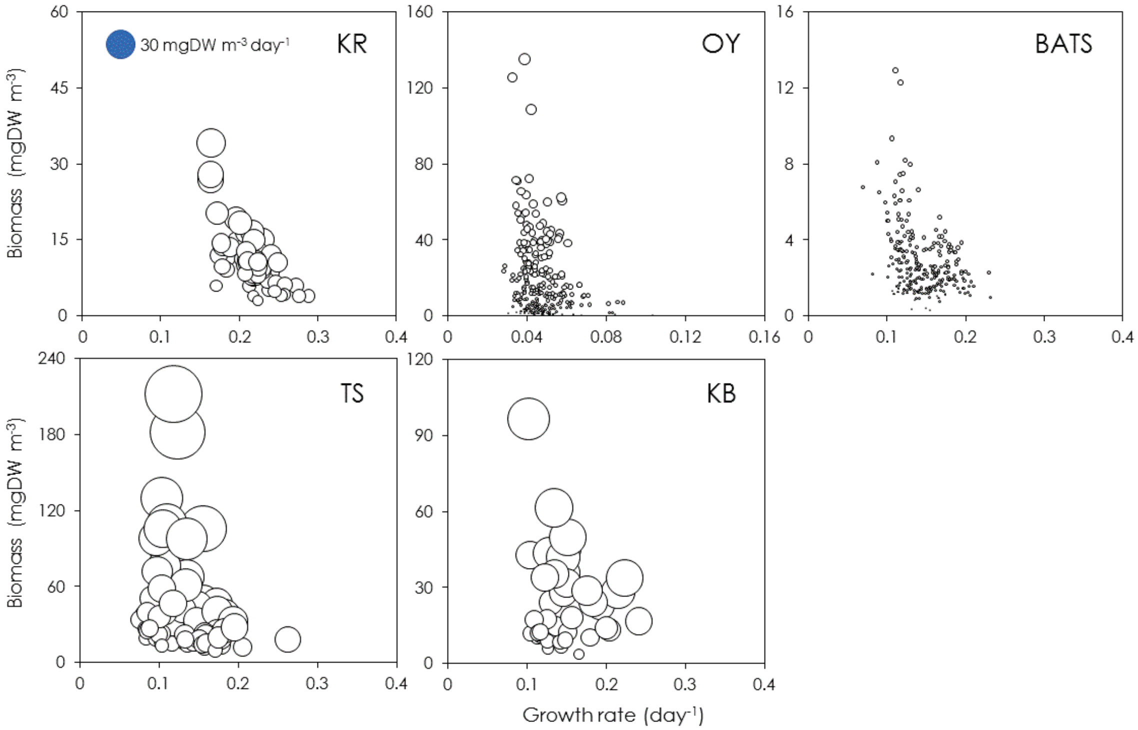

Fig. 4.1 Relationship of zooplankton biomass to its growth rate estimated with the physiological model based on several zooplankton data sets. Circle size means production rate. KR: Kuroshio. OY: Oyashio. BATS: Bermuda Atlantic Time-Series Study. TS: Tsushima Strait, southwestern NP Region 19. KB: Kagoshima Bay, southern Kyushu.

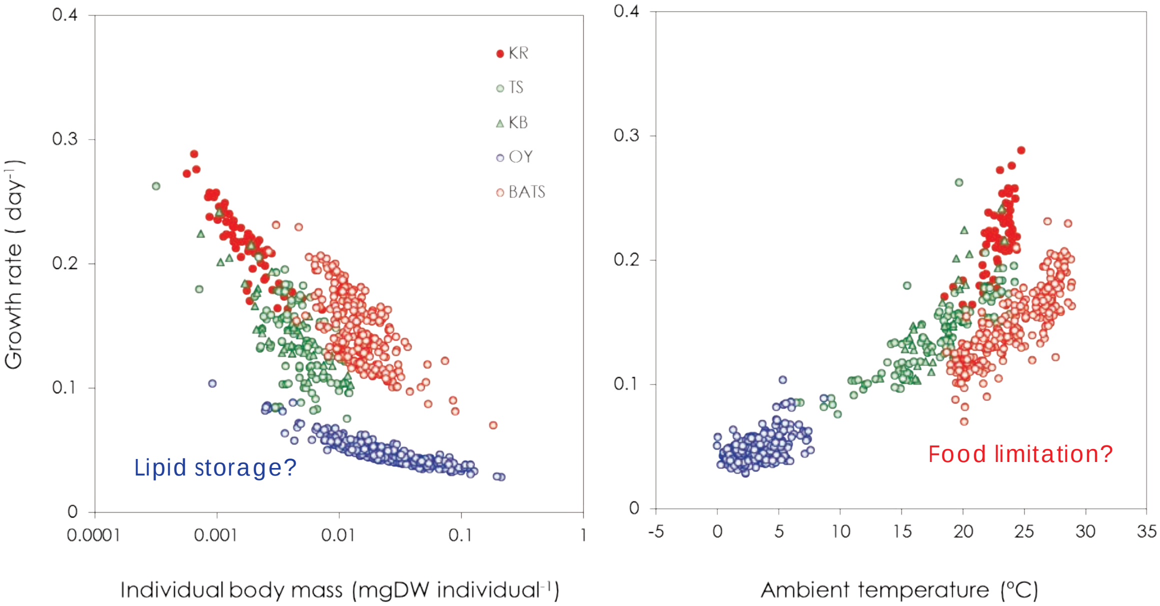

Fig 4.2 Relationship of zooplankton growth rate estimated with the physiological model to their individual body mass and ambient temperature based on several zooplankton data sets. KR: Kuroshio. TS: Tsushima Strait, southwestern NP Region 19. KB: Kagoshima Bay, southern Kyushu. OY: Oyashio. BATS: Bermuda Atlantic Time-Series Study.

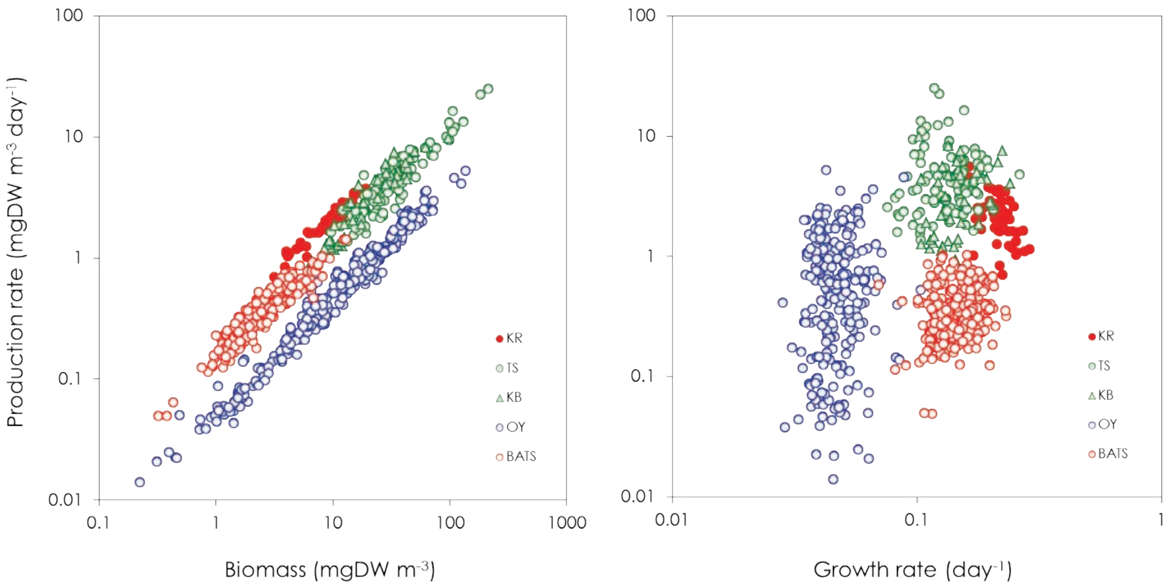

Fig 4.3 Relationship of zooplankton production rate to its biomass and growth rate estimated with the Ikeda-Motoda model (Ikeda and Motoda, 1978) based on several zooplankton data sets. KR: Kuroshio. TS: Tsushima Strait, southwestern NP Region 19. KB: Kagoshima Bay, southern Kyushu. OY: Oyashio. BATS: Bermuda Atlantic Time-Series Study.

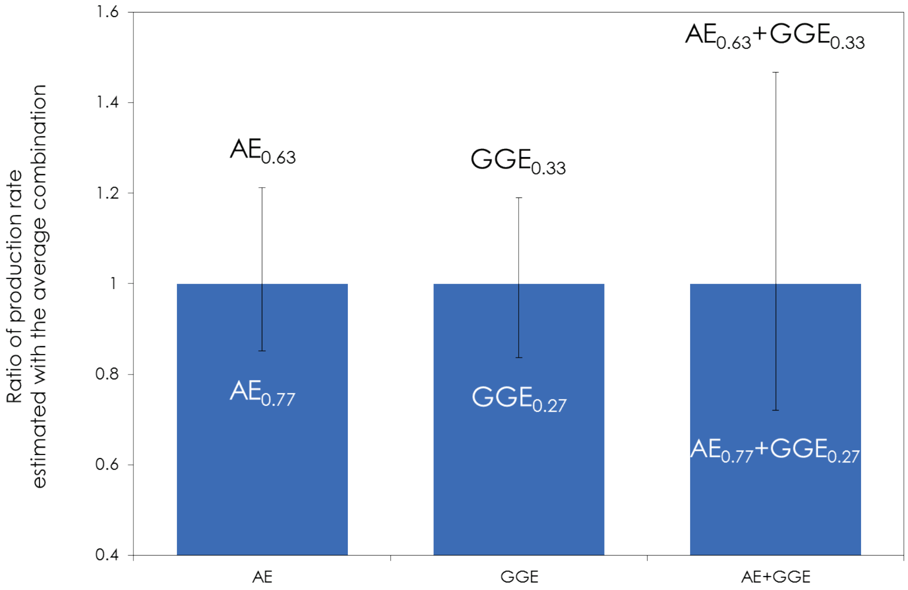

Fig 4.4 Sensitivity analysis of zooplankton production rates estimated with the Ikeda-Motoda model (Ikeda and Motoda, 1978). AE: assimilation efficiency. GGE: gross growth efficiency.

It is well known that the production rates estimated with the physiological model rely on two major constants: assimilation efficiency (AE) and gross growth efficiency (GGE). Indeed, AE and GGE have been assumed to be constant for production rate estimations (*e.g.*, Omori and Ikeda, 1984). Therefore, a sensitivity analysis was performed for the production rate estimates under 10% variability of the average AE (*i.e.*, 0.63 to 0.77) and GGE (*i.e.*, 0.27 to 0.33) and their combinations (Fig. 4.4). The production rate estimates were variable, ranging from 72 to 147% of the estimates with the average combinations of AE (0.7) and GGE (0.3), which were widely applied for the previous studies. These estimates were relatively sensitive to lower AE and higher GGE. As described earlier, the production rates estimated with the physiological model were strongly correlated with the directly measured biomass rather than the growth rates estimated even with a wide range of ambient temperature around Japanese waters. These results suggest that the physiological model is applicable for temporal and spatial comparisons of production rates using the zooplankton time-series.

4.3 NP Region 22: Inland Sea of Japan time-series

Kazuaki Tadokoro

The Inland Sea of Japan is one of the important fishery grounds in Japan. The fishery production is very high (20.6 tons m^{-2} $year^{-1}$) compared with production in the other areas such as the North Sea (5.7 tons m^{-2} $year^{-1}$) and Mediterranean Sea (0.8 tons m^{-2} $year^{-1}$) (Takeoka, personal communication). Eutrophication was a serious problem in the Inland Sea of Japan from the 1970s to the 1980s. However, nutrients concentration has decreased since the end of the 1980s because of government controls of the discharge of factory and domestic wastewaters. Fishery production (or catch amount of fishes) has also decreased since the 1980s. The decrease in nutrients concentration is suspected as one of the environmental factors for the decline in fish production. However, the mechanisms have not been clarified. Since copepods are important prey resources for fishes, their production rates are necessary for understanding the mechanisms related to the decline in fishery production in the Inland Sea of Japan.

During April 2016 and January 2018, we collected mesozooplankton samples by NORPAC net (45 cm diameter, 0.1 mm mesh size) vertical haul from bottom to sea surface. These samples were fixed by buffered formaldehyde. Copepod abundance was counted at species level using a dissecting microscope. The body length of each copepod species was measured and individual body wet weight was estimated using empirical equations (Uye, 1982). We estimated individual carbon content from the weight estimates as shown in Equation 4 (see above). Water temperature was measured from sea surface to bottom using the AAQ 1183 (JFE Advantech). The Ikeda-Motoda equation (Ikeda and Motoda, 1978) was then used to estimate copepod growth rates using the individual carbon contents of each copepod and mean water temperature in the water column.

We classified the copepod community using cluster analysis based on their production rates from April 2016 to January 2018. The copepod community was classified into 4 groups. Copepods collected from January to June were classified as group C appearing in Hyogo, Osaka, and Hiroshima (Fig. 4.5). Copepods in July belonged to group D. Copepods in September and November were classified into groups B and A, respectively. These results suggested that the seasonal variations of the copepod community were more prominent than geographical variations.

Next, production rates of predominant copepods were estimated in fiscal year (FY) 2016 (from April 2016 to January 2017) and FY2017 (from April 2017 to January 2018). Total copepod production rates were relatively low from April to June, increased in July, and then high values continued in September in both years (Fig. 4.6). The production rates in November were different between the two years (low in 2016 but high in the 2017), while they decreased in January in both years. Since individual carbon content and ambient water temperature are variables for the physiological model of Ikeda and Motoda (1978), the production rate estimates are dependent on water temperature. Thus, the high production rates during July to September are likely associated with the high thermal regime in summer in the Inland Sea of Japan.

Seasonal variations in production rates of the copepod community were represented by those of the predominant copepods; *Oithona similis* and *Calanus sinicus* from April to June, *Paracalanus parvus*, *O. davisae* and *Microsetella norvegica* in July, and *P. parvus* and *M. norvegica* from September to January. Contribution of *M. norvegica* to total copepod production rates was relatively greater in FY2017 compared to FY2016.

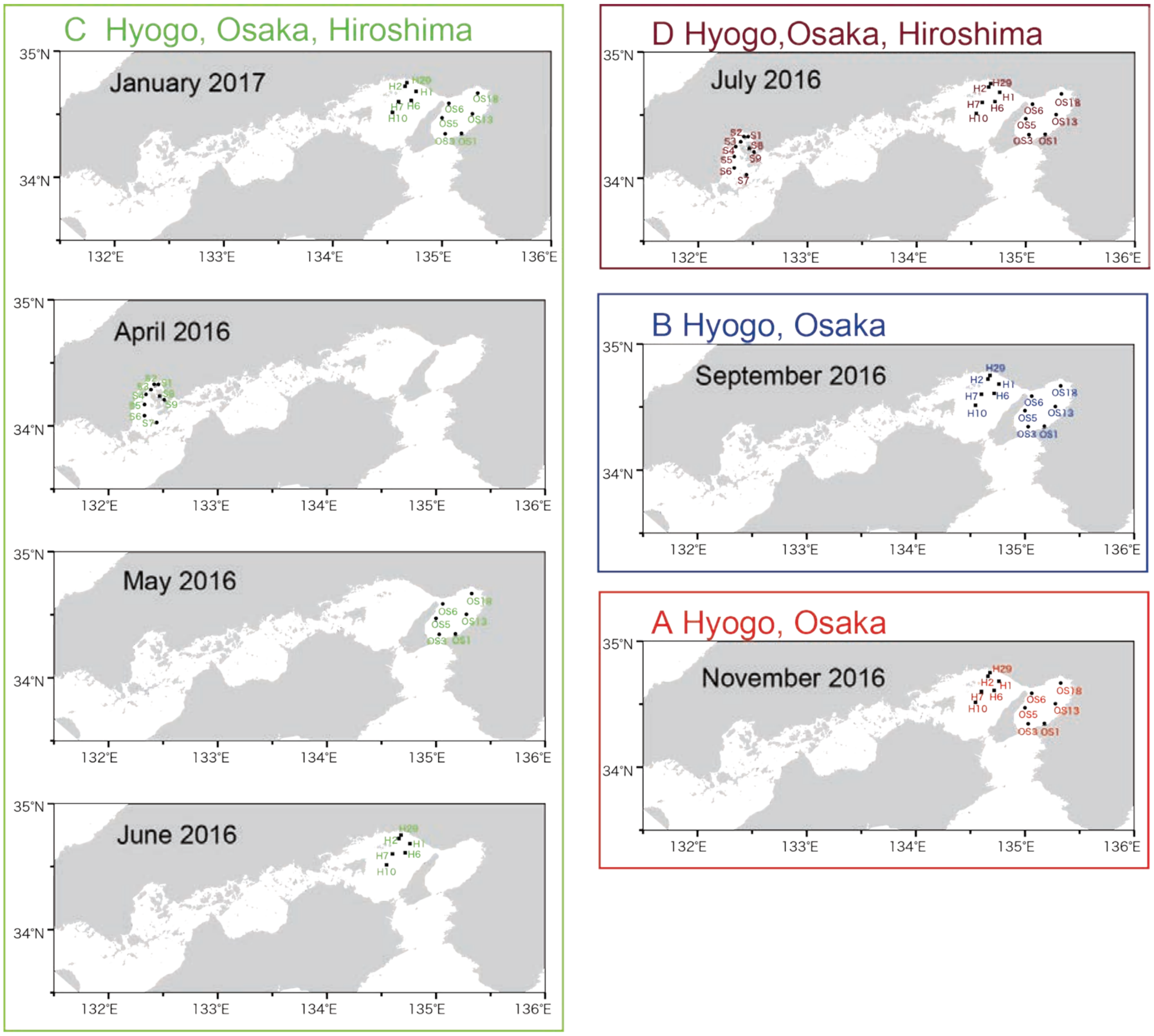

Fig 4.5 Spatial and monthly appearance of 4 groups identified by cluster analysis for the mesozooplankton community in the Inland Sea of Japan.

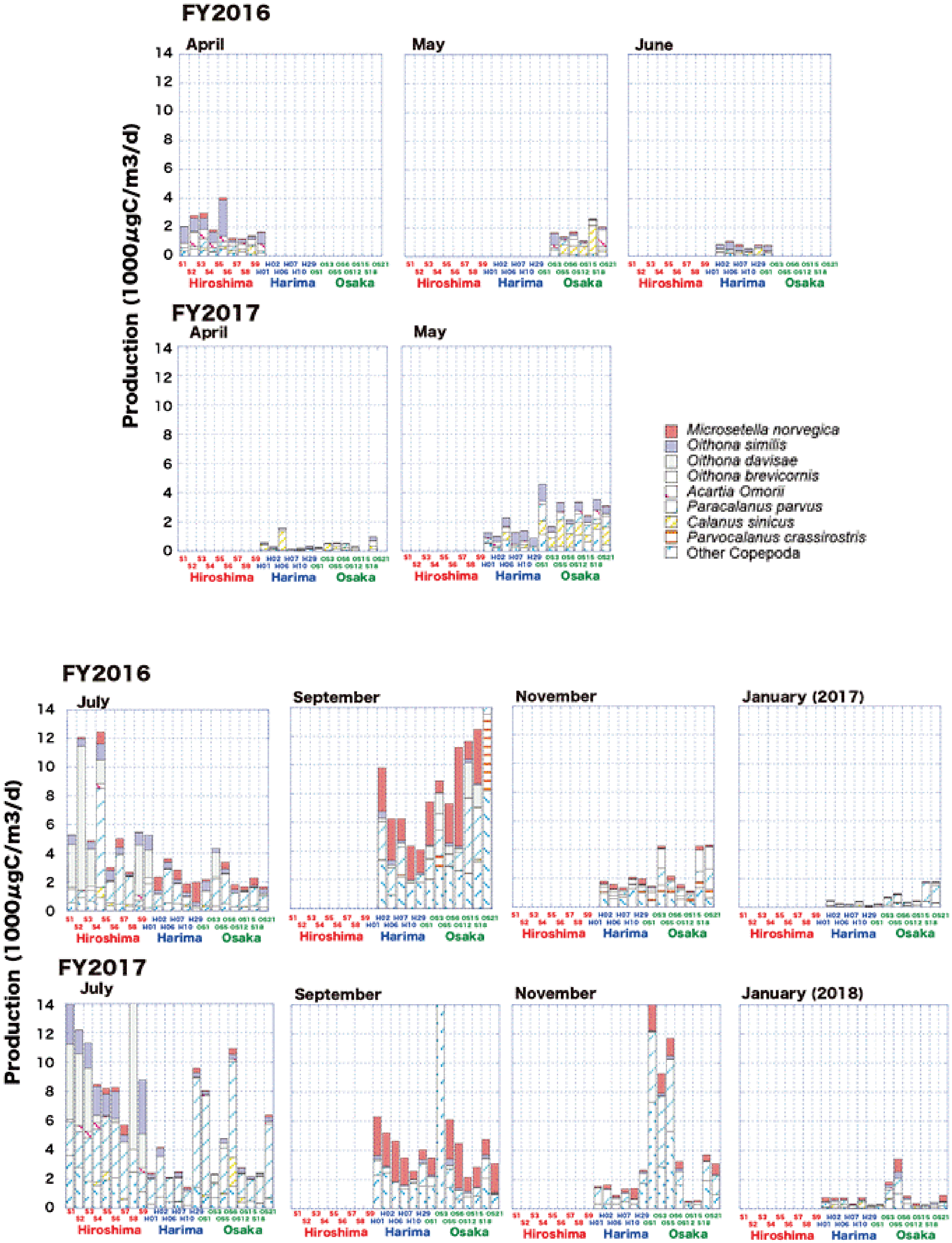

Fig 4.6 Regional and monthly comparisons of productivity for the predominant copepods in the Inland Sea of Japan during FY2016 (April 2016 to January 2017) and FY2017 (April 2017 to January 2018).

4.4 NP Region 11: California Current time-series

Samantha M. Zeaman, Eric Bjorkstedt and William T. Peterson

The Newport Hydrographic Line (NHL) is a 20+ year time-series of biophysical ocean conditions collected in the shelf waters off Newport, Oregon, USA. This high-frequency ocean monitoring program began in May 1996 and the oceanographic data have been key to informing an understanding of the connectivity between changes in the ocean–atmosphere and ecosystem structure and function. Sampling is conducted bi-monthly at 7 stations evenly spaced from ~1.5 to 40 km from shore. At the sentinel station NH05 (44.65.17ºN, −124.17.5ºE), 9 km from shore, vertical plankton nets are subsampled to quantify copepod biomass by species and stage.

Using plankton data collected at NH05 from 1997 to 2019, copepod secondary production was estimated using physiological models developed by Ikeda and Motoda (1978). Copepod secondary production rates were highly correlated with biomass estimates ($r = 0.95$, $p < 0.0001$, Fig 4.7), as biomass is more variable than growth rates estimated using the physiological model. Production rates were highest in August (1.27 ± 0.91 mgC m^{-3} day^{-1}) and lowest in December (0.34 ± 0.14 mgC m^{-3} day^{-1}). This seasonal pattern in production rates parallels increased copepod biomass in the summer upwelling season. These rates compare to earlier studies in the northern California Current (Peterson *et al.*, 2002) where on-shelf copepod production was estimated from female egg production, measurements of copepodite molting rate and assumptions of growth rates.

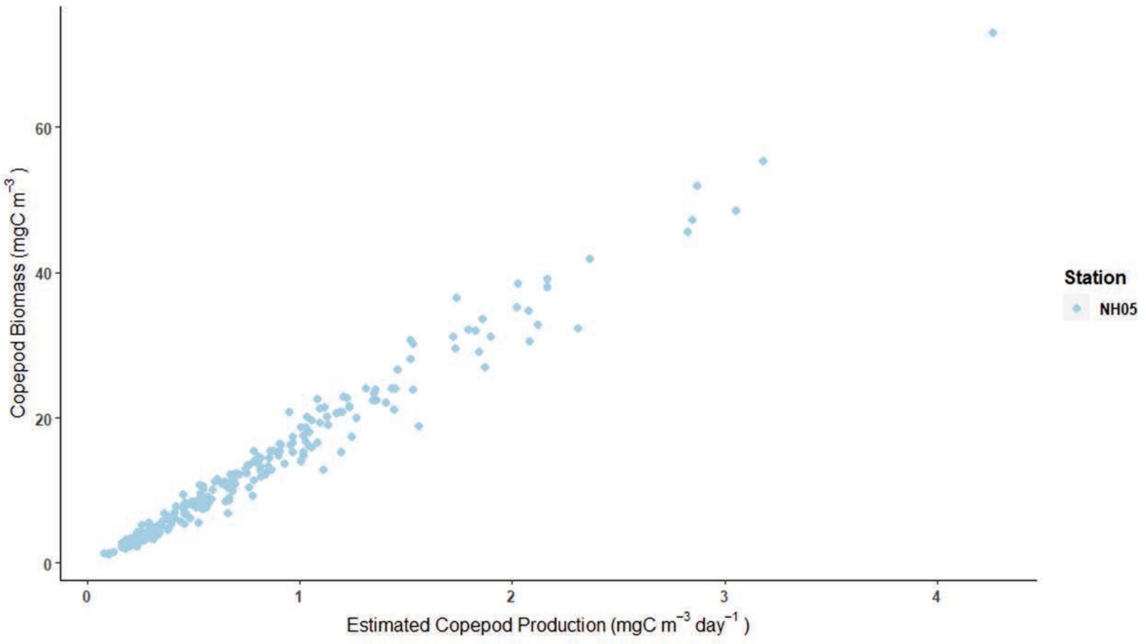

Fig 4.7 Summed copepod biomass by estimated copepod production at a high-frequency sampling station NH05 (44.65.17ºN, −124.17.5ºE) in the California Current. This sentinel station has been sampled bi-monthly since 1996.

In summer months, between May and September, ~75% of production was dominated by *Pseudocalanus* spp., *Centropages abdominalis*, and *Calanus marshallae*. In the winter months, *Pseudocalanus* spp., *Oithona similis*, and *Calanus marshallae* contributed the largest proportions (62%) to secondary production estimates. The contribution of *Pseudocalanus* spp. in summer and winter demonstrates the important role of smaller copepods in transferring primary production to higher trophic levels.

The utility of using physiological models to estimate secondary production lies in the ability to compare between oceanic regions with different temperature ranges and biomass. The Trinidad Head Line (41.05.833ºN, −124.26.67ºE) is another high-frequency oceanographic time-series in the California Current system. The Trinidad Head program began in 2008 with similar sampling methods, including monthly sampling and enumerating copepod species and stage from vertical plankton nets. We can now apply the physiological methods to the Trinidad Head data set using copepod counts from station TH02.

Overall, copepod production at the NH05 station is slightly higher across the time-series (Fig. 4.8). Production decreased for both sites in more recent years, 2015–2019. Interestingly, TH02 has higher production in the winter months and noticeably decreased production in summer months (Fig. 4.9). Secondary production at NH05 follows a more characteristic seasonal cycle, while seasons at TH02 are not as dramatically different (Fig. 4.9). These trends are comparable in the copepod biomass. While these two stations are characterized by different bathymetry and physics (shelf width, lee of headland, retention), they share similar copepod assemblages and temperature ranges. *Pseudocalanus* and *Calanus* species make up the majority of copepod production at Trinidad Head, but with greater contribution from southern-affiliated genera, such as *Clausocalanus* and *Paracalanus*.

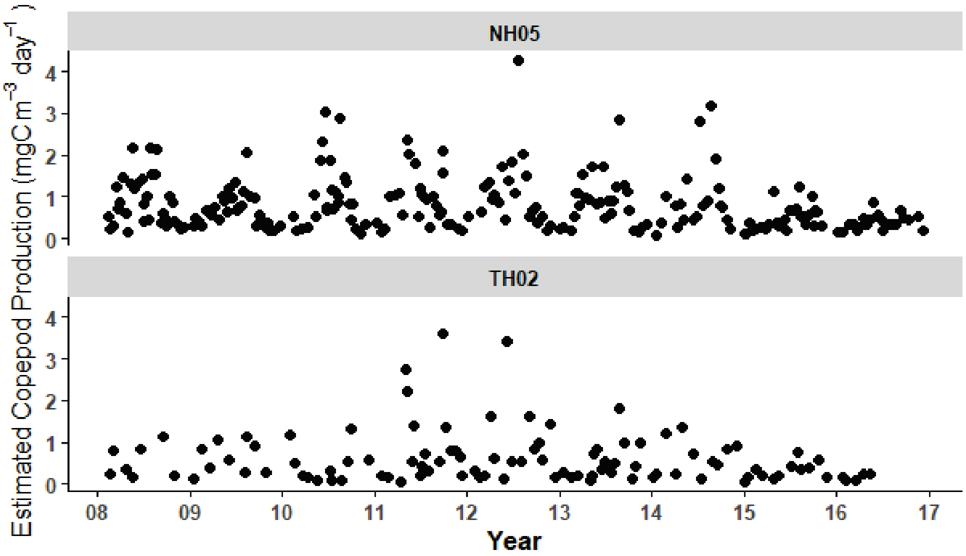

Fig 4.8 Copepod secondary production rates by sampling date estimated at two high-frequency stations, NH05 and TH02, in the California Current.

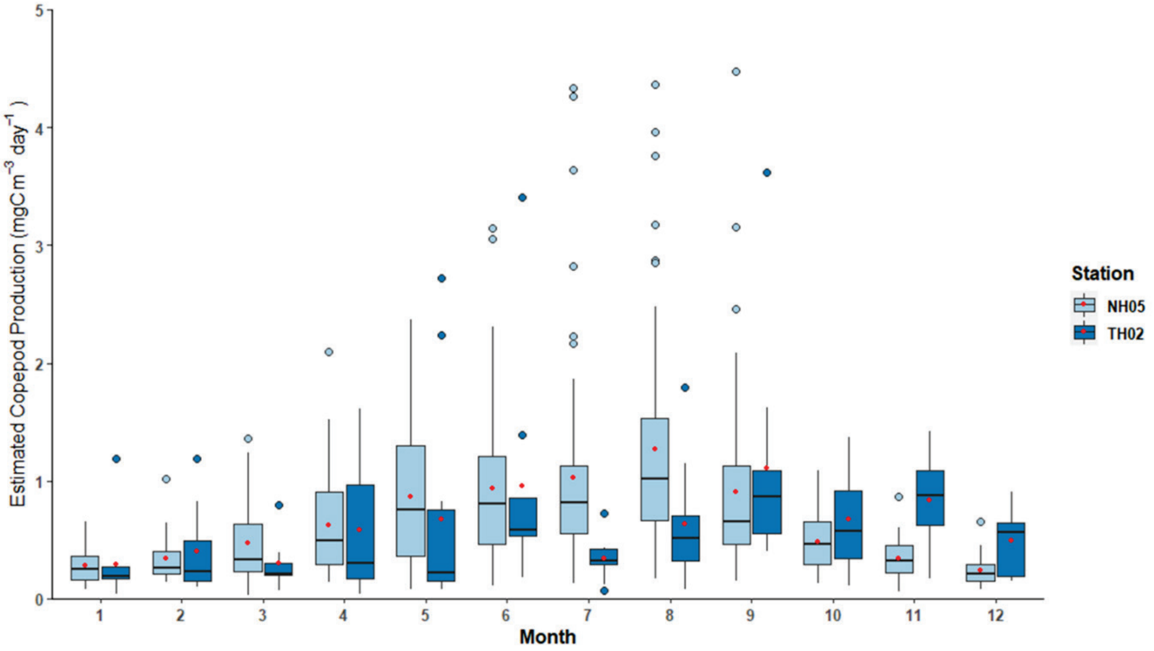

Fig 4.9 Box plots of monthly copepod secondary production rates (mgC m^{-3} day^{-1}) for two coastal observing stations, NH05 and TH02. Box represents first (bottom), second (bar) and third (top) quartiles. Whiskers indicate minimum and maximum values. Red and blue solid circles represent averages and outliers of production for each station and month. Production estimates are summed across species and life stages.

These data sets are unique not only because of the high-frequency of sampling, but also because of the detailed taxonomic resolution. Using physiological models, we can focus on production of important copepod species by life history stage. For example, the medium-sized copepods *Calanus marshallae* and *Calanus pacificus* are important lipid-rich members of the plankton at each site. Production rates by month show the importance of late-stage (IV-Adult) *Calanus*, especially in the summer months for TH02 (Fig. 4.10). Of note, TH02 has elevated production rates for *C. pacificus* stages in the winter months.

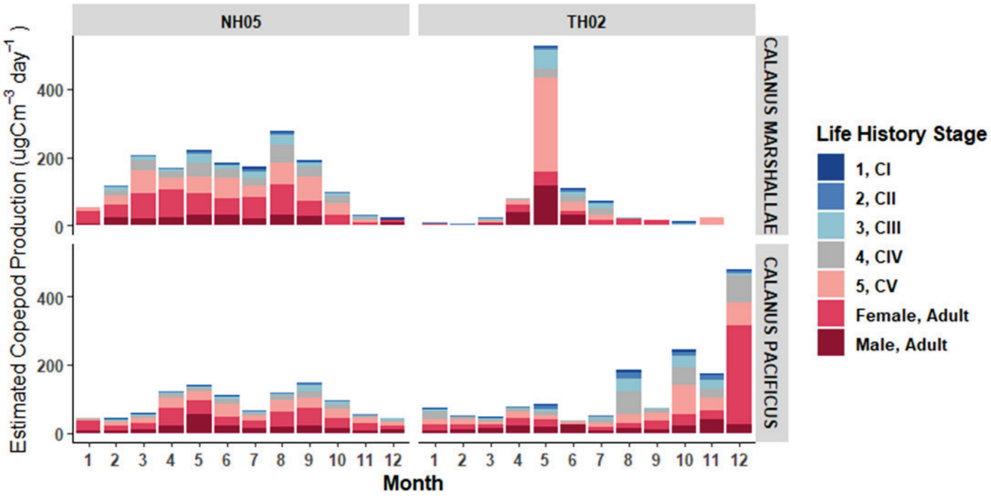

Fig 4.10 Secondary production rates for *Calanus marshallae* and *Calanus pacificus* by life history stage at stations NH05 and TH02.

Many of these patterns can be elucidated by examining copepod biomass (mgC m^{-3}) for each time series. More interesting comparisons can be achieved by calculating primary production rates at these sites. A more holistic examination of these systems could lead to calculation of copepod food chain efficiency and ecological efficiency temporally and spatially in the California Current. These data sets, in conjunction with physiological models, can also be compared to zooplankton sampling sites in other PICES member countries and across ocean basins.

4.5 NP Regions 11 and 24: Line P time series

Akash Sastri, Karyn Suchy, Lian Kwong, Moira Galbraith and Kelly Young

Here we estimate production rates for juvenile copepod assemblages sampled along the Line P oceanographic transect by Fisheries and Oceans Canada for the 1998–2010 period. The modern Line P program has sampled each of 26 stations (see Fig. 4.11) three times (winter, late spring, late summer) per year since 1981. The 1,420 km transect extends westward from productive continental margin (NP Region 11) and offshore waters (NP Region 24) to oligotrophic high nutrient low chlorophyll waters. The line can be broadly divided into "inner" stations characterized by stronger seasonal drawdown of surface nutrients and "outer" stations characterized by limited macronutrient utilization (Whitney and Freeland, 1999; Pomerleau *et al*., 2015). More finely resolved divisions of the line have been presented (*e.g*., Peña *et al*., 2019) and have been used by others (Kwong *et al*., 2022; Venello *et al*., 2022) to treat spatio-temporal variation of the mesozooplankton community along Line P. Here, however, we retain the approach taken by Whitney and Freeland (1999) and Pomerleau *et al*. (2015) as our objective is simply to characterize broad-scale interannual and seasonal patterns.

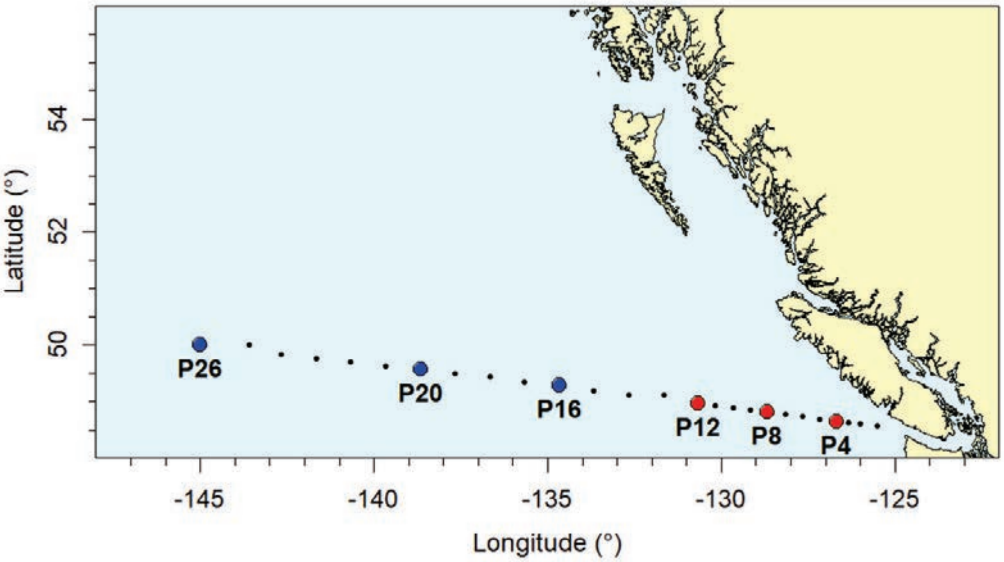

Fig 4.11 Map of Line P station locations. Coloured symbols represent zooplankton survey stations: Red symbols represent "inner" line stations and blue symbols represent "outer" line stations. P26 is Ocean Station Papa (145ºW, 50ºN).

During the study period, mesozooplankton have been consistently sampled at the inner stations, P4 (shelf break/slope, 1,300 m bottom depth), P8 and P12 (offshore, 2,440 and 3,300 m bottom depths, respectively). Bottom depths for the outer mesozooplankton stations, P16, P20 and P26, are 3,550, 3,890 and 4,300 m, respectively. Copepod community composition at all stations includes representation by the large (often biomass dominant) subarctic copepods, *Neocalanus plumchrus*, *N. flemingeri*, *N. cristatus* and *Eucalanus bungii*. Inner stations, and station P4 in particular, also include seasonally varying representation by relatively small, fast-growing, continental margin/coastal species such as *Centropages abdominalis* and *Acartia* spp. Coastal species are also occasionally transported to and sampled along the outer line *via* westward propagation of coastally generated Haida Eddies (Crawford, 2002).

Consistent with each contribution to this section, we calculate and present juvenile copepod production rates for Line P using the physiological model (Ikeda and Motoda, 1978; IM). For comparative purposes, we have also calculated production rates using specific growth rates estimated with empirical models of increasing complexity (see Table 4.1). Briefly, 1) the Huntley and Lopez (1992) model (HLo) characterizes variation of specific growth rate, estimated as the change in mass from egg through adult over the generation time varying solely on the basis of temperature; 2) the Hirst and Sheader (1997: HS) and Ikeda and Motoda (1978: IM) models rely on temperature but also include a dependence on body size to describe growth rate; 3) Hirst and Lampitt (1998: HLa) found that growth rate could be described on the basis of both temperature and body size for broadcast spawning copepods and only temperature for sac spawners, with broadcasters growing more quickly; and 4) Hirst and Bunker (2003: HB) includes temperature, discriminates between broadcast- and sac-spawners, and includes a food-term (chlorophyll a) for broadcast spawners.

Table 4.1 Physiological and empirical growth rate regression equations used in this study.

Model	Regression equation(s)	Reference
IM	$g = 0.75 \times RO_i \times 10^{-3} \times RQ \times 12/22.4 \times 24/W$	Ikeda and Motoda (1978), Ikeda (1985); as per section 4.1
HLo	$g = 0.0222e^{0.094\mathrm{T}}$	Huntley and Lopez (1992)
HS	$\log_{10}(g) = 0.0246\mathrm{T} - 0.2962 \log_{10}(W) - 1.1355$	Hirst and Sheader (1997)
HLa	$\log_{10}(g) = 0.0111\mathrm{T} - 0.2917 \log_{10}(W) - 0.6447$; [BS] $\log_{10}(g) = 0.0358\mathrm{T} - 1.4647$; [SS]	Hirst and Lampitt (1998)
HB	$\log_{10}(g) = -0.0143\mathrm{T} - 0.363 \log_{10}(W) + 0.135 \log_{10}(F) - 0.105$; [BS] $\log_{10}(g) = 0.0333\mathrm{T} - 0.163 \log_{10}(W) - 1.528$; [SS]	Hirst and Bunker (2003)

IM: Ikeda and Motoda (1978) and Ikeda (1985); HLo: Huntley and Lopez (1992); HS: Hirst and Sheader (1997); HLa: Hirst and Lampitt (1998); HB: Hirst and Bunker (2003). *RO* represents oxygen consumption rate (mL^{-2} individual hour^{-1}); *RQ* represents the respiratory quotient, 0.97; *W* represents individual carbon biomass, T represents temperature in the depth range sampled by the nets; *F* represents sea surface chlorophyll a concentration (mg Chl-*a* m^{-3}); and BS represents “broadcast spawner” and SS represents “sac spawner”.

Community-level biomass production rate for each sampling event was calculated as the product of stage-specific growth rate predicted by each model and total biomass for that stage summed across all developmental stages (see Equation 4). Growth rates were predicted for all juvenile copepod species identified in our samples. Each species was also identified as broadcast- or sac-spawner for the HLa and HB models. The temperature from CTD profiles for each sampling event was averaged through the upper 250 m (upper 150 m pre-2002) corresponding to the range of the vertical net haul range. Here we used a satellite-derived surface chlorophyll a for the HB broadcast-spawner model. Satellite-derived chlorophyll a values are the "NASA combined-satellite chlorophyll time series" resolved to within ~50 km of each station and to the mid-point of each month; values were obtained through the NOAA COPEPOD Spatiotemporal Data and Time Series Toolkit website[2]. Production rates predicted by each model were plotted relative to juvenile copepod biomass in Figure 4.12. We also present a reference value, the average of all event-specific production rate estimates ("E") using production rates estimated with the HLo, HS, HLa models. The averaged outputs of these particular models were chosen because they are based on similar assumptions and growth rate measurements (*i.e.*, moulting rate method). The HB method was not included because of uncertainties with respect to the efficacy of using satellite-derived surface chlorophyll a.

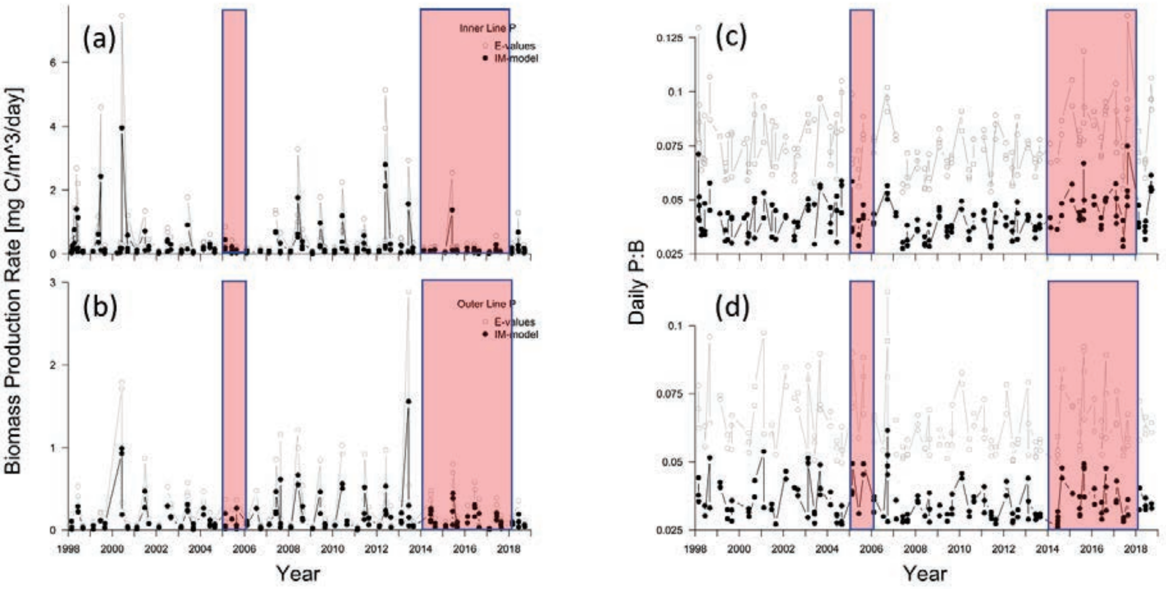

Fig. 4.12 Interannual patterns of: juvenile copepod biomass production rates (mgC m^{-3} day^{-1}) sampled along (a) the "inner" line and (b) "outer" sections of Line P; interannual patterns of juvenile daily P:B sampled along (c) the "inner" and (d) "outer" sections of Line P. Black symbols represent mean seasonal production rates (late winter, late spring, late summer) estimated using the Ikeda and Motoda (1978) physiological model and white symbols represent average of rates ("E") estimated using the Huntley and Lopez (1992), Hirst and Sheader (1997) and Hirst and Lampitt (1998) relationships for specific juvenile copepod growth rates.

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[2] https://www.st.nmfs.noaa.gov/copepod/toolkit/

As expected, the correspondence between production rate and biomass values is strong given that biomass is used in the calculation of production rate and because it is much more variable than growth rate (Huntley and Lopez, 1992). We take advantage of these relationships to compare (Table 4.2) model slopes (equivalent to daily P:B values) and variance not explained by biomass (residual standard error). Increasing model complexity was associated with greater residual standard error (RSE) or variation not explained solely by biomass. The HB model is the most complex (temperature, individual body size, spawning type and food concentration) and this is reflected in an RSE of 0.345. The IM and HS models are similar (temperature and body size dependence) and have similarly low RSE values *i.e.*, production rates are mostly described by biomass. Curiously, the least complex model, HLo, had a relatively high RSE value, suggesting a potential decoupling between temperature and biomass for our data set. The HLo model and the HB models also predicted the greatest production rates and daily P:B values (Fig. 4.13, Table 4.2).

Temporal patterns of production rates for inner and outer Line P stations (Fig. 4.12 a, b) are similar for both the IM and “E” production rates. The “E” rates, however, are ~1.5 to 2 times greater than the IM model for both inner and outer line time series. The temporal pattern for daily P:B for both IM and “E” daily P:B estimates are also similar for both inner and outer sections of Line P (Fig. 4.12 c, d). Note, however, that IM predictions for both sections are consistently lower than the average “E” daily P:B estimates. Production rates during the anomalously warm 2005–2006 and post-2014 periods (Fig. 4.12, shaded areas) are relatively depressed in both the inner and outer lines, reflecting reduced total biomass. These relatively low rates are also reflected in lower daily P:B for 2005 but not during the post-2014 period, again indicating that variation of juvenile biomass is largely responsible for variation in production rates. Note, however, that neither model identifies productivity-related responses to strong compositional shifts from large-bodied subarctic copepod biomass to small-bodied California Current species observed in during the moderate 2010 El Niño event. Median production rates (IM model) during both winter and late summer are greater (but with similar spread) for inner relative to outer stations (Fig. 4.14), reflecting expectations of higher ecosystem-scale productivity. Median production rates during the late spring/early summer period are similar (~2 mgC m^{-3} day^{-1}) between both regions. However, there is a greater spread about the median and skewedness toward higher production rates for the inner stations during late spring/early summer. Differences in peak biomass timing of *Neocalanus* spp. may account for some of the apparent similarity between inner and outer stations during the spring. On average, sampling along Line P happens within a 7-day window in early June, closer to peak biomass timing for outer stations but not for inner stations, which typically takes place 3 to 5 weeks earlier (Mackas *et al.*, 2007).

Table 4.2 Regression coefficients for Figure 4.12.

Model	Regression equation	Residual standard error	Daily P:B (regression slope)
Ikeda and Motoda (1978: IM)*	**P = 0.032 B + 0.01732; $p < 0.0001$**	**0.055**	**0.032**
Huntley and Lopez (1992: HLo)	P = 0.106 B – 0.00115; $p < 0.0001$	0.139	0.106
Hirst and Sheader (1997: HS)	P = 0.022 B + 0.02902; $p < 0.0001$	0.070	0.022
Hirst and Lampitt (1998: HLa)	P = 0.054 B + 0.00050; $p < 0.0001$	0.121	0.054
Hirst and Bunker (2003: HB)*	P = 0.070 B + 0.11348; $p < 0.0001$	0.345	0.070
E values	P = 0.061 B + 0.02633; $p < 0.0001$	0.092	0.061

Asterisk denotes models not represented by the averaged empirical model production rates (E values). Bolded line denotes model illustrated in Figure 4.12.

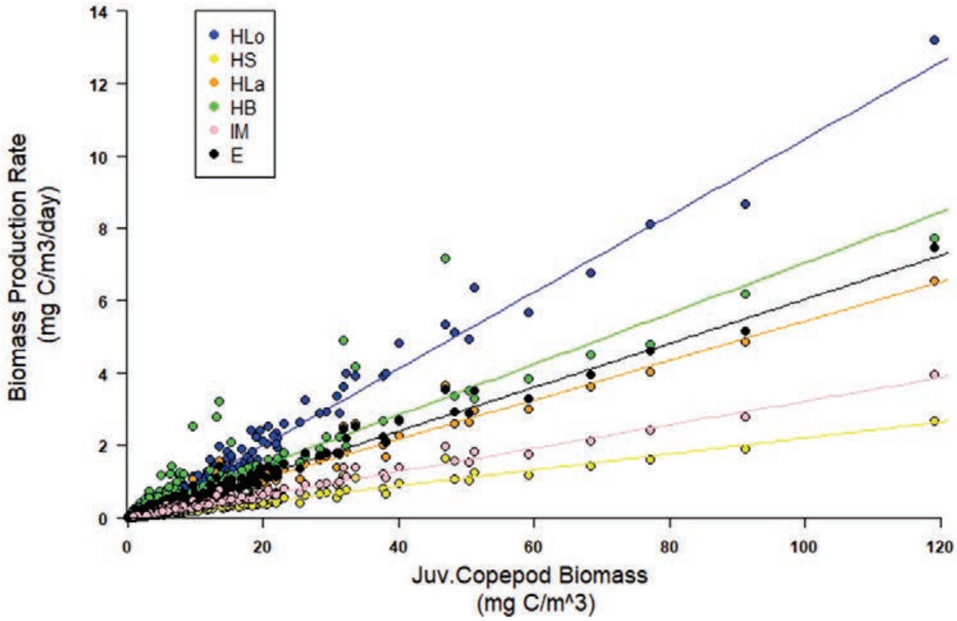

Fig. 4.13 Comparison of juvenile copepod production rates (mgC m^{-3} day^{-1}) relative to biomass (mgC m^{-3}). Biomass production rate was calculated as the product of biomass and individual weight-specific growth rate (day^{-1}) summed across all juvenile copepod life stages using the Huntley and Lopez (1992) (HLo: blue line and symbols), Hirst and Sheader (1997) (HS: yellow line and symbols), Hirst and Lampitt (1998) (HLa: orange line symbols), Hirst and Bunker (2003) (HB: green line and symbols) and Ikeda and Motoda (1978) (IM: pink lines and symbols) empirical/physiological growth rate models (see Table 4.1 for equations). Linear regression for each relationship was used to estimate mean predicted daily P:B for the Line P (1998–2018) time series and model choice on influence of biomass on variation of estimated production rate. Black line and symbols represent averaged (E) total production estimated with the HS, HLo and HLa models for each event.

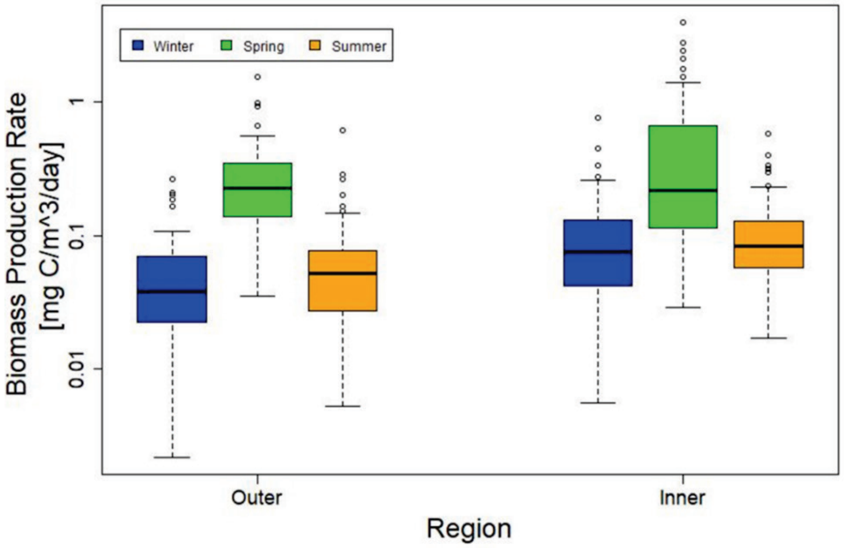

Fig 4.14 Box plot illustrating median (1998–2018) and spread about the regional biomass production rates (mgC m^{-3} day^{-1}) partitioned by season. Outliers are represented by individual symbols. "Outer" line includes stations, P16, P20 and P26. "Inner" line includes stations, P4, P8 and P12.

The IM model is useful for production rate estimates because it can be applied retrospectively to long-term time series of zooplankton body size, total biomass and temperature. This approach provides a tool to quickly assess how spatial and temporal changes of average body size and temperature will influence mesozooplankton productivity. These estimates may also be used in conjunction with primary production rates to provide estimates of ecological efficiency. However, application of the IM (or any of the empirical models discussed here) should be used with caution in the Northeast subarctic Pacific as these model syntheses do not include species typically sampled in our region. Region-specific models (*e.g.*, Liu and Hopcroft, 2006a,b, 2007, 2008) and/or region-specific model validation may provide greater sensitivity which would presumably include more realistic relationships between growth rate, temperature, body size and food proxies. Lastly, the copepod production rates calculated here assume that all animals are growing at rates predicted by the model. Mixed-species assemblages will include animals which are not actively growing (see Hirst and Sheader, 1997) due to differences of feeding preference and/or thermal range.

5 Comparisons of Zooplankton Production among Methodologies

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5.1 Introduction

Toru Kobari

While a few biochemical methods were introduced in the ICES Zooplankton Methodology Manual (Runge and Roff, 2000), alternative approaches like chitobiase activity (*e.g.*, Oosterhuis *et al.*, 2000; Sastri and Roff 2000) and aminoacyl tRNA synthetases (AARS) activity (*e.g.*, Yebra and Hernández-León, 2004) have been developed for zooplankton growth or productivity since 2000. As mentioned in Yebra *et al*. (2017), these biochemical approaches have many advantages like wide applicability to various taxonomic groups and good replicability, allowing for quick measurements. For evaluating wide applicability to natural zooplankton population or community, comparisons among these biochemical methodologies have been conducted (*e.g.*, Holmborn *et al.*, 2009; Yebra *et al.*, 2011). However, there is limited information on comparisons and validations of the biochemical proxies to the zooplankton production rate with the traditional methodologies (*e.g.*, Kobari *et al.*, 2018, 2019a,b). Here, we demonstrate examples of comparisons of production estimates with the natural cohort and modified natural cohort methods (section 5.3), the biochemical proxy (AARS activity and chitobiase activity) to the production estimates with the natural cohort methods using the cultured copepod population (sections 5.4, 5.6) and biochemical proxies (AARS activity) to the production estimates with the physiological model using field collected samples (section 5.5).

5.2 Copepod culture for inter-comparison

Toru Kobari, Tomonari Kotani, Yuka Matsuura and Yui Nakata

Pseudodiaptmus inopinus was collected from the coastal site of Amami Island, Japan, and cultured in a polycarbonate 100-L tank and fed two haptophytes (*Isochrysis* sp. and *Pavlova lutheri*) and one diatom (*Phaeodactylum tricornutum*) for more than 1 year (hereafter referred to as the batch culture). A size-fractionated cohort was created in the batch culture by slowly lowering a container with mesh (0.2-mm openings). Animals smaller than the mesh aperture were present in the container and siphoned out from the inside into another polycarbonate 100-L tank (hereafter referred to as the experiment culture). The incubation temperature of the experimental culture was 20°C during the 14-day observation period (August 25 to September 8) and was initiated with the same algae from the batch culture. The cultured copepods were siphoned daily from the experiment culture for biochemical samples (each 1000 mL for AARS activity and protein contents) and microscopic samples (250 mL). Biochemical samples were filtered on 0.1 mm Nitex filters. Samples for AARS activity and protein contents were frozen with liquid nitrogen and stored at –80ºC. Protein-specific AARS activity and protein contents were measured (see Yebra *et al*. (2017) for detailed procedures). Filtrate (culture water free of copepods) was retained in a 400 mL Nalgene bottle for a 12-hour incubation for monitoring the change in chitobiase activity. The bottles were incubated at 20°C and sub-sampled every three hours using a 0.2 μm syringe filter (as per Sastri and Dower, 2006). Chitobiase activity in each sub-sampled aliquot was assayed as per Sastri and Dower (2006) and change in activity over time was used to estimate daily biomass production rates according to calculations for a synchronously developing population by Oosterhuis *et al*. (2000). The microscopic samples were fixed with 5% borax-buffered formaldehyde, counted at each developmental stage under a dissecting microscope, and abundance (ZA) was determined. Body lengths were also measured for all development stages.

For measuring body length and stage duration, each adult female was individually incubated in a multiwell plate and fed the two haptophytes and one diatom diet as mentioned above. Once nauplii hatched from the adult female, they were transferred individually into another well. Development stages were checked twice a day for nauplius stages and once a day for copepodite stage under a dissecting microscope.

Population production rates were estimated with the two different approaches, natural cohort (ZP_{NC}) and modified natural cohort (ZP_{mNC}). ZP_{NC} (mgC L^{-1} day^{-1}) was calculated using the equation (Lalli and Parsons, 1993):

$$ZP_{NC} = (ZA_i - ZA_{i+1}) \times (CM_i/2 + CM_{i+1}/2) + (ZB_{i+1} - ZB_i) \quad (5)$$

where ZA_i and ZA_{i+1} are population abundance (10^3 individuals L^{-1}) at stage i and $i + 1$, CM_i and CM_{i+1} were individual carbon mass (μgC individual^{-1}) at stage i and $i + 1$, ZB_{i+1} and ZB_i were population biomass stage i and $i + 1$, respectively. Mean body weight was estimated from body length (BL: mm) using the equations (Uye *et al*., 1983):

$$\text{Log } CW = 2.00 \times \text{Log } BL - 5.67 \text{ for nauplius stages} \quad (6)$$

$$\text{Log } CW = 2.81 \times \text{Log } BL - 8.03 \text{ for copepodite stages} \quad (7)$$

ZP_{mNC} (mgC L^{-1} day^{-1}) was calculated using the equation:

$$ZP_{NC} = \Sigma\,(ZA_i \times BW_i \times g_i) \quad (8)$$

where g_i (day^{-1}) was weight-specific growth rate at stage i.

Body length and weight increased exponentially with development (Fig. 5.1, Table 5.1). Stage duration was 7.5 days during nauplius stage 1 to 6 and variable from 1.6 to 2.5 days for copepodite stages (Fig. 5.2, Table 5.1). Weight-specific growth rates were higher for nauplius stages (0.18 day^{-1}) and ranged from 0.06 day^{-1} to 0.11 day^{-1} for copepodite stages.

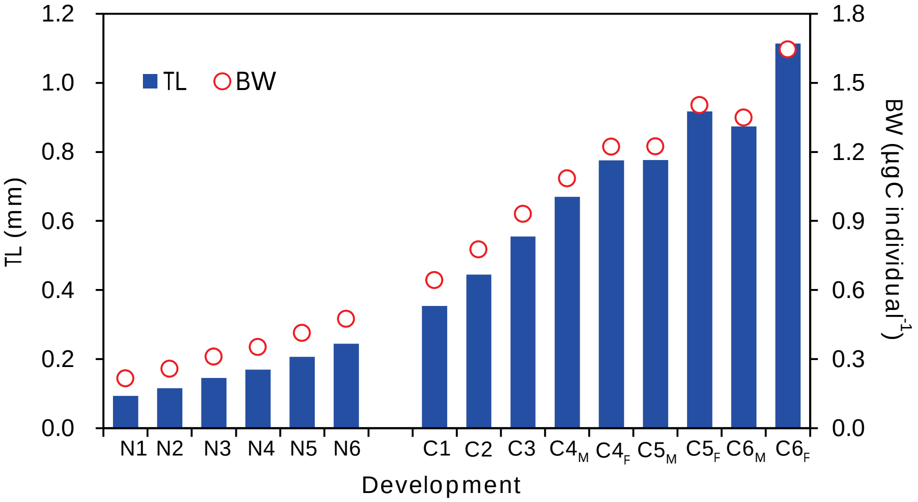

Fig. 5.1 Development changes in total body length (TL) and individual body weight (BW) of *Pseudodiaptomus inopinus* in the culture. N: nauplius stage. C: copepodite stage. M: male. F: female.

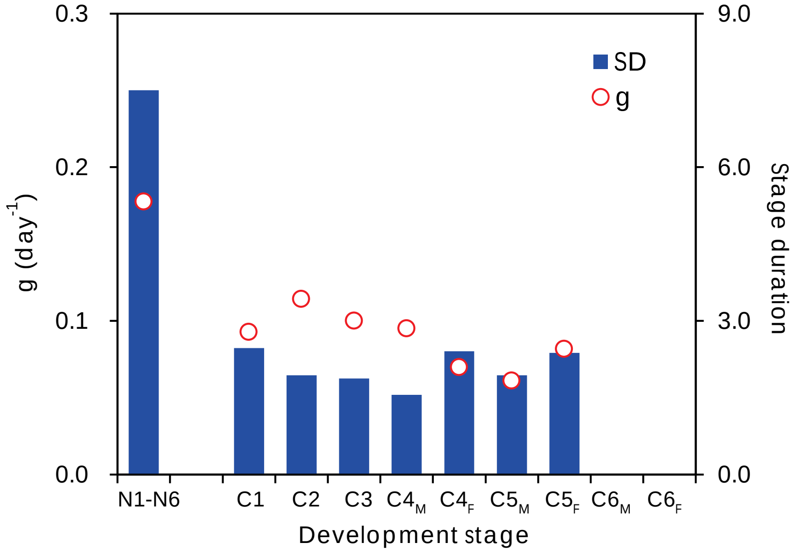

Fig. 5.2 Development changes in weight-specific growth rate (g) and stage duration (SD) of *Pseudodiaptomus inopinus* in the culture. N: nauplius stage. C: copepodite stage. M: male. F: female.

Table 5.1 Development changes in total body length (TL), individual body weight (BW), stage duration (SD), weight increment (G) and weight-specific growth rate (g) of *Pseudodiaptomus inopinus* in the culture.

Stage	TL ($10^3\mu$m)		BW (μgC)		SD (days)		G (μgC day^{-1})	g (day^{-1})
	Mean ± SE	***n***	**Mean ± SE**	***n***	**Mean ± SE**	***n***		
Nauplius								
N1	0.144 ± 0.001	30	0.140 ± 0.002	30	7.5	1	0.052	0.178
N2	0.171 ± 0.002	30	0.174 ± 0.002	30				
N3	0.207 ± 0.001	30	0.219 ± 0.001	30				
N4	0.235 ± 0.001	30	0.255 ± 0.002	30				
N5	0.276 ± 0.001	30	0.310 ± 0.002	30				
N6	0.317 ± 0.002	30	0.367 ± 0.003	30				
Copepodite								
C1	0.428 ± 0.002	30	0.530 ± 0.003	30	2.5 ± 0.2	32	0.055	0.093
C2	0.517 ± 0.004	30	0.667 ± 0.006	30	1.9 ± 0.1	24	0.085	0.114
C3	0.620 ± 0.003	30	0.832 ± 0.005	30	1.9 ± 0.2	20	0.092	0.100
C4M	0.723 ± 0.003	30	1.004 ± 0.005	30	1.6 ± 0.2	9	0.103	0.095
C4F	0.815 ± 0.005	30	1.163 ± 0.008	30	2.4 ± 0.3	11	0.089	0.070
C5M	0.816 ± 0.004	30	1.165 ± 0.007	30	1.9 ± 0.1	8	0.076	0.061
C5F	0.936 ± 0.004	30	1.376 ± 0.007	30	2.4 ± 0.1	8	0.124	0.082
C6M	0.900 ± 0.003	30	1.311 ± 0.005	30	ND		ND	ND
C6F	1.097 ± 0.007	30	1.671 ± 0.014	30	ND		ND	ND

n: number of individuals for measurements, SE: standard error, ND: no data

5.3 *Natural cohort and modified natural cohort methods*

Toru Kobari, Yuka Matsuura, Yui Nakata, Yuichiro Yamada and Tomonari Kotani

While late copepodite stages were mixed in the artificial cohort, early naupliar stages comprised more than 90% of the cultured copepod population at the beginning of the incubation (Fig. 5.3). *P. inopinus* increased significantly in abundance in the early phase of the incubation when they exhibited subsequent development from early to middle naupliar stages. Early copepodite stages appeared during Day 7 to Day 9, whereas early naupliar stages increased in relative abundance. Thereafter, subsequent development from early to middle naupliar stages occurred again and early copepodites increased in abundance in the population. A maximum abundance (1.6×10^3 individuals L^{-1}) was observed on Day 11.

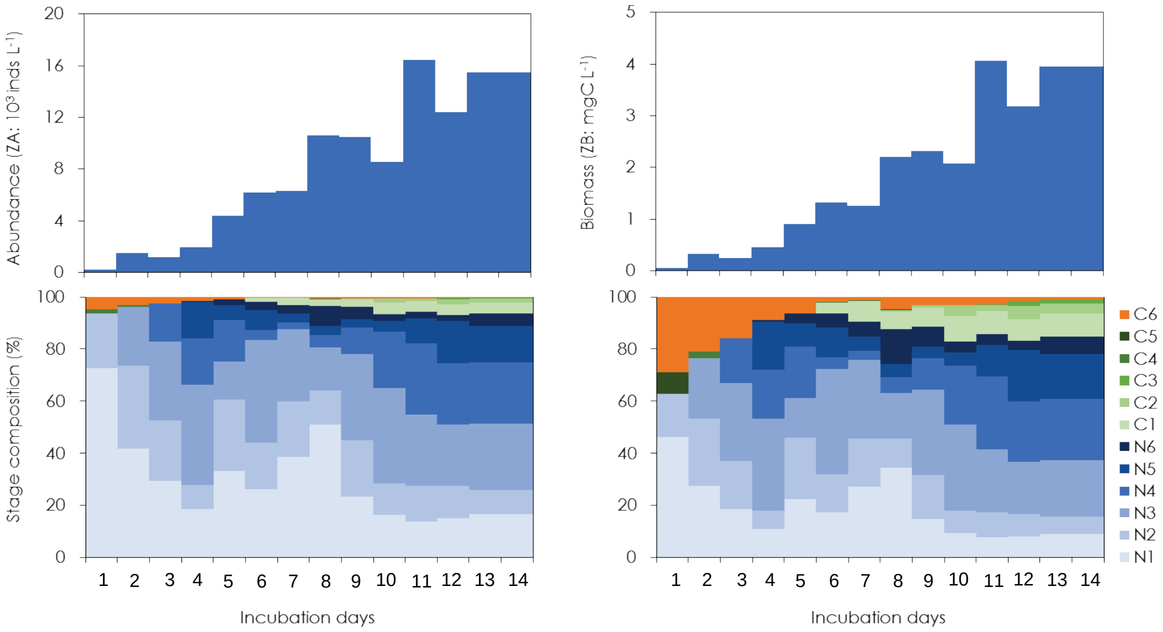

Fig. 5.3 Daily changes in population abundance (*ZA*), biomass (*ZB*) and stage compositions of *Pseudodiaptomus inopinus* in the culture. N: nauplius stage. C: copepodite stage.

Copepodite stage 6 contributed to 38% of the population biomass at the beginning of the incubation and declined in relative biomass in the early incubation phase. Population biomass increased with the contribution of early naupliar stages but their relative composition started to decline when they were replaced by early copepodites which made up 4 to 15% of the biomass. Maximum biomass (4.1 mgC L^{-1}) was observed on Day 12.

While similar temporal changes were evident for production rates estimated with the natural cohort and modified natural cohort methods, the production estimates with the modified natural cohort method corresponded to abundance and biomass to a greater degree (Fig. 5.4). Production rates estimated with the natural cohort method increased throughout the incubations and reached a maximum (0.8 mgC L^{-1} day^{-1}) at the end of the incubation. A maximum production rate (0.7 mgC L^{-1} day^{-1}) appeared on Day 11 for the modified natural cohort method. Early to middle naupliar stages contributed to the production rate during the early incubation phase and late nauplii and early copepodites increased their relative composition.

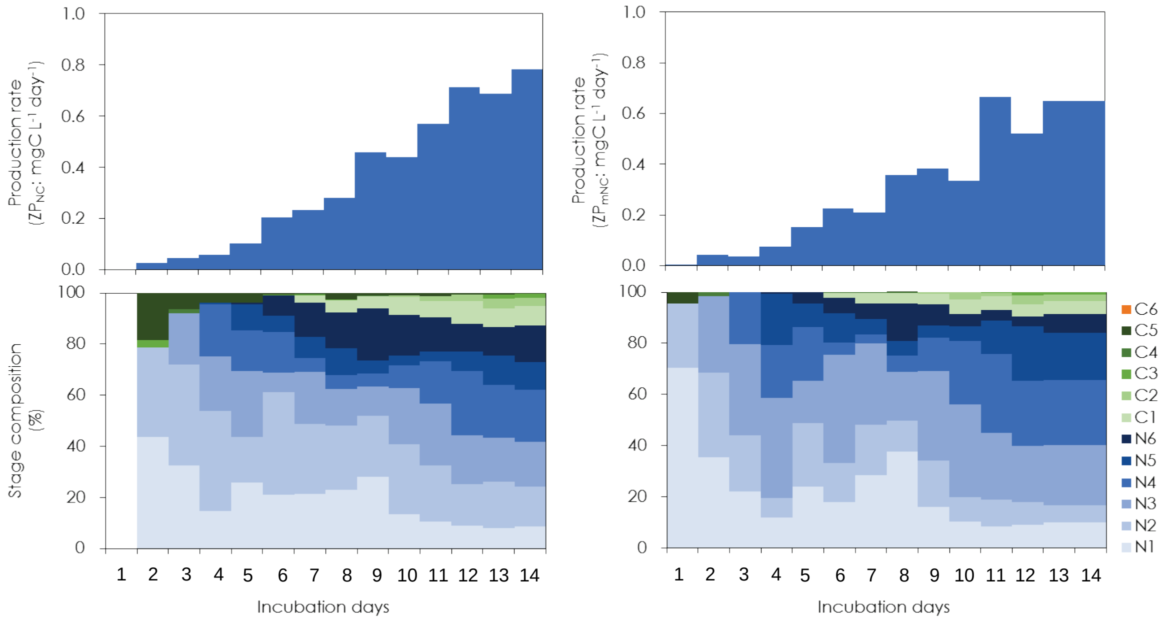

Fig. 5.4 Daily changes in population production rates (*ZP*) of *Pseudodiaptomus inopinus* and their stage composition in the culture estimated with the natural cohort (*NC*) and modified natural cohort (*mNC*) methods. N: nauplius stage. C: copepodite stage.

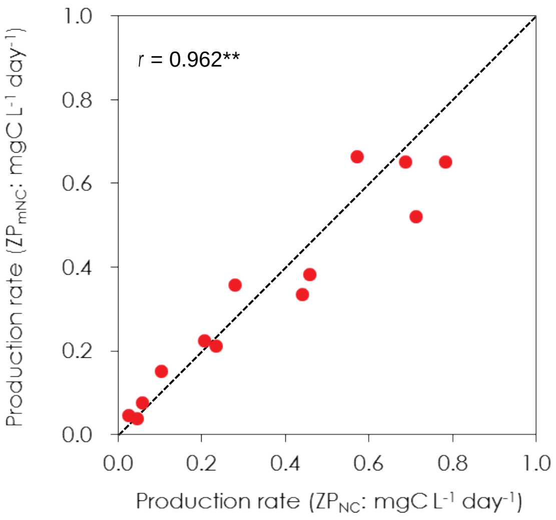

Fig. 5.5 Comparison of population production rates (*ZP*) and stage composition of *Pseudodiaptomus inopinus* in the culture estimated with the natural cohort (*NC*) and modified natural cohort (*mNC*) methods and their stage compositions. *r*: Pearson correlation coefficient. **: $p < 0.01$.

Significant positive correlation was found between the production estimates using the natural cohort and modified natural cohort methods (Fig. 5.5). Compared to the production estimates using the natural cohort method, the production rates with the modified natural cohort method were overestimated during the early incubation phase when early to middle naupliar stages were predominant and underestimated in the late incubation phase when late nauplii and early copepodites increased.

5.4 AARS activity and natural cohort method

Toru Kobari, Yuichiro Yamada, Megu Iwazono, Yuka Matsuura, Yui Nakata

Protein-specific AARS activity exhibited a maximum (7.6 μmolPPi mg-Protein^{-1} day^{-1}) at the beginning of the incubation and tended to be high in the early incubation phase when the production rates were low (Fig. 5.6). Protein-specific AARS activity declined with increasing production rates and tended to be low in the late incubation phase. Total AARS activity was low in the early incubation phase and increased thereafter. Total AARS activity reached a maximum (26.8 μmolPPi L^{-1} day^{-1}) at the end of incubation. The temporal changes of the total AARS activity were consistent with those of the production estimates.

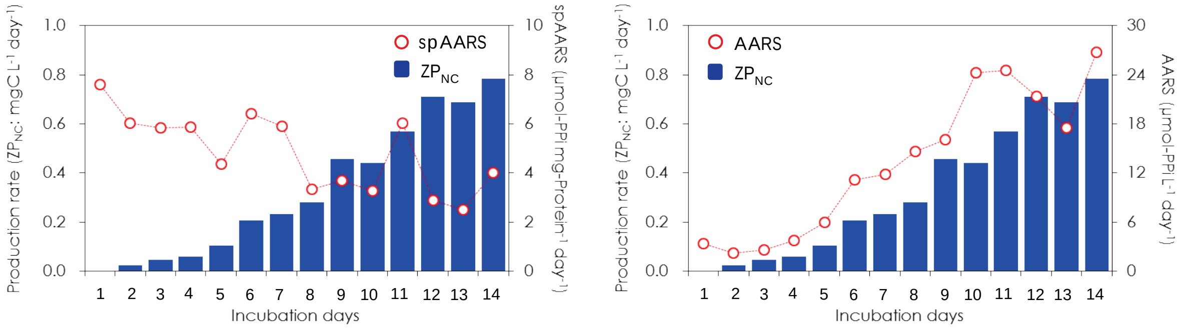

Fig. 5.6 Daily changes in population production rates (*ZP*, columns) estimated with the natural cohort (*NC*) and modified natural cohort (*mNC*) methods and (left) protein-specific (spAARS, open circles) and (right) total aminoacyl tRNA synthetases (AARS, open circles) activity of *Pseudodiaptomus inopinus* in the culture.

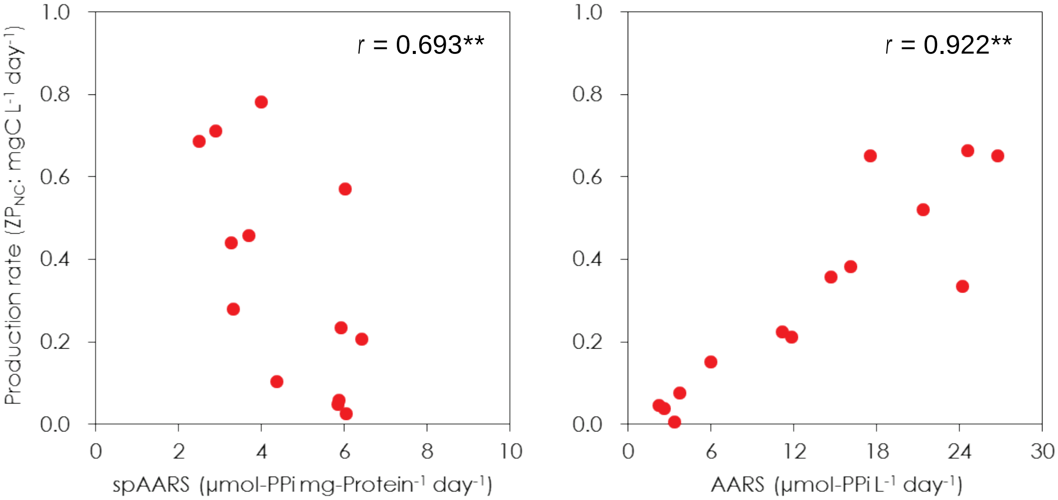

Fig. 5.7 Comparison of population production rates (*ZP*) estimated with the natural cohort (*NC*) and modified natural cohort (mNC) methods to (left) protein-specific (spAARS) and (right) volume-specific (AARS) aminoacyl tRNA synthetases activity of *Pseudodiaptomus inopinus* in the culture. *r*: Pearson correlation coefficient. **: $p < 0.01$.

While protein-specific AARS showed significantly negative correlation to the production rates, significant positive correlations were found between total AARS activity and the production rates (Fig. 5.7). According to previous reports (McKinnon *et al*., 2015), high protein-specific AARS activity was evident for zooplankton communities dominated by smaller individuals compared with those dominated by larger individuals. Protein-specific AARS activity might occur before the increase of population or community production and thus would be representative of growth potential. On the other hand, as demonstrated by Yebra *et al*. (2006a), total AARS activity can be a proxy for production rates.

5.5 Chitobiase activity and natural cohort

Akash Sastri, John Dower, Alex Clancy, Yuichiro Yamada, Tomonari Kotani, Toru Kobari and Yuka Matsuura

Chitobiase activity in the culture vessel varied between 21 and 104 nmol methylumbelliferone liberated L^{-1} $hour^{-1}$ during the 14-day (August 25 to September 8) observation period. This *in situ* enzyme activity ("CBAnat" Sastri and Dower 2006) was converted to biomass produced (delta biomass) using the generalized CBAnat-delta biomass relationship for crustacean zooplankton (Sastri and Dower, 2009). CBAnat is expected to vary with developing (or in this case juvenile copepod) biomass, as was generally observed in our culture vessel (Fig. 5.8). Under steady-state conditions, the rate of biomass production is calculated as the delta biomass divided by enzyme turnover rate which is itself calculated as the negative reciprocal of the slope of the exponential decay of enzyme activity measured via daily incubations. Note however, that the population was developing synchronously, so, we corrected for non-steady state as per Oosterhuis *et al*. (2000).

Chitobiase activity increased with population biomass through time for the first 12 days, with activity lagging biomass by approximately one day (Fig. 5.8). Estimated chitobiase-based rates of biomass production rates also varied with the biomass of juvenile copepods (NI–CV) with a lag of one day (Fig. 5.9a). The correspondence between chitobiase-based biomass production rates and biomass was strong (Fig. 5.9b, $R^2_{adj} = 0.86$, $p < 0.001$). (Lagged correlations are not presented here as they yield only moderate improvement of R^2_{adj} values.) Finally, we compared chitobiase-based production rates to natural cohort-based production estimates (see Equation 5, section 5.2). As per juvenile biomass, chitobiase-based production rates tended to vary but with lagged natural cohort-based production rates by approximately one day (Fig. 5.10a). The temporal pattern for both production rate estimates is similar. However, chitobiase-based estimates were much lower. Correspondence between the two rate estimates was strong (Fig. 5.10b, $R^2_{adj} = 0.74$, $p < 0.001$). All field estimates of chitobiase-based production rates (*e.g*., Oosterhuis *et al*., 2000; Sastri and Dower, 2009; Sastri *et al*., 2012; Suchy *et al*., 2016a) have yielded estimates comparable or greater (never lower) than biomass and/or production rates derived from corresponding plankton net-based estimates. It is not clear why chitobiase-based estimates in this study were considerably lower (1/3 to 1/4) than the corresponding natural cohort estimates. However, one possibility is that animals were sampled daily from the surface with a siphon (section 5.2) and density calculated as the number of individuals divided by volume siphoned. This approach may have led to the observed discrepancy if animals tended to aggregate at the surface (chitobiase activity assumed to be homogenous throughout the culture vessel). It is difficult to reconcile this issue in the absence of additional measurements. Nevertheless, correspondence between both biomass and natural cohort-based production rates and chitobiase-based production rates was strong and indicates that this method is useful for experimental laboratory cultures of copepods.

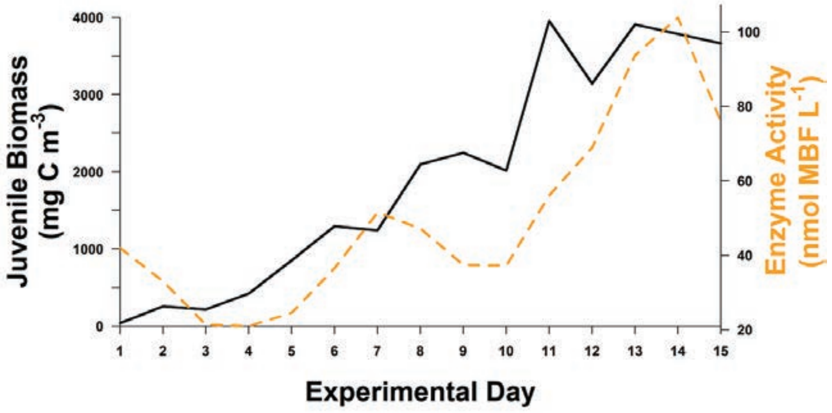

Fig. 5.8 Temporal patterns of juvenile copepod biomass (black line; mgC m^{-3}) and native chitobiase activity (dashed orange line; nmol methylumbelliferone liberated L^{-1} $hour^{-1}$) in the experimental *Pseudodiaptomus inopinus* culture vessel.

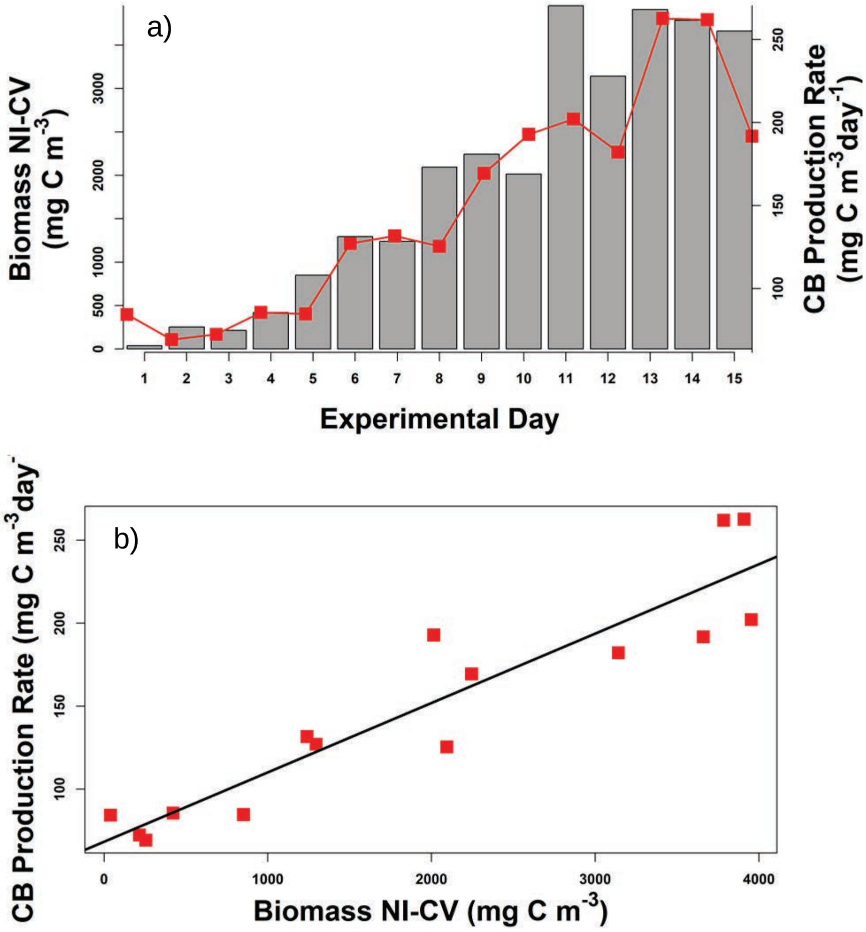

Fig. 5.9 a) Temporal patterns of juvenile copepod biomass (grey bars; mgC m^{-3}) and chitobiase-based biomass production rates (red line and symbols; mgC m^{-3} day^{-1}) in the experimental *Pseudodiaptomus inopinus* culture vessel and b) relationship ($R^2_{adj} = 0.86$, $p < 0.001$) between juvenile copepod biomass (mgC m^{-3}) and chitobiase-based biomass production rates (mgC m^{-3} day^{-1}).

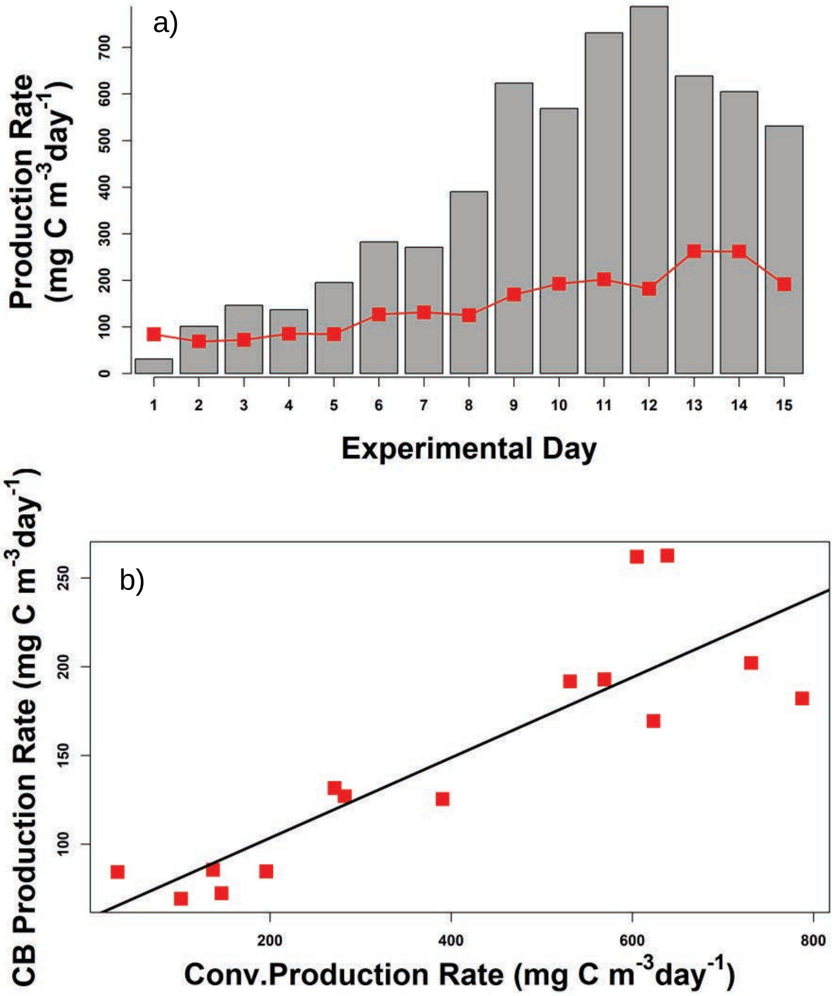

Fig. 5.10 a) Temporal patterns of juvenile copepod production rate (grey bars; mgC m^{-3} day^{-1}) estimated with the natural cohort method and chitobiase-based biomass production rates (red line and symbols; mgC m^{-3} day^{-1}) in the experimental *Pseudodiaptomus inopinus* culture vessel and b) relationship (R^2_{adj} = 0.74, $p < 0.001$) between juvenile copepod production rate (mgC m^{-3} day–1) estimated with the natural cohort method and chitobiase-based biomass production rates (mgC m^{-3} day^{-1}).

5.6 AARS activity and physiological model

Toru Kobari, Megu Iwazono, Yuichi Nishikawa, Yuka Matsuura and Yui Nakata

Aminoacyl tRNA synthetases (AARS) activity and the physiological model (*ZP*) were the methods which productivity can be evaluated for zooplankton community guilds. However, there is little knowledge whether these measurements are comparable between the two methods. To compare these measurements with AARS and *ZP*, zooplankton samples were collected using a twin-type NORPAC net (mesh size: 0.1 mm) from a coastal site (OS: Osumi Strait) and a pelagic site (KR: Kuroshio). AARS and *ZP* were measured for the community guild and the size-fractionated guilds (three size groups) at both sites.

AARS of the community guild were greatly variable, ranging from 5.4 to 171.9 μmolPPi m^{-3} day^{-1} at the coastal site and from 0.7 to 70.1 μmolPPi m^{-3} day^{-1} at the pelagic site (Figs. 5.11, 5.12). AARS were lower for the pelagic community compared with those for the coastal community. The community guild *ZP* was variable, ranging from 0.2 to 8.4 mgC m^{-3} day^{-1} at the coastal site and 0.2 to 2.6 mgC m^{-3} day^{-1} at the pelagic site. The pelagic community included some measurements with high *ZP* at low AARS, but such measurements were not observed for the coastal community. Variation range was much greater for the community-guild AARS compared with that for the community-guild *ZP*. Significant correlation was found for ZP_P to AARS at both coastal (Pearson correlation coefficient, $r = 0.741$, $p < 0.01$) and pelagic sites (Pearson correlation coefficient, $r = 0.319$, $p < 0.05$).

The size-fractionated AARS were more variable among the three groups and between the two sites, ranging from <0.1 to 90.2 μmolPPi m^{-3} day^{-1} at the coastal site and from 1.1 to 289.9 μmolPPi m^{-3} day^{-1} at the pelagic site (Fig. 5.13). The size-fractionated *ZP* ranged from <0.1 to 4.4 mgC m^{-3} day^{-1} at the coastal site and <0.1 to 0.7 mgC m^{-3} day^{-1} at the pelagic site. The variation ranges of AARS and *ZP* were the highest for the largest guild at the pelagic site and for the smallest guild at the coastal site, while the size-fractionated *ZP* to AARS revealed significant correlations for the medium and largest groups at the coastal sites and the three size-groups at the pelagic sites.

AARS and *ZP* are likely comparable for evaluating community guild productivity; however, there are some exceptions. At the coastal sites, *ZP* would be more variable (or unreliable) for the smaller size groups due to the overestimation of *ZB* with the mixture of large colonial phytoplankton like chain-forming diatoms.

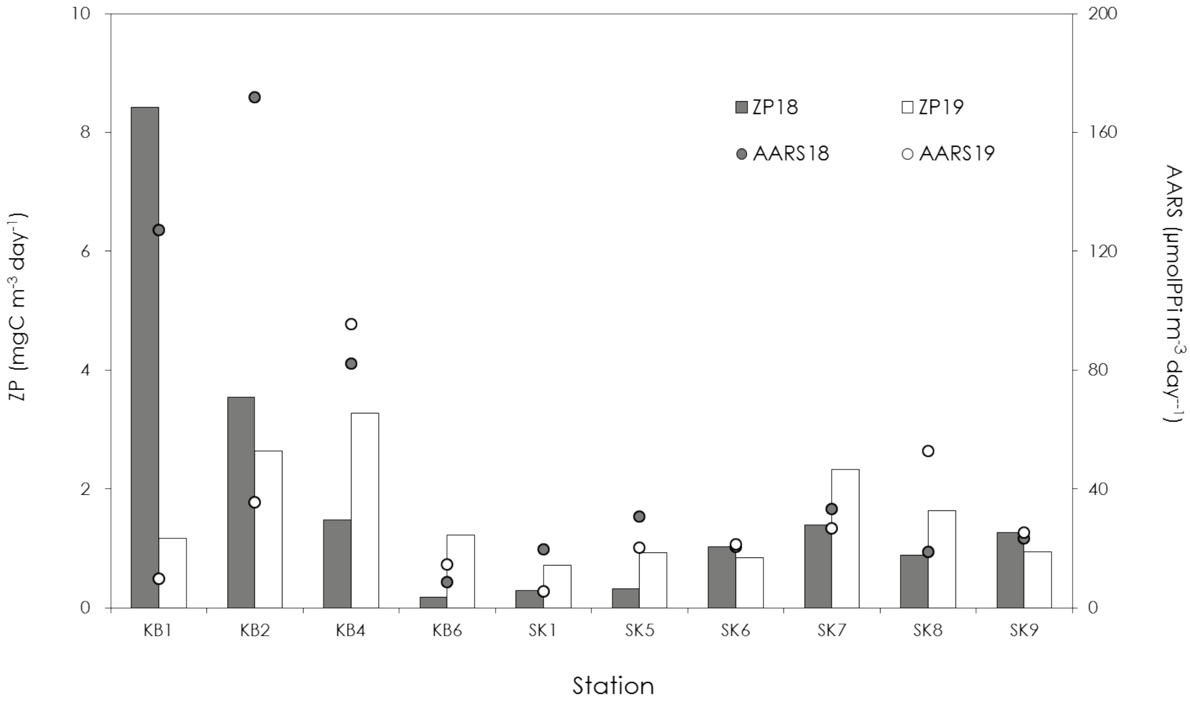

Fig. 5.11 Spatial changes in production rates (*ZP*: mgC m^{-3} day^{-1}) and total aminoacyl tRNA synthetases activity (AARS: μmolPPi m^{-3} day^{-1}) of the net zooplankton community at the coastal site (Osumi Strait, OS) during two cruises, in spring 2018 (18) (grey) and 2019 (19) (white).

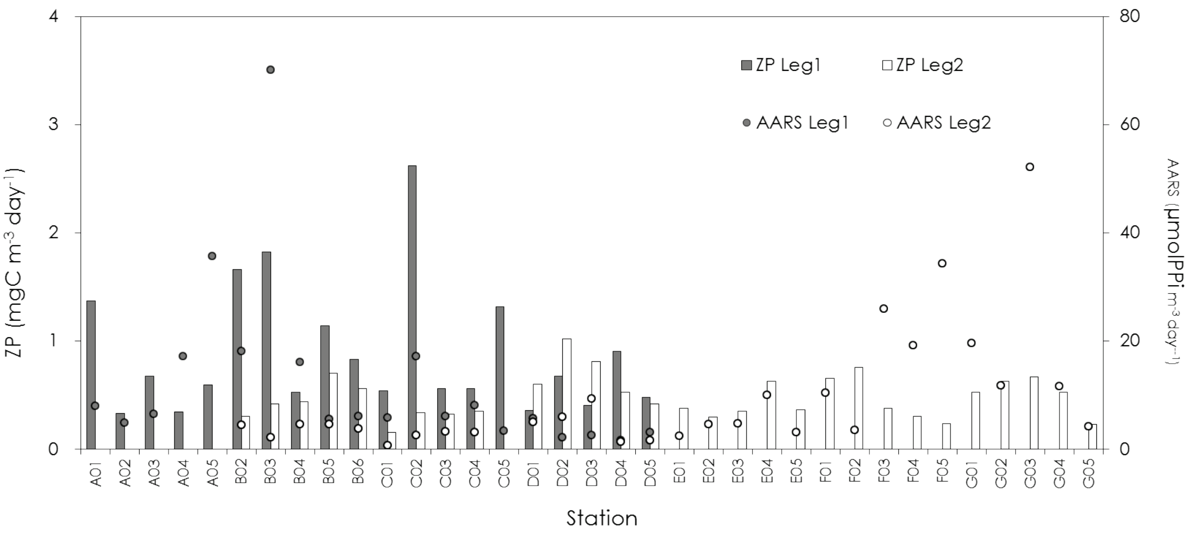

Fig. 5.12 Spatial variations in production rates (*ZP*: mgC m^{-3} day^{-1}) and aminoacyl tRNA synthetases activity (AARS: µmolPPi m^{-3} day^{-1}) of net zooplankton community at the pelagic site (Kuroshio, KR) during two cruises (Leg1 (grey) and Leg2 (white) in 2018.

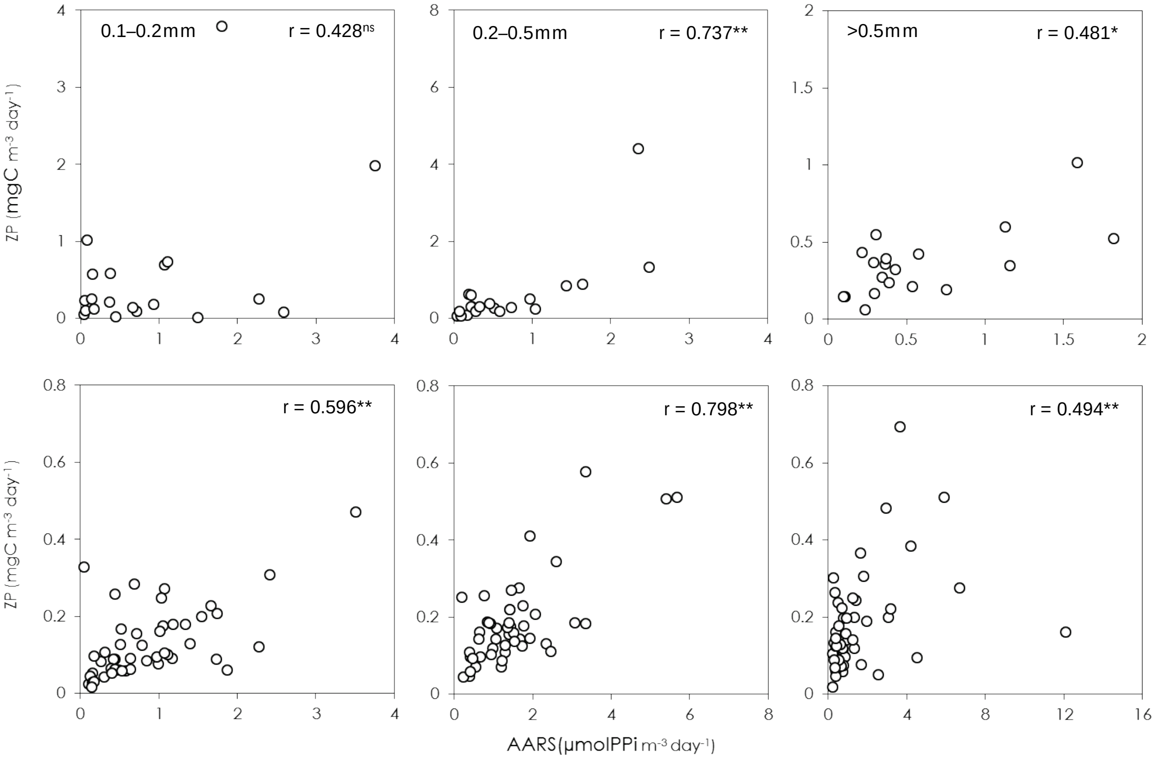

Fig. 5.13 Comparison of production rates estimated with a physiological model (ZP_P) on a size-fractionated zooplankton community at the coastal site (Osumi Strait: OS, top row) and pelagic site (Kuroshio: KR, bottom row) to the directly measured aminoacyl tRNA synthetases (AARS) activity on a size-fractionated zooplankton community. *r*: Pearson correlation coefficient. ns: no significance. *: $p < 0.05$. **: $p < 0.01$.

6 Concluding Remarks

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6.1 Recommendations

Toru Kobari, Akash Sastri and Lidia Yebra

Some recommendations have already been described and discussed in review papers (Yebra *et al.*, 2017; Kobari *et al.*, 2019a). To specify the most suitable method(s), they compared the advantages, disadvantages and limitations against target groups, locations and situations. However, due to the trade-offs imposed by their advantages, disadvantages and limitations of each method, we still have no globally standardized or accepted methodology for estimating zooplankton growth and production rates. Table 6.1 provides a comparison of advantages, disadvantages/problems and requirements among the traditional and biochemical methodologies.

The most compelling advantage of the traditional methodologies is that they provide direct rates of zooplankton growth rate applicable to calculations of production rate. In contrast, it may be difficult to constrain error due to the artifacts induced by the user's skill, artificial conditions and scaling issues. On the other hand, the most compelling advantages of biochemical approaches are reproducibility and high resolution in time and space. Unfortunately, with the exception of the chitobiase method, most biochemical methods need a calibration against direct rates of zooplankton growth and/or production due to the lack of a general biochemical-based equation to assess growth and production rates. The chitobiase method relies on a general relationship (Sastri and Dower, 2009) between growth increment and enzyme activity applicable across a wide-range of crustacean taxa. However, these specifics suggest that such disadvantages and problems might be overcome or better understood by a combined application of both traditional and biochemical methods. It is also important to choose the most appropriate method among the traditional and biochemical methods, depending on the study objectives and goals (coverage in time and space, either rates or indices, *etc*.) and the time, resources and facilities available (either in a laboratory or on a cruise, any existing data sets, *etc*.).

As discussed above, cases requiring direct growth and/or production rates cannot rely on many of the biochemical methods, except for chitobiase which does provide production estimates in relevant units (*i.e.*, mass T^{-1}). If growth potential or productivity is required, however, those biochemical indices based on nucleic acid ratios or nucleic acid linked enzyme activities are suitable. The detailed descriptions on the traditional and biochemical methodologies in this guideline would be useful for applying the most appropriate ones to zooplankton individual, population and community in nature.

Table 6.1 Advantages, disadvantages/problems and requirements of the traditional methodologies and biochemical approaches for applying zooplankton population or community in nature.

Methods	Advantages	Disadvantages/Problems	Requirements
Traditional methodologies			
Natural cohort	Applicable to wide taxonomic groups including community guild	Difficult or impossible identification of cohorts	High sampling frequency
Artificial cohort	Applicable to wide taxonomic groups including community guild	Labor intensive, No or less detection for slow growth	Incubation, Close to *in situ* density
Molting rate	Reproducible, High resolution in time and space	Limited taxonomic groups and life stages	Incubation, Calculation with the modified equations
Egg production	Reproducible, High resolution in time and space	Only for adult female, Not always representative to growth	Incubation
Empirical models	Applicable to wide locations	Only for copepods, Inconsistent with directly-measured growth	Some variables for each model
Physiological model	Applicable to wide taxonomic groups including community guild and wide locations	Highly dependent on assumptions used	Some variables in model and assumptions
Biochemical approaches			
Nucleic acid ratio	Reproducible, High resolution in time and space, Applicable to wide taxonomic groups	Individual based, Dimensional correction to growth, Necessary for calibration against growth rates	Deep freezing
Chitobiase activity	Reproducible, High resolution in time and space, Applicable across crustacean taxonomic groups, Applicable at the community/assemblage level	Limited to crustaceans	Short seawater incubation (12 hours), enzyme assays within two weeks of incubation
Aminoacyl tRNA synthetases activity	Reproducible, High resolution in time and space, Applicable to wide taxonomic groups including community guild	Dimensional calibration to growth, Necessary for calibration against direct rates	Quick and deep freezing

6.2 Future perspectives

Toru Kobari, Akash Sastri and Lidia Yebra

Zooplankton growth and production measurements are still limited for major taxonomic groups despite the various methodologies now available. There are still growth and productivity studies missing on many taxa such as protozoans, pelagic tunicates or gelatinous forms, which may represent an important proportion of community production. On the other hand, growth and production rates for zooplankton are still less frequently measured and with lesser coverage than those for phytoplankton. In this sense, contemporary biochemical methodologies or other approaches might be applicable to these groups and situations. Ideally, a general equation relating certain biochemical indices with growth rates of zooplankton community guild would lead to stimulate more measurements on zooplankton growth and production and a wider coverage of taxonomic groups, time and space. To achieve a more generalized equation, a focus on further laboratory studies designed to calibrate some of the biochemical methods on a wider range of taxa is recommended.

Some different approaches might be suggested as future prospects. The first approach is to establish regional empirical models to estimate growth or production rates assessed with the traditional methodologies based on region-specific environmental and zooplankton variables. Since all empirical models represent global trends, the estimated rates encompass broad variance (*i.e.*, underestimation or overestimation) with respect to the directly measured rates. Regional empirical models would minimize such variance when applied to communities of target regions. The second approach is to apply the physiological model which is only applicable to wide taxonomic groups and locations on the existing zooplankton time-series and data sets. Nowadays, numerous time-series on zooplankton standing stock and environmental parameters are available. Such application would produce regional and global maps of zooplankton productivity as potential indices of the complex responses of marine ecosystems to global warming and ocean acidification. The third approach is inter-comparison or calibration (as needed) of biochemical indices against growth and production rates estimated with the traditional methods. These tasks would allow for a global comparison of growth and production rates estimated with the different methods and their high-resolution mapping in time and space by incorporation of biochemical indices in monitoring activities.

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Appendix 1

WG 37 Terms of Reference

WG 37 term: 2016–2021
Extended 1 year to 2022
Parent Committee: BIO

1. Summarize assumptions, recent advances and limitations of both traditional and biochemical methodologies for measuring zooplankton production of natural populations and communities.

2. Produce recommendations and procedures for both traditional and biochemical zooplankton production rate measurement methodologies and make them available on a website for worldwide access.

3. Develop practical models for estimating zooplankton production from time-series observations.

4. Develop an interactive website for exchange of information on zooplankton production measurements for regional and/or global mapping.

5. Build a network of scientists and laboratories measuring zooplankton production among PICES member nations.

6. Promote international collaborations among zooplankton production researchers with other international organizations or programs (*e.g.*, ICES and IMBeR).

7. Publish a final report summarizing results.

Appendix 2

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Appendix 3

Laboratories Working on Zooplankton Production

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2	Erica Head	Canada	Fisheries and Oceans Canada, Bedford Institute of Oceanography	Erica.Head@dfo-mpo.gc.ca	Egg production
3	Karyn D. Suchy	Canada	Department of Earth, Ocean and Atmospheric Sciences, University of British Columbia	ksuchy@eoas.ubc.ca	Chitobiase activity, Bio-physical models
4	Marc Ringuette	Canada	Fisheries and Oceans Canada, Bedford Institute of Oceanography	Marc.Ringuette@dfo-mpo.gc.ca	Egg production
5	Delphine Bonnet	France	MARBEC, University of Montpellier	delphine.bonnet@umontpellier.fr	Egg production, Somatic growth, AARS
6	Fabien Lombard	France	Laboratoire d'océanographie de Villefranche sur mer	lombard@obs-vlfr.fr	Somatic growth, Empirical models
7	Epaminondas Christou	Greece	Hellenic Center for Marine Research/Institute of Oceanography	edc@hcmr.gr	Egg production
8	Soultana Zervoudaki	Greece	Hellenic Center for Marine Research/Institute of Oceanography	tanya@hcmr.gr	Egg production, AARS, Natural cohort, Somatic growth
9	Astthor Gislason	Iceland	Marine and Freshwater Research Institute	astthor.gislason@hafogvatn.is	Egg production
10	Hildur Petursdottir	Iceland	Marine and Freshwater Research Institute	astthor.gislason@hafogvatn.is	Egg production
11	Lisa Anne Libungan	Iceland	Marine and Freshwater Research Institute	astthor.gislason@hafogvatn.is	Egg production
12	Teresa Silva	Iceland	Marine and Freshwater Research Institute	astthor.gislason@hafogvatn.is	Egg production
13	Ylenia Carotenuto	Italy	Stazione Zoologica Anton Dohrn	ylenia.carotenuto@szn.it	Egg production
14	Atsushi Yamaguchi	Japan	Faculty of Fisheries, Hokkaido University	a-yama@fish.hokudai.ac.jp	Empirical models, Egg production

	Name	Nation	Institute	Email	Methodology used
15	Hiroomi Miyamoto	Japan	Tohoku National Fisheries Research Institute	miyamotohiroomi@affrc.go.jp	Egg production
16	Kazuaki Tadokoro	Japan	Tohoku National Fisheries Research Institute, FRA	den@affrc.go.jp	Empirical models
17	Kazutaka Takahashi	Japan	University of Tokyo	akazutak@mail.ecc.u-tokyo.ac.jp	Egg production, Natural cohort
18	Koichi Ara	Japan	College of Bioresource Sciences, Nihon University	arakoich@brs.nihon-u.ac.jp	Natural cohort, Empirical models
19	Ryota Nakajima	Japan	Japan Agency for Marine-Earth Science and Technology	nakajimar@jamstec.go.jp	Natural cohort, Empirical models
20	Shinji Shimode	Japan	Manazuru Marine Center, Yokohama National University	shimode@ynu.ac.jp	Egg production
21	Toru Kobari	Japan	Faculty of Fisheries, Kagoshima University	kobari@fish.kagoshima-u.ac.jp	Molting rate, Nucleic acid ratio, AARS, Physiological model, Empirical models
22	Hyung-Ku Kang	Korea	Marine Ecosystem and Biological Research Center, KIOST	kanghk@kiost.ac.kr	Natural cohort
23	Jung Hoon Kang	Korea	Korea Institute of Ocean Science and Technology	jhkang@kiost.ac.kr	Natural cohort
24	Min-Chul Jang	Korea	Korea Institute of Ocean Science and Technology	mcjang@kiost.ac.kr	Egg production
25	Se-Jong Ju	Korea	Korea Institute of Ocean Science and Technology	sjju@kiost.ac.kr	Egg production
26	Webjørn Melle	Norway	Institute of Marine Research	webjorn@hi.no	Egg production
27	Nejib Daly Yahia	Qatar	College of Arts and Sciences, Qatar University	nejibdaly@qu.edu.qa	Egg production
28	Elena Hubareva	Russia	A.O. Kovalevsky Institute of Marine Biological Research	ehubareva@mail.ru	
29	Albert Calbet	Spain	Institut de Ciències del Mar, CSIC	acalbet@icm.csic.es	Egg production, Somatic growth
30	Enric Saiz	Spain	Institut de Ciències del Mar, CSIC	enric@icm.csic.es	Egg production, Somatic growth
31	Ibon Uriarte	Spain	University of the Basque Country (UPV/EHU)	ibon.uriarte@ehu.eus	Egg production
32	Lidia Yebra	Spain	Centro Oceanográfico de Málaga, IEO	lidia.yebra@ieo.es	AARS, Artificial cohort, Egg production
33	Ziortza Barroeta	Spain	University of the Basque Country (UPV/EHU)	ziortzabarroetalegarreta@gmail.com	Egg production
34	Elena Gorokhova	Sweden	Stockholm University	elena.gorokhova@su.se	Nucleic acid ratio, AARS
35	Neila Annabi-Trabelsi	Tunisia	Laboratory of biodiversity and Aquatic ecosystems, University of Sfax	neila.trabelsi@isbs.usf.tn	Egg production
36	Zaher Drira	Tunisia	Sfax Faculty of Sciences, University of Sfax	zaherdrira@yahoo.fr	Natural cohort

	Name	**Nation**	**Institute**	**Email**	**Methodology used**
37	Dalida Bedikoglu	Türkiye	Institution of Marine Sciences and Management, Istanbul University	dalidabedikoglu@gmail.com	Egg production
38	Funda Üstün	Türkiye	Fisheries Faculty, Sinop University	fundaustun@gmail.com	Egg production
39	Angus Atkinson	UK	Plymouth Marine Laboratory	aat@pml.ac.uk	Egg production
40	Dan Mayor	UK	National Oceanography Centre	Dan.Mayor@noc.ac.uk	Egg production, Molting rate
41	Kathryn Cook	UK	National Oceanography Centre	Kathryn.Cook@noc.ac.uk	Egg production, Molting rate
42	Leonid Svetlichny	Ukraine	I.I. Schmalhausen Institute of Zoology	leonid.svetlichny@gmail.com	Natural cohort, Somatic growth, Egg production
43	Hui Liu	USA	TAMU Galveston Marine Biology	liuh@tamug.edu	Artificial cohort
44	Russell R Hopcroft	USA	Institute of Marine Science, University of Alaska	rrhopcroft@alaska.edu	Artificial cohort

Appendix 4

Bibliography of Zooplankton Production in the PICES Region

	Authors	Year	Title	Journal, volume and pages	Location	Methodology used
1	T. Ikeda, S. Motoda	1978	Estimated zooplankton production and their ammonia excretion in the Kuroshio and adjacent seas	*Fishery Bulletin* **76**: 357–367	Kuroshio	Physiological models
2	S. Uye	1981	Fecundity studies of neritic calanoid copepods *Acartia clausi* Giesbrecht and *Acartia steueri* Smirnov - a simple empirical model of daily egg production	*Journal of Experimental Marine Biology and Ecology* **50**: 255–271	Laboratory	Egg production
3	S. Uye	1982	Population dynamics and production of *Acartia clausi* Giesbrecht (Copepoda, Calanoida) in inlet waters	*Journal of Experimental Marine Biology and Ecology* **57**: 55–83	Inland Sea of Japan, Gulf of Mexico	Natural cohort
4	S. Uye, Y. Iwai, S. Kasahara	1983	Growth and production of the inshore marine copepod *Pseudodiaptomus marinus* in the central part of the Inland Sea of Japan	*Marine Biology* **73**: 91–98	Inland Sea of Japan	Natural cohort
5	T. Ikeda	1985	Metabolic rates of epipelagic marine zooplankton as a function of body mass and temperature	*Marine Biology* **85**: 1–11	Global	Physiological models
6	K. Kimoto, S. Uye, T. Onbé	1986	Growth characteristics of a brackish-water calanoid copepod *Sinocalanus tenellus* in relation to temperature and salinity	*Bulletin of Plankton Society of Japan* **33**: 43–57	Laboratory	Incubation
7	S. Uye, H. Kuwata, T. Endo	1986	Standing stocks and production rate of phytoplankton and planktonic copepods in the Inland Sea of Japan	*Journal of the Oceanographic Society of Japan* **42**: 421–434	Inland Sea of Japan	Physiological models
8	W.J. Kimmerer, A.D. McKinnon	1987	Growth, mortality, and secondary production of the copepod *Acartia tranteri* in Westernport Bay, Australia.	*Limnology and Oceanography* **32**: 14–28	Australian coast	Artificial cohort
9	S. Uye	1988	Temperature dependent development and growth of *Calanus sinicus* (Copepoda, Calanoida) in the laboratory	*Hydrobiologia* **167**: 285–293	Laboratory	Incubation

	Authors	Year	Title	Journal, volume and pages	Location	Methodology used
10	K. Nakata	1990	Abundance of nauplii and protein synthesis activity of adult female copepods in the Kuroshio front during the Japanese sardine spawning season	*Journal of Oceanographic Society of Japan* **46**: 219–229	Kuroshio	Nucleic acid ratio
11	D.M. Checkley, M.J. Dagg, S. Uye	1992	Feeding, excretion and egg production by individuals and populations of the marine, planktonic copepods, *Acartia* spp. and *Centropages furcatus*	*Journal of Plankton Research* **14**: 71–96	Inland Sea of Japan, Gulf of Mexico	Egg production
12	S. Uye, N. Shibuno	1992	Reproductive biology of the planktonic copepod *Paracalanus* sp. in the Inland Sea of Japan.	*Journal of Plankton Research* **14**: 343–358	Inland Sea of Japan	Egg production
13	C. Huang, S. Uye, T. Onbé	1993	Geographic distribution, seasonal life cycle, biomass and production of a planktonic copepod *Calanus sinicus* in the Inland Sea of Japan and its neighboring Pacific Ocean	*Journal of Plankton Research* **15**: 1229–1246	Onagawa Bay, Japan	Natural cohort
14	D. Liang, S. Uye, T. Onbé	1994	Production and loss of eggs in the calanoid copepod *Centropages abdominalis* Sato in Fukuyama Harbor, the Inland Sea of Japan	*Bulletin of the Plankton Society of Japan* **4**: 131–142	Inland Sea of Japan	Egg production
15	K. Nakata, H. Nakano, H. Kikuchi	1994	Relationship between egg productivity and RNA/DNA ratio in *Paracalanus* sp. in the frontal waters of the Kuroshio	*Marine Biology* **119**: 591–596	Kuroshio	Nucleic acid ratio
16	S. Uye, K. Sano	1995	Seasonal reproductive biology of the small cyclopoid copepod *Oithona davisae* in a temperate eutrophic inlet	*Marine Ecology Progress Series* **118**: 121–128	Inland Sea of Japan	Egg production
17	S. Uye, S. Ichino	1995	Seasonal variations in abundance, size composition, biomass and production rate of *Oikopleura dioica* (Fol) (Tunicata, Appendicularia) in a temperate eutrophic inlet	*Journal of Experimental Marine Biology and Ecology* **189**: 1–11	Inland Sea of Japan	Natural cohort
18	D. Liang, S. Uye, T. Onbé	1996	Population dynamics and production of the planktonic copepods in eutrophic inlet of the Inland Sea of Japan. I. *Centropages abdominalis*	*Marine Biology* **124**: 527–536	Inland Sea of Japan	Natural cohort
19	D. Liang, S. Uye	1996	Population dynamics and production of the planktonic copepods in eutrophic inlet of the Inland Sea of Japan. II. *Acrtia omorii*	*Marine Biology* **125**: 109–117	Inland Sea of Japan	Natural cohort
20	D. Liang, S. Uye	1996	Population dynamics and production of the planktonic copepods in eutrophic inlet of the Inland Sea of Japan. III. *Paracalanus* sp.	*Marine Biology* **127**: 219–227	Inland Sea of Japan	Natural cohort
21	D. Liang, S. Uye	1997	Seasonal reproductive biology of the egg-carrying calanoid copepod *Pseudodiaptomus marinus* in a eutrophic inlet of the Inland Sea of Japan	*Marine Biology* **128**: 409–414	Inland Sea of Japan	Egg production
22	D. Liang, S. Uye	1997	Population dynamics and production of the planktonic copepods in a eutrophic inlet of the Inland Sea of Japan. IV. *Pseudodiaptomus marinus*, the egg-carrying calanoid	*Marine Biology* **128**: 415–421	Inland Sea of Japan	Natural cohort

	Authors	Year	Title	Journal, volume and pages	Location	Methodology used
23	S. Uye, A. Murase	1997	Relationship of egg production rates of the planktonic copepod *Calanus sinicus* to phytoplankton availability in the Inland Sea of Japan	*Plankton Biology and Ecology* **44**: 3–11	Inland Sea of Japan	Egg production
24	S. Uye, T. Shimazu	1997	Geographical and seasonal variations in abundance, biomass and estimated production rates of meso-and macrozooplankton in the Inland Sea of Japan	*Journal of Oceanography* **53**: 529–538	Inland Sea of Japan	Empirical models
25	H.K. Kang, Y.J. Kang	1998	Egg production of the copepod *Acartia steueri* in Ilkwang Bay, southeastern coast of Korea	*Journal of Korean Fisheries Society* **31**: 288–295	Korean coast	Egg production
26	H.K. Kang, Y.J. Kang	1998	Growth and development of *Acartia steueri* (Copepoda: Calanoida) in the laboratory	*Journal of Korean Fisheries Society* **31**: 842–851	Korean coast	Artificial cohort
27	S. Uye, D. Liang	1998	Copepods attain high abundance, biomass and production in the absence of large predators but suffer cannibalistic loss	*Journal of Marine Systems* **15**: 1–4	Inland Sea of Japan	Natural cohort
28	S. Uye, K. Sano	1998	Seasonal variations in biomass, growth rate and production rate of the small cyclopoid copepod *Oithona davisae* in a temperature eutrophic inlet	*Marine Ecology Progress Series* **163**: 37–44	Inland Sea of Japan	Natural cohort
29	S. Uye, N. Nagano, T. Shimazu	1998	Biomass, production and trophic roles of micro- and net-zooplankton in Dokai Inlet, a heavily eutrophic inlet, in summer	*Plankton Biology and Ecology* **4**: 171–182	Dokai Inlet, Japan	Empirical models
30	M. Kotori	1999	Life cycle and growth rate of the chaetognath *Parasagitta elegans* in the northern North Pacific	*Plankton Biology and Ecology* **46**: 153–158	Oyashio	Natural cohort
31	T. Ikeda, N. Shiga	1999	Production, metabolism and production/biomass (P/B) ratio of *Themisto japonica* (Crustacea: Amphipoda) in Toyama Bay, southern Japan Sea	*Journal of Plankton Research* **21**: 299–308	Toyama Bay, Japan	Natural cohort, Empirical models
32	M. Tomita, T. Ikeda	1999	Production of *Oikopleura longicauda* (Tunicata: Appendicularia) in Toyama Bay, southern Japan Sea	*Journal of Plankton Research* **22**: 2421–2430	Toyama Bay, Japan	Natural cohort
33	N. Iguchi, T. Ikeda	1999	Production, metabolism and P:B ratio of *Euphausia pacifica* (Crustacea; Euphausiacea) in Toyama Bay, southern Japan Sea	*Plankton Biology and Ecology* **46**: 68–74	Toyama Bay, Japan	Natural cohort
34	S. Uye, N. Nagano, T. Shimazu	2000	Abundance, biomass, production and trophic roles of micro- and net-zooplankton in Ise Bay, central Japan, in winter	*Journal of Oceanography* **56**: 389–398	Ise Bay, Japan	Physiological models
35	A. Shinada, T. Ikeda, S. Ban, A. Tsuda	2001	Seasonal dynamics of planktonic food chain in the Oyashio region, western subarctic Pacific	*Journal of Plankton Research* **23**: 1237–1247	Oyashio	Natural cohort, Empirical models
36	K. Ara	2001	Daily egg production rate of the planktonic copepod *Acaitia lilljeborgi* in the Cananéia Lagoon estuarine system, São Paulo, Brazil	*Hydrobiologia* **45**: 205–215	Brazilian coast	Egg production

	Authors	Year	Title	Journal, volume and pages	Location	Methodology used
37	K. Ara	2001	Temporal variability and production of *Euterpina acutifrons* (Copepoda: Harpacticoida) in the Cananeia Lagoon estuarine system, Sao Paulo, Brazil	*Hydrobiologia* **453**: 177–187	Brazilian coast	Natural cohort
38	K. Ara	2001	Temporal variability and production of the planktonic copepods in the Cananéia Lagoon estuarine system, São Paulo, Brazil. II. *Acaitia lilljeborgi*	*Plankton Biology and Ecology* **48**: 35–45	Brazilian coast	Natural cohort
39	T. Ikeda, Y. Kanno, K. Ozaki, A. Shinada	2001	Metabolic rates of epipelagic marine copepods as a function of body mass and temperature	*Marine Biology* **139**: 587–596	Global	Physiological models
40	D. Takahashi, T. Ikeda	2002	Abundance, vertical distribution and life cycle patterns of the hydromedusa *Aglantha digitale* in the Oyashio region, western subarctic Pacific	*Plankton and Benthos Research* **1**: 91–96	Oyashio	Natural cohort
41	K. Ara	2002	Temporal variability and production of *Temora turbinata* (Copepoda: Calanoida) in the Cananéia Lagoon estuarine system, São Paulo, Brazil	*Scientia Marina* **66**: 399–406	Brazilian coast	Natural cohort
42	S. Uye, I. Aoto, T. Onbé	2002	Seasonal population dynamics and production of *Microsetella norvegica*, a widely distributed but little-studied marine planktonic harpacticoid copepod	*Journal of Plankton Research* **24**: 143–153	Inland Sea of Japan	Natural cohort
43	T. Ikeda, K. Hirakawa, N. Shiga	2002	Production, metabolism and production/biomass (P/B) ratio of *Metridia pacifica* (Crustacea: Copepoda) in Toyama Bay, southern Japan Sea	*Plankton Biology and Ecology* **49**: 58–65	Toyama Bay, Japan	Natural cohort
44	W.T. Peterson, J. Gómez-Gutiérrez, C.A. Morgan	2002	Cross-shelf variation in calanoid copepod production during summer 1996 off the Oregon coast, USA	*Marine Biology* **141**: 353–365	Oregon coast, USA	Egg production
45	K. Shin, M. Jang, P. Jang, S. Ju, M. Chang	2003	Influence of food quality on egg production and viability of marine planktonic copepod *Acartia omorii*	*Progress in Oceanography* **57**: 265–277	Korean coast	Egg production
46	T. Kobari, A. Shinada, A. Tsuda	2003	Functional roles of interzonal migrating mesozooplankton in the western subarctic Pacific	*Progress in Oceanography* **57**: 279–298	Oyashio	Empirical models
47	K. Ara	2004	Temporal variability and production of the planktonic copepod community in the Cananéia Lagoon estuarine system, São Paulo, Brazil	*Zoological Studies* **43**: 179–186	Brazilian coast	Natural cohort
48	S. Ju, H.R. Harvey	2004	Nutritional condition of the Antarctic krill, *Euphausia superba* and *Euphausia crystallorophias*, during austral winter.	*Deep-Sea Research II* **51**: 2199–2214	Antarctica	Lipid biomarkers
49	S. Ju, K. Scolardi, K. Daly, H.R. Harvey	2004	Understanding trophic roles of Ctenophore *Callianira antarctica* in Antarctic ecosystem using lipid biomarkers.	*Polar Biology* **27**: 782–792	Antarctica	Lipid biomarkers

	Authors	Year	Title	Journal, volume and pages	Location	Methodology used
50	S. Uye, S. Nakai, M. Aizaki	2004	Potential use of extremely high biomass and production of copepods in an enclosed brackish water body in Lake Nakaumi, Japan, for the mass seed production of fishes	*Zoological Studies* **43**: 165–172	Lake Nakaumi, Japan	Natural cohort
51	Y. Jung, H.K. Kang, Y.J. Kang	2004	In situ egg production rate of the planktonic copepod *Acartia steueri* in Ilkwang Bay, southeastern coast of Korea	*Journal of Plankton Research* **26**: 1547–1553	Korean coast	Egg production
52	H.K. Kang, Y.J. Kang	2005	Production of *Acartia steueri* (Copepoda: Calanoida) in Ilkwang Bay, southeastern coast of Korea	*Journal of Oceanography* **61**: 327–334	Korean coast	Natural cohort
53	A. Shinada, S. Ban, Y. Yamada, T. Ikeda	2005	Seasonal variations of plankton food web structure in the coastal water off Usujiri Southwestern Hokkaido, Japan	*Journal of Oceanography* **61**: 645–654	Oyashio	Natural cohort, Empirical models
54	S. Hernández-León, T. Ikeda	2005	A global assessment of mesozooplankton respiration in the ocean	*Journal of Plankton Research* **27**: 153–158	Global	Physiological models
55	S. Uye, H. Shimauchi	2005	Population biomass, feeding, respiration and growth rates, and carbon budget of the scyphomedusa *Aurelia aurita* in the Inland Sea of Japan	*Journal of Plankton Research* **27**: 237–248	Inland Sea of Japan	Natural cohort
56	H. Liu, R.R. Hopcroft	2006	Growth and development of *Neocalanus flemingeri/plumchrus* in the northern Gulf of Alaska: validation of the artificial-cohort method in cold waters	*Journal of Plankton Research* **28**: 87–101	Gulf of Alaska	Artificial cohort
57	H. Liu, R.R. Hopcroft	2006	Growth and development of *Metridia pacifica* in the northern Gulf of Alaska	*Journal of Plankton Research* **28**: 769–781	Gulf of Alaska	Artificial cohort
58	S. Ju, J. Gómez-Gutiérrez, W.T. Peterson, H.R. Harvey	2006	The role of lipid during embryonic development and sedimentation in eggs of the euphausiids *Euphausia pacifica* and *Thysanoessa spinifera*	*Limnology and Oceanography* **51**: 2398–2408	California coast	Lipid biomarkers
59	Y. Yamada, T. Ikeda	2006	Production, metabolism and trophic importance of four pelagic amphipods in the Oyashio region, western subarctic Pacific	*Marine Ecology Progress Series* **308**: 155–163	Oyashio	Natural cohort, Empirical models
60	A.I. Pinchuk, R.R. Hopcroft	2007	Seasonal variations in the growth rate of euphausiids (*Thysanoessa inermis*, *T. spinifera*, and *Euphausia pacifica*) from the northern Gulf of Alaska	*Marine Biology* **151**: 257–269	Gulf of Alaska	Molting rate
61	H.K. Kang, Y.J. Kang, C. Park	2007	Production of *Acartia omorii* (Copepoda: Calanoida) in Ilkwang Bay, southeastern coast of Korea	*Journal of Marine Systems* **67**: 236–244	Korean coast	Natural cohort
62	K. Ara, J. Hiroumi	2007	Temporal variability in primary and copepod production in Sagami Bay, Japan	*Journal of Plankton Research* **29**: 185–196	Sagami Bay, Japan	Natural cohort

	Authors	Year	Title	Journal, volume and pages	Location	Methodology used
63	T. Ikeda, F. Sano, A. Yamaguchi, T. Matsuishi	2007	RNA:DNA ratios of calanoid copepods from the epipelagic through abyssopelagic zones of the North Pacific Ocean	*Aquatic Biology* **1**: 99–108	Oyashio	Nucleic acid ratio
64	T. Ikeda, F. Sano, A. Yamaguchi	2007	Respiration in marine pelagic copepods: a global-bathymetric model	*Marine Ecology Progress Series* **339**: 215–219	Global	Physiological models
65	W.J. Kimmerer, A.G. Hirst, R.R. Hopcroft, A.D. McKinnon	2007	Estimating juvenile copepod growth rates: corrections, inter-comparisons and recommendations	*Marine Ecology Progress Series* **336**: 187–202	Australian coast	Artificial cohort
66	H. Liu, R.R. Hopcroft	2008	A comparison of seasonal growth and development of the copepods *Calanus marshallae* and *C. pacificus* in the northern Gulf of Alaska	*Journal of Plankton Research* **29**: 569–581	Gulf of Alaska	Artificial cohort
67	H. Liu, R.R. Hopcroft	2008	Growth and development of *Pseudocalanus* spp. in the northern Gulf of Alaska	*Journal of Plankton Research* **30**: 923–935	Gulf of Alaska	Artificial cohort
68	T. Ikeda, N. Shiga, A. Yamaguchi	2008	Structure, biomass distribution and trophodynamics of the pelagic ecosystem in the Oyashio region, western subarctic Pacific	*Journal of Oceanography* **30**: 577–585	Oyashio	Natural cohort, Empirical models
69	M. Hayashi, S. Uye	2008	Geographical and seasonal variations in biomass and estimated production rates of net zooplankton in Yatsushiro Bay, Japan	*Journal of Oceanography* **64**: 877–889	Yatsushiro Bay, Japan	Empirical models
70	A. Ko, S. Ju, C.R. Lee	2009	The physiological and ecological comparisons between warm (*Pleuromamma* sp.) and cold water copepod species (*Neocalanus plumchrus*) in the northwestern Pacific Ocean using lipid contents and compositions	*Ocean and Polar Research* **31**: 121–131	Northwestern Pacific	Lipid biomarkers
71	K. Ara, J. Hiroumi	2009	Seasonal variability in plankton food web structure and trophodynamics in the neritic area of Sagami Bay, Japan	*Journal of Oceanography* **65**: 757–775	Sagami Bay, Japan	Natural cohort
72	K. Takahashi, A. Kuwata, H. Sugisaki, K. Uchikawa, H. Saito	2009	Downward carbon transport by diel vertical migration of *Metridia pacifica* and *M. ohotensis* in the Oyashio region of the western subarctic Pacific Ocean	*Deep-Sea Research* **56**: 1777–1791	Oyashio	Empirical models
73	S. Ju, H. Kang, W. Kim, H.R. Harvey	2009	Comparative lipid dynamics of euphausiids from the Antarctic and Northeast Pacific Oceans	*Marine Biology* **156**: 1459–1473	Antarctic and California coast	Lipid biomarkers
74	A.R. Sastri, J.F. Dower	2009	Interannual variability in chitobiase based production rates of the crustacean zooplankton community in the Strait of Georgia	*Marine Ecology Progress Series* **388**: 147–157	Strait of Georgia, British Columbia, Canada	Chitobiase enzyme

	Authors	Year	Title	Journal, volume and pages	Location	Methodology used
75	H.R. Harvey, S. Ju, S. Son, L.R. Feinberg, C.T. Shaw, W.T. Peterson	2010	The biochemical estimation of age in Euphausiids: Laboratory calibration and field comparisons	*Deep-Sea Research II* **57**: 663–671	California coast	Natural cohort using biochemical aging method
76	A. Yamaguchi, Y. Onishi, A. Omata, M. Kawai, M. Kaneda, T. Ikeda	2010	Population structure, egg production and gut content pigment of large grazing copepods during the spring phytoplankton bloom in the Oyashio region	*Deep-Sea Research II* **57**: 1679–1690	Global	Physiological models
77	E.J. Yang, S. Ju, J. Choi	2010	Feeding activity of the copepod *Acartia hongi* on phytoplankton and microzooplankton in Gyeonggi Bay, Yellow Sea	*Estuarine and Coastal Shelf Science* **88**: 292–301	Yellow Sea	Feeding experiment with natural cohort
78	H.S. Kim, S. Ju, A. Ko	2010	Comparisons of feeding ecology of *Euphausia pacifica* from Korean waters using lipid composition	*Ocean and Polar Research* **32**: 165–175	Korea coast	Lipid biomarkers
79	T. Kobari	2010	Measurements of growth rate for natural population of planktonic copepods: a review (in Japanese with English abstract)	*Oceanography in Japan* **19**: 213–232	–	Review
80	T. Kobari, A. Ueda, Y. Nishibe	2010	Development and growth of ontogenetically migrating copepods during the spring phytoplankton bloom in the Oyashio region	*Deep-Sea Research II* **57**: 1715–1726	Oyashio	Molting rate
81	K. Takahashi, K. Ide	2011	Reproduction, grazing and development of the large subarctic calanoid *Eucalanus bungii*: is spring diatom bloom the key to controlling their recruitment?	*Hydrobiologia* **666**: 99–109.	Oyashio	Egg production, Starvation tolerance
82	S. Ju, A. Ko, C.R. Lee	2011	Latitudinal variation of nutritional condition and diet for copepod species, for *Euchaeta* sp. and *Pleuromamma* spp., from the Northwest Pacific Ocean using lipid biomarkers	*Ocean and Polar Research* **33**: 349–358	Northwestern Pacific	Lipid biomarkers
83	T. Ikeda	2011	Metabolic activity of pelagic copepods from 5,000 to 7,000 m depth of the western subarctic Pacific, as inferred from electron transfer system (ETS) activity	*Journal of Oceanography* **67**: 785–790	Global	Physiological models
84	T. Ikeda	2012	Metabolism and chemical composition of zooplankton from 500 to 5,000 m depth of the western subarctic Pacific Ocean	*Journal of Oceanography* **68**: 641–649	Global	Physiological models
85	T. Okutsu, K. Ara, J. Hiromi	2012	Microbial food web structure of the plankton ecosystem in the neritic area of Sagami Bay, Japan: seasonal variability in chlorophyll a<20 μm, bacteria, heterotrophic nanoflagellates and microzooplankton (in Japanese with English abstract)	*Bulletin of the Plankton Society of Japan* **59**: 101–119	Sagami Bay, Japan	Natural cohort

	Authors	Year	Title	Journal, volume and pages	Location	Methodology used
86	A.R. Sastri, R.J. Nelson, D.E. Varela, I. Wrohan, W.J. Williams	2012	Variation of chitobiase-based estimates of crustacean zooplankton production rates in high latitude waters	*Journal of Experimental Marine Biology and Ecology* **414–415**: 54–61	Gulf of Alaska, Bering Sea, Chuckchi Sea, Beaufort Sea	Chitobiase enzyme
87	K.Y. Lin, A.R. Sastri, G.C. Gong, C.H. Hsieh	2013	Copepod community growth rates in relation to body size, temperature, and food availability in the East China Sea - a test of metabolic theory	*Biogeosciences* **10**: 1–16	East China Sea	Artificial cohort
88	F.H. Chang, E. Marguis, C.W. Chang, G.C. Gong, C.H. Hsieh	2013	Scaling of growth rate and mortality with size and its consequence on size spectra of natural microphytoplankton assemblages in the East China Sea	*Biogeosciences* **10**: 5267–5280	East China Sea	Artificial cohort
89	K. Chikugo, A. Yamaguchi, K. Matsuno, R. Saito, I. Imai	2013	Life history and production of pelagic mysids and decapods in the Oyashio region, Japan	*Crustaceana* **86**: 449–474	Oyashio	Empirical models
90	T. Kobari, H. Mori, H. Tokushige	2013	Nucleic acids and protein content in ontogenetically migrating copepods in the Oyashio region as influenced by development stage and depth distribution	*Journal of Plankton Research* **35**: 97–104	Oyashio	Nucleic acid ratio
91	L.B. Feinberg, C.T. Shaw, W.T. Peterson, M. Decima, Y. Okazaki, S. Ju	2013	*Euphausia pacifica* brood sizes: a North Pacific synthesis	*Journal of Plankton Research* **36**: 1192–1206	North Pacific	Natural cohort
92	T. Ikeda	2013	Metabolism and chemical composition of marine pelagic amphipods: synthesis toward a global bathymetric model	*Journal of Oceanography* **69**: 339–355	Global	Physiological models
93	T. Ikeda	2013	Metabolism and chemical composition of pelagic decapod shrimps: synthesis toward a global bathymetric model	*Journal of Oceanography* **69**: 671–686	Global	Physiological models
94	R. Nakajima, T. Yoshida, B.H.R. Othman, T. Toda	2014	Biomass and estimated production rates of metazoan zooplankton community in a tropical coral reef of Malaysia	*Marine Ecology* **35**: 112–131	Coral reef, Japan	Natural cohort
95	T. Ikeda	2014	Metabolism and chemical composition of marine pelagic gastropod molluscs: a synthesis	*Journal of Oceanography* **70**: 289–305	Global	Physiological models
96	A. Ko, E.J. Yang, M. Kim, S. Ju	2016	Trophodynamics of euphausiids in the Amundsen Sea during the austral summer by fatty acid and stable isotopic signatures	*Deep-Sea Research II* **123**: 78–85	Antarctica	Lipid biomarkers
97	H. Yoon, A. Ko, J. Kang, J. Choi, S. Ju	2016	Diet of chaetognaths *Sagitta crassa* and *S. nagae* in the Yellow Sea inferred from gut content and fatty acid analyses	*Ocean and Polar Research* **38**: 35–46	Yellow Sea	Gut contents, Lipid biomarker

	Authors	Year	Title	Journal, volume and pages	Location	Methodology used
98	K.D. Suchy, J.F. Dower, D.E. Varela, M.G. Lagunas	2016	Interannual variability in the relationship between in situ primary productivity and somatic crustacean productivity in a temperate fjord	*Marine Ecology Progress Series* **545**: 91–108	Saanich Inlet, British Columbia, Canada	Chitobiase enzyme
99	A. Yamaguchi, K. Matsuno, Y. Abe, D. Arima, I. Imai	2017	Latitudinal variations in the abundance, biomass, taxonomic composition and estimated production of epipelagic mesozooplankton along the 155°E longitude in the western North Pacific during spring	*Progress in Oceanography* **150**: 13–19	North Pacific	Empirical models
100	T. Kobari, S. Miyake, W.T. Peterson, J. Peterson, T. Shaw	2017	Nucleic acid ratio as a proxy for starvation of coastal and pelagic copepods in the North Pacific Ocean	*Plankton and Benthos Research* **12**: 25–33	North Pacific	Nucleic acid ratio
101	R. Nakajima, H. Yamazaki, L.S. Lewis, A. Khen, J.E. Smith, N. Nakatomi, H. Kurihara	2017	Planktonic trophic structure in a coral reef ecosystem – Grazing versus microbial food webs and the production of mesozooplankton	*Progress in Oceanography* **156**: 104–120	Coral reef, Japan	Natural cohort
102	L. Yebra, T. Kobari, A.R. Sastri, F. Gusmão, S. Hernández-León	2017	Advances in biochemical indices of zooplankton production	*Advances in Marine Biology* **76**: 157–240	Global	Review
103	T. Ikeda	2017	An analysis of metabolic characteristics of planktonic heterotrophic protozoans	*Journal of Plankton Research* **39**: 479–490	Global	Physiological models
104	T. Kobari, W. Makihara, T. Kawafuchi, K. Sato, G. Kume	2018	Geographic variability in taxonomic composition, standing stock, and productivity of the mesozooplankton community around the Kuroshio Current in the East China Sea	*Fisheries Oceanography* **27**: 336–350	Kuroshio	Physiological models, AARS
105	T. Kobari, A.R. Sastri, L. Yebra, H. Liu, R.R. Hopcroft	2019	Evaluation of trade-offs in traditional methodologies for measuring metazooplankton growth rates: Assumptions, advantages and disadvantages for field applications	*Progress in Oceanography* **178**: 102137	Global	Review
106	T. Kobari, Y. Kobari, H. Miyamoto, Y. Okazaki, G. Kume, R. Kondo, A. Habano	2019	Variability in taxonomic composition, standing stock and productivity of the plankton community in the Kuroshio and its neighboring waters	*Geophysical Monograph* **243**: 223–350	Kuroshio	Physiological models, AARS
107	T.A. Venello, A.R. Sastri, K.D., Suchy, M.D. Galbraith, J.F. Dower	2022	Drivers of variation in crustacean zooplankton production rates differ across regions off the west coast of Vancouver Island and in the subarctic NE Pacific	*ICES Journal of Marine Sciences* **79**: 741–760	West Coast Vancouver Island, Gulf of Alaska	Chitobiase enzyme

	Authors	Year	Title	Journal, volume and pages	Location	Methodology used
108	L.E. Kwong, K.D. Suchy, A.R. Sastri, J.F. Dower, E.A. Pakhomov	2022	Comparison of mesozooplankton production estimates from Saanich Inlet (British Columbia, Canada) using the chitobiase and biomass size spectra approaches	*Marine Ecology Progress Series* **655**: 59–75	Saanich Inlet, British Columbia, Canada	Size-based models and chitobiase enzyme

Appendix 5

Meeting Reports and Workshop Summaries from Past Annual and Inter-sessional Meetings Related to WG 37

PICES-2012, Hiroshima, Japan

ICES/PICES 6th International Zooplankton Production Symposium, Bergen, Norway, 2016

PICES-2017, Vladivostok, Russia

AGU 2018 Ocean Sciences Meeting, Portland, Oregon

WG 37 Practical Workshop, Manazuru, Japan, 2018

PICES-2018, Yokohama, Japan

WG 37 Practical Workshop, Quadra Island, British Columbia, 2019

PICES-2019, Victoria, Canada

PICES-2020, virtual

PICES-2021, virtual

PICES-2012
October 12–21, 2012, Hiroshima, Japan

Excerpted from:

Summary of Scientific Sessions and Workshops at PICES-2012

BIO Workshop (W2)
Secondary production: Measurement methodology and its application on natural zooplankton community

Co-Convenors: *Toru Kobari (Japan) and William Peterson (USA)*

Invited Speaker:
Lidia Yebra (Oceanographic Center of Málaga, Instituto Español de Oceanografía (IEO), Spain)

Zooplankton communities play important roles on the transfer of primary production to higher trophic levels of marine ecosystems. In the past two decades, the quantitative evaluation of the energy flow has been emphasized for better understanding how marine ecosystems respond to climate change and global warming. To date, primary production can be globally estimated with remote sensing techniques and validated with *in situ* experiments using radio or stable isotopes. Although secondary production has been estimated with various methods (natural cohort, artificial cohort, molting rate, egg production, nucleic acids ratio, enzyme activity and empirical models), there is little information which method is relevant for natural zooplankton population or community. Thereby, we have little knowledge or confidence of secondary production measurements compared with that of primary production. In this workshop, the intent was to review current methodologies to measure secondary production. Through published reports of secondary production on natural zooplankton population or community, this workshop aimed to clarify the assumptions, advantages and disadvantages for each method. New techniques (nucleic acids ratio, enzyme activity, chitobiase, or other methods) and challenges in the calibration between the estimates using different methods were also discussed.

Summary of Workshop

Throughout the oral presentations, we clarified not only advantages but also disadvantages of the current methodologies used to estimate zooplankton production of natural zooplankton populations or communities. More direct measurements on body mass would be recommended for those who use the traditional methods (such as the “molt rate”), while these methods are laborious and time-consuming and need special care to eliminate artifacts. Biochemical approaches would take advantages to the traditional methods due to the simple protocols and quick measurements, but they need some calibrations of the parameters to the direct measurements.

Before discussion, we confirmed consensus to specify the target group for production estimation because “secondary production” means sum of production for wide taxonomic groups. As a first issue to be discussed, we confirmed the necessity of writing a review paper on current methodologies for estimating zooplankton growth rate because it is very helpful for our prospective activities. Second, we agreed that we should propose a new working group on zooplankton production (including a workshop/symposium at the PICES 2014 annual meeting) to the BIO Committee before PICES-2013. In the working group we will conduct an exchange program to compare methodologies by cross-calibration of biochemical methods (Nucleic acids ratio, AARS, Chitobiase) of growth and validation against traditional methods (Direct growth, Molting rate, Egg production, Physiological rate). The value to PICES and FUTURE is as follows. Researchers involved with modeling and monitoring as well as scientists associated with BIO, FIS and MONITOR consider aspects of zooplankton biomass and species composition in their work, but little attention is given to "rates" of growth and production. Since "rates" are likely to be more sensitive to environmental change than "biomass", "rates" could be more sensitive to, and excellent early indicators of, environmental change than biomass alone. We suggest that both AP-COVE and AP-SOFE would be interested in incorporating a better understanding of zooplankton growth and production rates into (a) understanding of effects of climate variability on ecosystems (COVE) and (b) outlooks and ecosystem status (SOFE). A new PICES Working Group on Zooplankton Production would clarify (1) methods of measurements of rates, and (2) recommend a set of techniques that could be adopted by scientists of not only PICES but also ICES member countries.

Prospective activities

1. Make guidance to review advantages and disadvantages of the current methodologies for zooplankton production
2. Establish a PICES Working Group on Zooplankton Production.
3. Champion an international research program to compare methodologies (including proposal for funding)
4. Establish a cooperative network between PICES Working Group on Zooplankton Production and ICES Working Group on Zooplankton Ecology

Proposed Steering Committee for the proposed new Working Group
T. Kobari (KUFF), B.T. Peterson (NOAA), R. Escribano (IIO), L. Yebra (IEO), A. Sastri (UQAM), Hyung-Ku Kang (KIOST)

PICES-2012 Workshop (W2) (front row, from left) Lidia Yebra, Julie Keister, Rie Nakamura, Bill Peterson, Tracy Shaw, Pamela Hidalgo, Akash Sastri; (back row, from left) Hyung-Ku Kang, Keisuke Unno, Rubén Escribano, Atsuhiro Hirata, Sachi Miyake, Michael Dagg, Toru Kobari, Yasuhide Nakamura, and Jennifer Fisher

List of papers

Oral presentations

Lidia Yebra (Invited)
Biochemical indices of zooplankton production

Akash R. Sastri
Chitobiase-based measurements of crustacean zooplankton community biomass production rates: Method development and application in the NE subarctic Pacific

William T. Peterson, Jay Peterson and Jennifer L. Fisher
Use egg production of adult female copepods as a measure of secondary production

Hyung-Ku Kang
Secondary production of *Acartia steueri* and *A. omorii* (Copepoda: Calanoida) in a small bay, southeastern coast of Korea: The growth rate approach

Rubén Escribano and Pamela Hidalgo
Can temperature-dependent growth be used to measure secondary production of copepods in coastal upwelling systems?

Pamela Hidalgo and Rubén Escribano
The importance of rapid development to produce more biomass on a year cycle: Comparing some copepod species from the Humboldt Current

Yasuhide Nakamura, Atsushi Yamaguchi and Noritoshi Suzuki
Characteristics of zooplankton community in the Japan Sea: Biomass, stable isotope ratio and dominant taxa

Poster presentations

Lidia Yebra, Elisa Berdalet, Rodrigo Almeda, Verónica Pérez, Albert Calbet and Enric Saiz
AARS activity and RNA/DNA ratio as proxies for growth and fitness of *Oithona davisae* early developmental stages

Lidia Yebra, Sébastien Putzeys, Dolores Cortés, Ana Luisa Da Cruz, Francisco Gómez, Pablo León, Jesús M. Mercado and Soluna Salles
Application of biochemical tools to assess zooplankton metabolism in the coastal North Alboran Sea (SW Mediterranean)

Toru Kobari, Shigeki Kori and Haruko Mori
Nucleic acids and protein contents as proxies for protein-specific growth of *Artemia salina*

Sachi Miyake and Toru Kobari
Nucleic acids and protein contents as proxies for starvation of marine copepods

Andrew G. Hirst, Julie E. Keister and numerous contributors
Assessing copepod growth rates using the Modified Moult Rate Method

ICES/PICES 6th International Zooplankton Production Symposium

May 9–13, 2016, Bergen, Norway

Workshop
ICES/PICES cooperative research initiative - towards a global measurement of zooplankton production

Conveners:
Lidia Yebra (IEO, Spain)
Toru Kobari (Kagoshima University, Japan)

Invited speaker:
Lutz Postel (Germany)

Zooplankton communities play a central role in the flow of matter and energy passing from primary producers to higher trophic levels in marine ecosystems. Over the past two decades, quantitative evaluation of zooplankton production and its driving forces has been emphasized as a critical component to improved understanding of the responses of marine ecosystems to global climate change. While many methodologies have been proposed for estimating zooplankton production, we have limited knowledge of which methods are the most practical and relevant for measuring the production rates of natural zooplankton populations and/or communities across a wide range of phyla and trophic levels. A quantitative evaluation of existing, new, and emerging methodologies is required.

This workshop will share the applicability of existing methods (*i.e.* traditional approaches) as well as the development of novel methods (*i.e.* biochemical-based approaches and others) for measuring zooplankton production rates. We welcome abstract submissions on topics that concern:

- Assumptions, limitations, and recent advances of the traditional and novel biochemical-based approaches used to estimate production of zooplankton populations or communities;
- Validation and calibration of zooplankton production rate estimates measured by biochemical-based approaches, models, and traditional methodologies.

Through this workshop, we aim to foster cooperative research activities and working groups on zooplankton production among members of the PICES (North Pacific Marine Science Organization) and ICES (International Council for the Exploration of the Sea) communities.

List of papers

Oral presentations

Lutz Postel1, Gunta Rubene Aispure, Angus Atkinson, Kathryn Cook, Padmini Dalpadado, Tone Falkenhaug, Elaine Fileman, Astthor Gislason, Erica Head, Arantza Iriarte, Todd O'Brien, Maria Grazia Mazzocchi, Piotr Margonski, Antonina dos Santos, Patrik Strömberg, Alexandra Teodosio, Ibon Uriarte, Fernando Villate, Peter Wiebe and Lidia Yebra
Zooplankton production and metabolic activity in the North Atlantic and adjacent seas

Karyn Suchy, John Dower and Diana Varela
Interannual variability in the relationship between in situ primary productivity and chitobiase-based crustacean productivity in a temperate fjord

Koichi Ara, Satoshi Fukuyama, Yasuaki Nakajima and Akihiro Shiomoto
Seasonal and year-on-year variations in primary production and mesozooplankton secondary and tertiary production for 9 years (2006–2014) in the neritic area of Sagami Bay, Japan

PICES-2017

September 22–October 1, 2017, Vladivostok, Russia

Excerpted from:

Summary of Scientific Sessions and Workshops at PICES-2017

BIO Workshop (W6)

Advantages and limitations of traditional and biochemical methods of measuring zooplankton production

Co-Convenors: *Toru Kobari (Japan), Akash Sastri (Canada)*

Invited Speaker:
Andrew Hirst (School of Environmental Sciences, University of Liverpool, U.K.)

Background

Zooplankton communities occupy a central position in the flow of matter and energy from primary producers to animals at higher trophic levels in marine ecosystems. Over the past two decades, the increasing emphasis on quantitative assessments of marine ecosystem function has been focused on improving our understanding of how marine ecosystems respond to global climate change. Zooplankton (secondary) production represents a quantitative proxy for the functional response of marine ecosystems since it corresponds to the zooplankton biomass accrued through consumption of lower food-web levels. Zooplankton production traditionally has been estimated using methods which either: 1) follow the development of zooplankton populations/communities over the course of several weeks or months (cohort approaches); or 2) employ *ex situ* fixed-period incubations. Incubation-based techniques with simultaneous sampling of natural communities are the most widely used traditional methods in the field. Recent advances in biochemical methods for measuring zooplankton growth and production, such as quantification of RNA/DNA ratios, chitobiase, or aminoacyl-tRNA synthetases, have been developed and applied to a diverse range of organisms and habitats. The goal of the workshop was to examine and compare traditional and biochemical approaches to estimating zooplankton secondary production.

Summary of presentations

Akash Sastri and Toru Kobari (PICES WG 37 Co-Chair) convened the ½-day workshop in the morning of September 22. Eleven participants joined this workshop and 4 talks and 2 posters were presented.

Invited Speaker, Dr. Andrew Hirst (UK) demonstrated the errors and variations of copepod growth estimates in the molting rate method as an example for disadvantages of the traditional methodologies. He also described a global pattern of the copepod growth estimated with the natural cohort method indicating response of copepod growth to environmental variables. On behalf of Lian E. Kwong, Natalie Mahara described the relevance of ‘Biomass Size Spectra’ for estimating ecosystem productivity and transfer efficiency and noted that this approach may represent an additional method for estimating zooplankton production. She also demonstrated that zooplankton community structure was associated with oceanographic conditions and emphasized the importance of microscopic analysis. On behalf of Theresa A. Venello, Akash Sastri presented transfer efficiency measurements estimated directly from primary production (dissolved gas ratios and radio isotope incorporation) and zooplankton production by chitobiase activity. He mentioned there is limited information on direct measurements of transfer efficiency but that we are now starting to accumulate such data. For poster presentations, Akash Sastri and Toru Kobari presented the results from collaborative experiments which compared production estimates measured with different methodologies. Our discussions are summarized as follows.

- Specify advantages, disadvantages and limitations of available methodologies to apply natural population or community.
- The taxonomic groups for which the methodologies are not applicable should be specified.
- Errors and deviations of production estimates should be compared among the methodologies using zooplankton population or community in nature or in laboratory.

Active and extensive discussions among the experts were incredibly helpful for promoting the terms of reference for our working group and gave some new ideas to the WG members. This report and record of our discussion was shared among the WG members.

List of papers

Oral presentations

Revising our traditions: An overview on method and results of growth and production estimates for zooplankton
Andrew G. Hirst

A comparison of zooplankton secondary production in a high nutrient low chlorophyll (HNLC) and seasonally productive regions in the North Pacific
Natalie Mahara presenting for Lian E. Kwong, Evgeny A. Pakhomov

Zooplankton communities in the coastal northeast Pacific Ocean: A comparison of a highly productive region and a light-limited high nutrient, low chlorophyll region
Natalie Mahara, Brian V.P. Hunt, Evgeny A. Pakhomov

Coupling crustacean zooplankton production and primary production rates to estimate trophic transfer efficiencies in the NE Pacific
Theresa A. Venello, John F. Dower, Akash R. Sastri

Poster presentations

A comparison of protein synthetases activity to standing stock and productivity in a cultured copepod population, *Pseudodiaptomus inopinus*
Toru Kobari, Yuka Matsuura, Akash Sastri, Yuichiro Yamada and Tomonari Kotani

A comparison of chitobiase-based estimates to developing biomass and production rates of a laboratory culture of *Pseudodiaptomus inopinus*
Akash Sastri, John Dower, Alex Clancy, Yuichiro Yamada, Tomonari Kotani, Toru Kobari and Yuka Matsuura

Report of Working Group 37 on *Zooplankton Production Methodologies, Applications and Measurements in PICES Regions*

The first meeting of the Working Group on *Zooplankton Production Methodologies, Applications and Measurements in PICES Regions* (WG 37) was held on September 24, 2017 from 9:00 to 12:30 h in Vladivostok, Russia, under the chairmanship of Dr. Toru Kobari (Japan) and Dr. Akash Sastri (Canada). Three members and two observers attended the meeting (***WG 37 Endnote 1***). Several members who could not attend the meeting reported progress on their inter-sessional activities (see ***WG 37 Endnote 2***) and/or provided comments through the E-mail communication.

AGENDA ITEM 1

Background and recent activities of the Working Group

Dr. Kobari provided a brief rationale and background for the formation of the Working Group, problems in measuring zooplankton rates, and recent activities and progress made by the Group.

AGENDA ITEMS 2 AND 3

Terms of reference and future plans

Dr. Kobari reviewed the WG terms of reference (***WG 37 Endnote 3***) and provided details to address them.

1. Review papers on traditional and biochemical methodologies (ToR1).
    - Review paper for biochemical approaches was already published in *Advances in Marine Biology* (https://doi.org/10.1016/bs.amb.2016.09.001);
    - Guideline describing advantages, disadvantages and limitations was not deemed novel since such information is already described in the ICES manual and Kimmerer *et al*. (2007). In the proposed review paper, quantitative evaluation like error and variance should be compared among the estimates for available traditional methodologies;
    - Average and variance of growth rates estimated with the traditional methods can be compared with the estimates with the Ikeda-Motoda and Banse-Mosher models which are applicable to wide taxonomic groups with the least variables (*i.e*., temperature and individual body weight). Such comparison standards estimated with these models enable evaluation of the applicability of traditional methodologies to taxonomic groups, locations and situations.
    - *In situ* or laboratory experiments for comparing the traditional methodologies should be encouraged and promoted. WG 37 will seek and call for collaborative opportunities without funding like sample exchange, small field or laboratory projects (traveling on individual funding) and application to zooplankton data sets;
    - Colleagues who confirmed their interest in participating in the review paper on traditional methodologies are:
        - Toru Kobari, Akash Sastri (Co-Chairs),
        - Hui Liu (U.S. member: artificial cohort),
        - Andrew Hirst (UK colleague: empirical models).

2. Guidelines and recommendations of traditional and biochemical methodologies (ToR2).
    - Recommendations and procedures for the biochemical methodologies are completed and included in the review paper (Yebra *et al*., 2017) as supplements. The Co-Chairs and Dr. Lidia Yebra (WG 37 *ex officio* member, representing ICES) will draft recommendations and guidelines for the biochemical methodologies. A final version will be posted on the PICES website;
    - Similar guidelines for the traditional methodologies can be produced by the authors of that review paper. WG 37 asks for an outline of the following methods: molting rate by T. Kobari; natural cohort by Koichi Ara; artificial cohort by Hui Liu, egg production by H.K. Kang and M.C. Jang; and empirical models by Andrew Hirst. Dr. Kobari will draft an outline of this guideline by the next Ocean Sciences Meeting (February 2018);

3. Develop practical models for estimating zooplankton production to time-series (ToR3).
    - Ikeda-Motoda and Banse-Mosher models are recommended as the best methods for application to zooplankton time-series because of applicability to wide taxonomic groups, locations and situations, minimum requirements of variables only for temperature and animal body weight, and high temporal and spatial resolutions. Dr. Kobari is applying the Ikeda-Motoda model to the different time-series and comparing the estimates. He will demonstrate the results in the workshop during the PICES 2018 Annual Meeting in Japan, collaborating with T. Tadokoro (Japan) and D. Steinberg (USA);
    - Dr. Tadokoro will demonstrate the application of the Ikeda-Motoda model to zooplankton data sets in the Inland Sea of Japan in the proposed workshop (see ***WG 37 Endnote 4***) during PICES-2018.

4. Build a platform of information exchange on zooplankton production measurements through an interactive website for regional and/or global mapping (ToR4).
    - WG 37 asks Dr. Yebra to apply the Ikeda-Motoda and Banse-Mosher models to the zooplankton data base in collaboration with its organizer, Mr. Todd O'Brien (USA).

5. Build a network of scientists and laboratories measuring zooplankton production among PICES and ICES member countries as well as developing countries (ToR5).
    - WG members continue to seek scientists and laboratories measuring zooplankton production. They will report on and update this information at the WG meeting at PICES-2018. In particular, WG 37 needs information from China and Russia because we have none from those countries at the moment;
    - Each WG member is to update a list of the information (*e.g*., name, institute, email, methodology used, some publications). The Co-Chairs will contact the Secretariat about placing the information on the PICES website.

6. Promote international collaborations among zooplankton production researchers through international organizations such as PICES, ICES and IMBER (ToR6).
    - WG members should continue to seek and report on potential funding opportunities for international collaboration on zooplankton production estimates. They will report any updates at the WG meetings in 2018. Opportunities and ideas for collaborative research or experiments for zooplankton production estimate comparisons with small funding or without funding are also welcome to report (see above);
    - ToR6 will be simultaneously promoted with ToR2, ToR3 and ToR4.

7. Publish a final report summarizing results (ToR7).
    - The Co-Chairs will draft an outline for the final report referring to previous reports for the past working groups as examples;
    - WG members will discuss an outline (sections) of the report at PICES-2018. All of the members are associated with each section;
    - A bibliography of zooplankton growth and production in the North Pacific will be included in the report. WG members will assemble the literature for zooplankton growth and production studies for each country and report them at the next WG meeting. In particular, WG 37 strongly encourages China and Russia to submit this information because we have nothing from these countries at the moment.

Additional plans for WG 37 include a workshop proposed for PICES-2018 (***WG 37 Endnote 4***). This workshop is intended to provide a venue for both Working Group members and others to present either syntheses of secondary production work in their region and/or recent focused methodological studies on secondary production.

AGENDA ITEM 4

Other items

- *Bibliography for zooplankton production methodology and measurements in the PICES region*

Published papers in Korean and Japanese waters have been listed in a bibliography. Members were asked to continue collecting published papers, in particular for Canada, China, Russia and the U.S.

- *Review of BIO Workshop (W6) on "Advantages and limitations of traditional and biochemical methods of measuring zooplankton production" at PICES-2017*

Drs. Kobari and Sastri convened the ½-day W6 workshop on September 23. Eleven participants attended and 4 talks and 2 posters were presented (see PICES-2017 Session Summaries for a summary of the workshop).

- *Upcoming Ocean Sciences Meeting 2018 in Oregon*

Drs. Kobari, Sastri and Yebra will convene a topic session on "*Zooplankton productivity as a function of trophodynamics in marine ecosystems*" at the 2018 Ocean Sciences Meeting in Portland, Oregon (February 11–16, 2018). Nineteen abstracts have been submitted to the Science Steering Committee and will be reviewed by the conveners. The schedule will be determined in late September to early October 2017.

- *School or workshop for early career scientists*

Members discussed holding a fall school or workshop for early career scientists to practice zooplankton production procedures, sample analysis and types of traditional methodologies after the PICES 2018 Annual Meeting in Japan or in 2019 in Canada. The final decision was to hold a practical workshop prior to the Annual Meeting at the Manazuru Marine Center for Environmental Research and Education of Yokohama National University (***WG 37 Endnote 5***).

- *Membership*

Dr. Lidia Yebra (representing ICES) was approved as an *ex officio* member of WG 37 by Governing Council.

WG 37 Endnote 1

WG 37 participation list

Members

Toru Kobari (Co-Chair, Japan)
Akash Sastri (Co-Chair, Canada)
Kazuaki Tadokoro (Japan)

Observers

Ian Perry (Canada)
Ryan Rykaczewski (USA)

Members unable to attend

China: Qing Yang
Korea: Se-Jong Ju, Jung-Hoon Kang
Russia: Vladimir Napazakov
USA: Hui Liu, Todd O'Brien

WG 37 Endnote 2

WG 37 meeting agenda

1. Background of the Working Group on *Zooplankton Production Methodologies, Applications and Measurements in PICES Regions* and recent activities
2. Terms of reference
3. Future plans
4. Other items

WG 37 Endnote 3

WG 37 Terms of reference

1. Summarize assumptions, recent advances and limitations of both traditional and biochemical methodologies for measuring zooplankton production of natural populations and communities;
2. Produce recommendations and procedures for both traditional and biochemical zooplankton production rate measurement methodologies and make them available for worldwide users on a website;
3. Develop practical models for estimating zooplankton production to time-series;
4. Build a platform of information exchange on zooplankton production measurements through an interactive website for regional and/or global mapping;
5. Build a network of scientists and laboratories measuring zooplankton production among PICES and ICES nations as well as developing countries;
6. Promote international collaborations among zooplankton production researchers through international organizations such as PICES, ICES and IMBER;
7. Publish a final report summarizing results.

WG 37 Endnote 4

Proposal for a Workshop on
"Regional evaluation of secondary production observations and application of methodology in the North Pacific" at PICES-2018

Duration: ½ day

Convenors: Akash Sastri (Canada) and Toru Kobari (Japan)

Suggested Invited Speakers: Shin-ichi Uye (Japan), Chih-hao Hsieh (Chinese Taipei)

Zooplankton production represents a quantitative proxy for the functional response of marine ecosystems to regional and global climate change, because material and energy scattering in the lower food web is integrated by zooplankton communities. Although a variety of methodologies for measuring zooplankton production have been developed and applied over the last half century, our knowledge of which approaches are applicable to a diverse range of organisms and habitats remains limited. Recent advances in biochemical methods for measuring zooplankton production have been reviewed, however, such information is still lacking for the traditional methodologies. This workshop will share the current status on zooplankton production methodologies and measurements, to be reported by the working group members representative of each PICES nation. In addition, we also encourage presentations and discussion on advantages, applications and limitations of traditional methodologies on zooplankton production applicable to natural zooplankton populations and communities.

WG 37 Endnote 5

Proposal for a Practical Workshop on
"Production methodologies and measurements for in situ zooplankton: Phase 1"

PICES Working Group 37 and Yokohama National University are conducting a 3-day practical workshop (22–24 October, 2018) at Yokohama National University to introduce students and early career scientists to information about several approaches for estimating zooplankton production. Included in the course is both shipboard coastal sampling of zooplankton and instruction in the laboratory on methods of estimating production. This practical workshop is limited to 10 participants due to vessel capacity and classroom facility limitations. The workshop is aimed at early arrivals to the PICES Annual Meeting and is envisioned as the first of two workshops on the topic of estimation of zooplankton production.

Scope

Zooplankton production represents a quantitative proxy for the functional response of marine ecosystems to regional and global climate change because material and energy scattering in the lower food web is integrated by zooplankton communities. In the last half century, many methodologies for measuring zooplankton production have been developed as described in the ICES Zooplankton Methodology Manual. Unfortunately, the applications to zooplankton population and community in nature remain limited due to the specific knowledge and handlings for these methodologies. In this workshop, participants will estimate zooplankton growth or production with several methodologies using zooplankton samples and share the practical tricks. We also encourage international network and collaborations on zooplankton production measurements among early career scientists and students from PICES member countries through this workshop.

Sponsors

PICES BIO/Working Group on *Zooplankton Production Methodologies, Applications and Measurements in PICES Regions* (WG 37)
Yokohama National University
Japan Science and Promotion Society

Organizers

Toru Kobari (WG 37)
Akash Sastri (WG 37)

Local Organizing Committee (LOC)

Toru Kobari (Chair: Kagoshima University)
Shinji Shimode (Yokohama National University)
Koichi Ara (Nihon University)

Date

22–24 October, 2018 (Monday to Wednesday, just before the PICES 2018 Annual Meeting)

Venue

Manazuru Marine Center for Environmental Research and Education, Yokohama National University (http://www.mmcer.ynu.ac.jp/mmcer/top.html)

Maximum number of participants

10 early career scientists or students

Registration

- ✓ All applicants must email a curriculum vita including their name, institutional information, nationality, gender and email address to the Chair of the LOC (kobari@fish.kagoshima-u.ac.jp). Deadline for registration is 15 June 2018. Considering international balance among the PICES member countries, participants will be decided by the LOC on a first-come-first-served basis. All applicants will receive the decision by email from the LOC by 30 June.
- ✓ Note: PICES is not providing financial support for participants to attend the workshop.
- ✓ There is no registration fee, but participants will be required to pay their own meals and transportation costs to the Manazuru Marine Center during the workshop. Accommodation and facility are provided for the participants by grants-in-aid for scientific research from the Japan Science and Promotion Society (17K00522).

Practical Workshop Schedule

October 22 (Monday)
19:00–21:00 Opening ceremony and ice breaker

October 23 (Tuesday)
07:30–08:30 Breakfast (bring own meal)
08:30–09:30 Loading sampling gears and lecture for on-board sampling
09:30–12:00 On-board sampling
12:00–13:00 Lunch (pre-ordered lunch box)
13:00–15:00 Laboratory work
Sorting for egg production method (Dr. Shimode)
15:00–15:30 Coffee break
15:30–17:30 Laboratory work
Imaging for live zooplankton (TBA)
18:00–19:00 Dinner (make own meals)
19:00–21:00 Night session

October 24 (Wednesday)
07:30–08:30 Breakfast (bring own meals before coming)
08:30–12:00 Laboratory work
Counting eggs and estimating egg production (Dr. Shimode)
12:00–13:00 Lunch (pre-ordered lunch box)
13:00–15:00 Laboratory work
Application of empirical models to in situ zooplankton (Dr. Ara)
15:00–15:30 Closing ceremony
15:30 Break up

Note

✓ Participants should bring the following items:
  □ Laptop PC (MS Excel pre-installed)
  □ Rain suits, boots and work clothes for onboard sampling (if necessary)
  □ Medicine for motion sickness (if necessary)
  □ Bath amenity and towel

✓ The Chair of the LOC will send an “email” to all participants if this practical workshop is cancelled by severe storms on the day before this workshop (i.e., 21 October, 2018).

✓ Participants should bring their own meals for breakfast on Tuesday and Wednesday. The LOC will support all participants on transportation to local shops.

✓ All participants will make their own dinner on Tuesday. All participants and the others will pool funds to purchase food, which is cooked in a kitchen.

AGU 2018 Ocean Sciences Meeting
February 11–16, 2018, Yokohama, Japan

Session ME41A
Zooplankton Productivity as a Function of Trophodynamics in Marine Ecosystems

The functional role of zooplankton communities in marine food-webs represents an effective integration of material/energy transfers through multiple lower trophic level interactions (phytoplankton and the microbial loop) toward animals at higher trophic levels. Zooplankton productivity represents an overarching functional measure of this critical role and has been emphasized as important to our understanding of how fishery resources respond to cyclical regime shifts and longer-term responses of marine ecosystems to global climate change. However, evaluation of zooplankton productivity and its controlling factors in the field is still challenging because of the necessity of broad coverage applicable to multiple phyla and trophic levels, with high temporal and spatial resolution.

This session will share the information on zooplankton productivity measured by various contemporary methods and relevant applications including transfer efficiency and relationships to biogeochemistry and fisheries production. We also welcome theoretical and methodological topics such as comparison and applicability of existing methods as well as the development of novel methods. Through this session, we would like to foster a cooperative network and research activities for zooplankton production measurements and methodologies among members of the PICES and ICES communities.

Primary Chair
Akash R. Sastri
University of Victoria

Co-Chairs
Toru Kobari
Faculty of Fisheries, Kagoshima University

Lidia Yebra
Instituto Español de Oceanografía

Moderators
Akash R. Sastri
University of Victoria

Toru Kobari
Faculty of Fisheries, Kagoshima University

List of Presenations

Do doliolids eat eggs and juveniles of copepods?
Gustav Adolf Paffenhofer and Marion Koester

Temperature-dependent egg-hatching and production of the egg-carrying copepods *Microsetella norvegica* and *Oithona similis* in a high latitude fjord
Coralie Barth-Jensen, Camilla Svensen, Peter Glad and Ulrike Grote

Identification method for starved female *Calanus sinicus* (Calanoida: Copepoda) based on differential gene expression profile
Takuya Ohnishi, Junya Hirai, Shinji Shimode and Atsushi Tsuda

Estimating crustacean zooplankton production rates and energy transfer in the NE Pacific
Theresa Ann Venello, John Dower, and Akash R. Sastri

Copepod dynamics across warm and cold periods in the eastern Bering Sea: Implications for walleye pollock (*Gadus chalcogrammus*) and the Oscillating Control Hypothesis
Janet Duffy-Anderson, David Kimmel, Matthew Wilson and Lisa B. Eisner

WG 37 Practical Workshop on “*Production methodologies and measurements for in situ zooplankton: Phase 1*”

October 22–24, 2018, Yokohama, Japan

PICES Working Group 37 and Yokohama National University are conducting a 3-day practical workshop (22–24 October, 2018) at Yokohama National University to introduce students and early career scientists to information about several approaches for estimating zooplankton production. Included in the course is both shipboard coastal sampling of zooplankton and instruction in the laboratory on methods of estimating production. This practical workshop is limited to 10 participants due to vessel capacity and classroom facility limitations. The workshop is aimed at early arrivals to the PICES Annual Meeting and is envisioned as the first of two workshops (Phase 2 in 2019, date TBD) on the topic of estimation of zooplankton production.

Scope

Zooplankton production represents a quantitative proxy for the functional response of marine ecosystems to regional and global climate change because material and energy scattering in the lower food web is integrated by zooplankton communities. In the last half century, many methodologies for measuring zooplankton production have been developed as described in the ICES Zooplankton Methodology Manual. Unfortunately, the applications to zooplankton population and community in nature remain limited due to the specific knowledge and handlings for these methodologies. In this workshop, participants will estimate zooplankton growth or production with several methodologies using zooplankton samples and share the practical tricks. We also encourage international network and collaborations on zooplankton production measurements among early career scientists and students from PICES member countries through this workshop.

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PICES-2018
October 25–November 4, 2018, Yokohama, Japan

Excerpted from:

Summary of Scientific Sessions and Workshops at PICES-2018

BIO Workshop (W6)
Regional evaluation of secondary production observations and application of methodology in the North Pacific

Convenors: *Akash Sastri (Canada), Toru Kobari (Japan)*

Invited Speaker: *Koichi Ara (Nihon University, Japan)*

Background

Zooplankton production represents a quantitative proxy for the functional response of marine ecosystems to regional and global climate change, because material and energy scattering in the lower food web is integrated by zooplankton communities. Although a variety of methodologies for measuring zooplankton production have been developed and applied over the last half century, our knowledge of which approaches are applicable to a diverse range of organisms and habitats remains limited. Recent advances in biochemical methods for measuring zooplankton production have been reviewed, however, such information is still lacking for the traditional methodologies. The purpose of this workshop was to share the current status on zooplankton production methodologies and measurements, reported by the working group members representing each PICES country. In addition, presentations and discussion on advantages, applications and limitations of traditional methodologies on zooplankton production applicable to natural zooplankton populations and communities were also encouraged.

Summary of presentations

Drs. Akash Sastri and Toru Kobari (Co-Chairs, Working Group on *Zooplankton Production Methodologies, Applications and Measurements in PICES Regions*, WG 37) convened a workshop (W6) “Regional evaluation of secondary production observations and application of methodology in the North Pacific” in the morning of October 25 during PICES-2018 in Yokohama. About 25 participants from 5 countries joined this workshop. Nine talks and 4 posters were presented.

Drs. K. Ara (Japan), K. Tadokoro (Japan) and A. Sastri (Canada) demonstrated applications of some empirical models to zooplankton population or community in nature and emphasized that the models would be the most practical to existing zooplankton data sets among the contemporary methodologies. Drs. C.H. Hsieh and H. Liu reviewed the artificial cohort method which was widely used and described their results comparing with those by the other methods. Dr. L.E. Kwong introduced a good example of intercalibration for zooplankton productions between normalized biomass size spectra and chitobiase activity. Dr. S. Zeman demonstrated egg productions of two copepod species associated with environmental changes at the Oregon coast. Status reports of zooplankton productivity measurements in the Canadian and Japanese waters were done by Drs. A. Sastri and T. Kobari, respectively. At the end of the workshop, the following issues were discussed.

- What kind of information is necessary for promoting zooplankton production measurements?
- How should we promote zooplankton production measurements?

Dr. C.H. Hsieh proposed that the regional model for zooplankton growth or production applicable to the PICES region should be developed by sharing data-sets of the direct measurements and environmental variables. Also, participants confirmed that such data exchanges would be good collaborations to promote zooplankton production measurements. The Co-Chairs continued to discuss these issues at the Working Group meeting.

List of papers

Oral presentations

Traditional approaches for estimating zooplankton production rate and food requirement in the neritic area of the North Pacific (Invited)
Koichi Ara and Akihiro Shiomoto

Spatial and temporal variation of mesozooplankton productivity in the Seto Inland Sea, Japan
Kazuaki Tadokoro, Akihide Kasai, Katsuyuki Abo, Kazutaka Miyahara, Keigo Yamamoto, and Kazuhiko Koike

Copepod community growth rates in relation to body size, temperature, and food availability in the East China Sea: A test of metabolic theory of ecology
Kuan-Yu Lin, Akash R. Sastri, Gwo-Ching Gong, and Chih-hao Hsieh

An overview of artificial cohort method for estimating zooplankton production in the ocean
Hui Liu and Russell R. Hopcroft

Evaluation of the application of empirical growth rate models toward a long-term zooplankton biomass/ production time-series on the southern shelf of Vancouver Island
Akash R. Sastri, Moira Galbraith, and R. Ian Perry

A status report on Canadian marine zooplankton production rate measurements
Karyn D. Suchy and Akash R. Sastri

Status report on zooplankton productivity measurements in the western North Pacific Ocean and its neighboring waters
Toru Kobari and Kazuaki Tadokoro

An intercalibration of chitobiase and biomass size spectra zooplankton production estimates
Lian E. Kwong, Karyn D. Suchy, John F. Dower, and Evgeny A. Pakhomov

***Calanus marshallae* and *Calanus pacificus* egg production in relation to environmental variables in a productive upwelling zone in the northern California Current**
Samantha Zeman, Jay Peterson, Jennifer Fisher, and William Peterson

Poster presentations

Zooplankton secondary production in high nutrient low chlorophyll (HNLC) and seasonally productive regions in the North Pacific
Lian E. Kwong and Evgeny A. Pakhomov

Estimation of egg production rate of *Calanus sinicus* from preserved samples
Takashi Fushima, Takafumi Yamaguchi, Kiyotaka Hidaka, Mana Mikawa, Minamo Hirahara, Tomohiko Kikuchi, Tatsuki Toda, and Shinji Shimode

Diel rhythm of egg spawning of the planktonic copepod *Calanus sinicus* in Sagami Bay, Japan
Yuji Yoshinaga, Tomohiko Kikuchi, Tatsuki Toda, and Shinji Shimode

Individual growth rate (IGR) measurements negatively correlate with aminoacyl-tRNA synthetases (AARS) activity in North Pacific krill, *Euphausia pacifica*
Anna K. McLaskey and Julie E. Keister

Report of Working Group 37 on *Zooplankton Production Methodologies, Applications and Measurements in PICES Regions*

The second meeting of the Working Group on *Zooplankton Production Methodologies, Applications and Measurements in PICES Regions* (WG 37) was held on October 25, 2018 from 14:00 to 17:00 h in Yokohama, Japan, under the chairmanship of Dr. Toru Kobari (Japan) and Dr. Akash Sastri (Canada). 16 participants including the national representatives and observers attended the meeting (***WG 37 Endnote 1***). Several members who could not attend the meeting reported progress on their inter-sessional activities (see ***WG 37 Endnote 2***) and/or provided comments through the E-mail communication.

AGENDA ITEM 1
Description on terms of references

Dr. Kobari described the terms of references for the Working Group (see WG 37 webpage).

AGENDA ITEM 2
Activities in 2018

Drs. Kobari and Sastri reported the following WG activities achieved in 2018.

- Drs. Kobari, Sastri and Yebra Lidia convened a session on “*Zooplankton Productivity as a Function of Trophodynamics in Marine Ecosystems*” at the Ocean Sciences Meeting 2018 on February 15 in Portland, Oregon, USA. More than 30 people attended, and 6 talks and 9 posters were presented (see ***WG 37 Endnote 3***).
- Drs. Kobari, Shinji Shimode and Koichi Ara convened a Practical Workshop Phase 1 from October 22 to 24, 2018 (just before the PICES 2018 Annual Meeting) in Manazuru Marine Center for Environmental Research and Education, Yokohama National University. Nineteen participants, including conveners and support staff, attended. Onboard sampling, laboratory work and lectures on egg production and empirical models were provided (see PICES Press, Vol. 27, No. 1).
- The Co-Chairs convened a Workshop in the PICES 2018 Annual Meeting on October 25, 2018 in Yokohama. Twenty-eight people attended, and 8 talks and 4 posters were presented (see W6 in 2018 Session and Workshop Summaries).

AGENDA ITEM 3
Future plans

Plans to promote terms of reference

After Dr. Kobari described the tentative plans regarding the WG terms of references, the participants provided comments and suggestions.

1. Review papers on traditional and biochemical methodologies (ToR1).

- Review paper by L. Yebra, T. Kobari, A.R. Sastri *et al*. on biochemical approaches published in *Advances in Marine Biology*, 2017, 76: 157–240, https://doi.org/10.1016/bs.amb.2016.09.001.
- Review paper on traditional methodologies written by T. Kobari, A. Sastri and L. Yebra following comments and suggestions kindly provided by Dr. Charles Miller. Additional comments and

suggestions will be provided by Drs. R. Hopcroft and H. Liu. This review paper will be submitted to Special Issue on Climate, Zooplankton and Salmon (Dr. Bill Peterson Commemorative Issue) of *Progress in Oceanography* by the end of November 2018.

2. Guidelines and recommendations (procedures/protocols) of traditional and biochemical methodologies (ToR2).
   - Recommendations and procedures for the biochemical methodologies were included in the review paper by Yebra *et al*. (2017; see above) as supplements. The Co-Chairs asked Dr. Yebra (*ex officio* WG member, representing ICES) to make the draft based on the review paper. These documents will be posted on the PICES website and/or final report.
   - Similar guidelines for the traditional methodologies are now being developed by the WG members and colleagues. The Co-Chairs asked WG members and colleagues for guidelines on the following: molting rate by Dr. Hopcroft (USA member) and T. Kobari (Co-Chair), artificial cohort by H. Liu (USA member), egg production by Dr. Shinji Shimode (materials for Practical Workshop Phase 1), empirical models by Dr. Koichi Ara (materials for Practical Workshop Phase 1) and physiological models by T. Kobari. Dr. Kobari will circulate some examples of these guidelines after PICES-2018. These guidelines will be posted on the PICES website and/or final report.

3. Develop practical models for estimating zooplankton production to time-series (ToR3).
   - The Ikeda-Motoda method would be only one to be applicable to zooplankton time-series due to the wide coverage of various taxonomic groups, locations and situations, minimum requirements of variables for only temperature and animal body weight, and high temporal and spatial resolutions.
   - Dr. Kobari applied the Ikeda-Motoda model to some zooplankton data-sets (Kobari *et al*., 2018, *Fisheries Oceanography*, 27: 336–350, https://doi.org/10.1111/fog.12256). Drs. Kazuaki Tadokoro and Sastri demonstrated the applications of the Ikeda-Motoda model to zooplankton data-sets in the Inland Sea of Japan and on the Canadian coast at workshop W6 during PICES-2018 (see also Agenda Item 7).
   - WG members encouraged the use of such applications, using zooplankton time-series or data-sets in the PICES region. Drs. Kobari and Tadokoro will help in the estimation.
   - On the other hand, as suggested by Dr. C.H. Hsieh, the regional model for zooplankton growth or production applicable to the PICES region should be developed by sharing data-sets of the direct measurements on zooplankton growth/production and environmental variables. The Co-Chairs asked Drs. Liu, Hopcroft, and Hsieh to work on the development of the regional model using their data sets. Dr. Kobari will also contribute.

4. Build a platform of information exchange on zooplankton production measurements through an interactive website for regional and/or global mapping (ToR4).
   - The Co-Chairs asked Dr. Yebra to apply the Ikeda-Motoda and/or Banse-Mosher models to the COPEPOD data base in collaboration with its organizer, Dr. T. O’Brien (USA member). Unfortunately, it was reported that it was too difficult to get permission from each data owner.

- As alternative approaches, the Co-Chairs seek zooplankton data-sets or time-series in the PICES region, and permissions from the data owners. Available zooplankton data-sets or time-series and their data owners are as follows. Other data sets are welcome.
    - Station P and line P in the subarctic North Pacific (I. Perry, A. Akash, Canada)
    - BATS in the subtropical North Atlantic (D. Steinberg, T. Kobari, USA)
    - Newport Line in the western US coast (J. Fisher, USA)
    - Tsushima Strait in the Japan Sea (T. Kobari, Japan)
    - Kuroshio in the East China Sea (T. Kobari, Japan)
    - A-Line in the western North Pacific (T. Tadokoro, Japan)
    - Inland Sea of Japan (K. Tadokoro, Japan)
    - Strait of Georgia (I. Perry, A. Akash, Canada)
- Using these estimates, regional comparisons of zooplankton production estimates will be included in the final report.
- WG 37 will seek comparisons between the group’s mesozooplankton productions with the models at each time-series to the results of mesozooplankton biomass or abundance from ETSOs.

5. Build a network of scientists and laboratories measuring zooplankton production among PICES and ICES nations as well as developing countries (ToR5).
    - The Co-Chairs asked the WG members to seek scientists and laboratories measuring zooplankton production. In particular, information from Chinese and Russian representatives is especially welcome as there is nobody available at the moment. (Dr. Hong Xia Ming will contact Chinese WG member Dr. Qing Yang on this issue)
    - The Co-chairs are making a list of the information on the scientists and laboratories (*e.g.*, name, institute, email, methodology used, publications) which will be posted on the PICES website.
    - The Co-chairs will ask Dr. Yebra to join this list from ICES Working Group on Zooplankton Ecology.

6. Promote international collaborations among zooplankton production researchers through international organizations such as PICES, ICES and IMBER (ToR6).
    - The Co-Chairs asked the WG members to seek the information on potential funding opportunities for international collaboration on zooplankton production estimates. Some examples of Japanese funding were introduced at the meeting.
    - The Co-Chairs proposed “Practical Workshop Phase 2” to be held just before PICES-2019 (***WG 37 Endnote 4***). Biochemical approaches are the target methodologies in this workshop.
    - *In situ* or laboratory experiments for comparing the traditional methodologies will be conducted by Drs. Kobari and Sastri and preliminary results were already demonstrated at PICES-2017. These results will be published in the final report.
    - The Co-Chairs will seek a collaborative session or workshop with *ex officio* member, Dr. Yebra in the 2021 Zooplankton Production Symposium.

7. Publish a final report summarizing results (ToR7).
    - Dr. Kobari proposed a tentative plan of contents and responsible authors for the final report, referring the previous reports for the past working groups as follows.
      In Memoriam (Toru Kobari and Akash Sastri)
      Executive Summary (Toru Kobari, Akash Sastri and Lidia Yebra)

1) Introduction (Toru Kobari)
        Background and Rationale
        Working Group Timeline
2) Principle, advantages/disadvantages and recommendations
    2-1) Traditional methodologies (from review paper) (Toru Kobari)
        Natural Cohort
        Artificial Cohort
        Molting Rate
        Egg Production
        Empirical Models
    2-2) Biochemical approaches (from review paper) (Lidia Yebra)
        Nucleic Acid Indices
        Enzymatic Methods
        Chitobiase Activity
        Protein Synthetases Activity
3) Procedures
    3-1) Traditional methodologies
        Artificial Cohort (Russ Hopcroft and Hui Liu)
        Molting Rate (Russ Hopcroft and Toru Kobari)
        Egg Production (Shinji Shimode)
        Empirical models (Koichi Ara)
        Physiological models (Toru Kobari)
    3-2) Biochemical approaches (from review paper)
        Nucleic Acid Indices (Toru Kobari)
        Chitobiase Activity (Akash Sastri)
        Protein Synthetases Activity (Lidia Yebra)
4) Zooplankton Production Measurements in Regional Seas (review on the previous studies)
        Gulf of Alaska (Russ Hopcroft and Hui Liu)
        Bering Sea (Akash Sastri)
        Okhotsk Sea (Russian members?)
        Western North Pacific (Toru Kobari)
        Japanese Coast (Toru Kobari)
        Korean Coast (Se-Jong Ju and Jung-Hoon Kang)
        East China Sea (Chinese members?)
5) Application of Empirical Models to Zooplankton Data Sets in PICES region
        Station Papa (Akash Sastri)
        West Coast of Vancouver Island and Strait of Georgia (Akash Sastri)
        Inland Sea of Japan (Kazuaki Tadokoro)
        Western North Pacific (Toru Kobari)
        Oregon coast (Jennifer Fisher and Samantha Zeman)
        Bering Sea (Dave Kimmel? and/or Russ Hopcroft?)
6) Comparisons among Methodologies
        Protein Synthetase Activity vs. Natural Cohort (Toru Kobari)
        Chitobiase Activity vs. Natural Cohort (Akash Sastri)
7) Concluding Remarks (Toru Kobari, Akash Sastri and Lidia Yebra)
        Recommendations
        Future Prospects

8) Acknowledgements (Toru Kobari)
9) References
10) Supplemented Information (Toru Kobari)
    Appendix 1 WG37 Terms of References
    Appendix 2 WG37 Membership
    Appendix 3 Business Meeting Reports from Past PICES Annual Meetings
    Appendix 4 Session/Workshop Summaries of International Conference Related to WG 37
    Appendix 5 Bibliography
    Appendix 6 Information on Laboratories Working on Zooplankton Production

- WG members discussed the outline, sections and responsible authors of the report at the WG business meeting 2018. This tentative plan will be circulated in November 2018 and confirmed within 2018 (all responsible authors will start to write from 2019).
- Bibliography of zooplankton growth and production in the North Pacific will be included in the report. WG members will assemble the literature for zooplankton growth and production studies for each country and report them at the WG business meeting 2018. Currently, there is limited or no information on papers in the Chinese and Russian waters.

Workshop for PICES-2019

Drs. Sastri and Kobari proposed 1-day workshop for PICES-2019 (***WG 37 Endnote 5***). This workshop is intended to provide a venue for further projects collaborating with the ICES Working Group on Zooplankton Ecology. The proposed workshop supports the terms of reference and final report of WG 37.

Practical Workshop Phase 2

See ***WG 37 Endnote 4***.

AGENDA ITEM 4
Others

Bibliography for zooplankton production methodology and measurements in the PICES region

The published papers on Korean and Japanese waters are listed to the report bibliography. The Co-Chairs asked WG members to collect more literature, in particular, papers from the Chinese and Russian regions.

Report of Workshop at PICES-2018

Dr. Kobari showed the participants the summary report of W6 on "*Regional evaluation of secondary production observations and application of methodology in the North Pacific*" that will be submitted it to the PICES Secretariat after the Annual Meeting.

WG 37 members and participants at workshop W6.

WG members and guests enjoy dinner at a Japanese soba restaurant after a successful Workshop (W6) at PICES-2018.

Report of Practical Workshop Phase 1 in Manazuru

Dr. Kobari showed the participants a report of the Practical Workshop Phase 1 that will be submitted to PICES Press after the Annual Meeting.

WG 37 Endnote 1

WG 37 participation list

<u>Members</u>

Se-Jong Ju (Korea)
Jung-Hoon Kang (Korea)
Russ Hopcroft (USA)
Hui Liu (USA)
Toru Kobari (Co-Chair, Japan)
Akash Sastri (Co-Chair, Canada)
Kazuaki Tadokoro (Japan)

<u>Members unable to attend</u>

China: Qing Yang
Russia: Vladimir Napazakov
USA: Todd O'Brien

<u>Observers</u>

Jennifer Fisher (USA)
Chih-hao Hsieh (China)
Megu Iwazono (Japan)
Takeru Kanayama (Japan)
Lian Kwong (Canada)
Hong Xia Ming (China)
Emma Moritoshi (Japan)
Chailinn Park (Korea)
Atsushi Tsuda (Japan)
Naoki Yoshie (Japan)
Samantha Zeman (USA)

WG 37 Endnote 2

WG 37 meeting agenda

1. Terms of reference
2. Activities in 2018
    - Session in the Ocean Science Meeting
    - Practical Workshop Phase 1
    - Workshop in the PICES 2018 Annual Meeting
3. Future plans
    - Plans to promote terms of reference
    - Workshop in the PICES Annual Meeting 2019
    - Practical Workshop Phase 2
4. Others
    - Bibliography for zooplankton production methodology and measurements in the PICES region
    - Report of Workshop in PICES 2018 Annual Meeting
    - Report of Practical Workshop Phase 1

WG 37 Endnote 3

Session in the Open Science Meeting

Zooplankton Productivity as a Function of Trophodynamics in Marine Ecosystems
Oregon Convention Center, Oregon, USA
February 15, 2018

Presentations

6 Talks (4 abstracts withdrawn)

1. T. Kobari: Session introduction, Zooplankton Productivity as a Function of Trophodynamics in Marine Ecosystems
2. G.A. Paffenhofer: Do doliolids eat eggs and juveniles of copepods?
3. C. Barth-Jensen *et al*.: Temperature-dependent egg-hatching and production of the egg-carrying copepods *Microsetella norvegica* and *Oithona similis* in a high latitude fjord
4. T. Ohnishi *et al*.: Identification method for starved female *Calanus sinicus* (Calanoida: Copepoda) based on differential gene expression profile
5. T.A. Venello *et al*.: Estimating crustacean zooplankton production rates and energy transfer in the NE Pacific
6. J. Duffy-Anderson *et al*. (presented by David Kimmel): Copepod dynamics across warm and cold periods in the eastern Bering Sea: Implications for walleye pollock (*Gadus chalcogrammus*) and the Oscillating Control Hypothesis

9 Posters (1 abstract withdrawn)

1. B.T. Jaspe *et al*.: Abundance, distribution and species composition of cyclopoid copepods in the upwelling region off northern Zamboanga Peninsula, Philippines
2. T. Kobari *et al*.: Community structure, standing stock and productivity of mesozooplankton in the southern Kyushu, Japan
3. T. Honma *et al*.: Spatial and temporal variations in community structure, standing stock and productivity of mesozooplankton in the downstream of the Tsushima Strait
4. C. Mckinstry and R.W. Campbell: Seasonal variation of zooplankton abundance and community structure in Prince William Sound, Alaska, 2009–2016
5. A. Poje *et al*.: Growth of calanoid copepods on an Arctic shelf
6. K. Suchy *et al*.: Temporal variations in depth-specific crustacean community structure and productivity estimates in a temperate fjord
7. L. Brotz and D. Pauly: The scale of jellyfish fisheries
8. R. Abualhaija *et al*.: Variability of zooplankton production across temporal and spatial scales in the Eastern Mediterranean ultra-oligotrophic pelagic region
9. R. Wahle *et al*.: The ‘Great Disconnect’: New lows in Gulf of Maine lobster recruitment during a boom in egg production linked to changes in the pelagic food web

WG 37 Endnote 4

Proposal for an inter-sessional Practical Workshop Phase 2

Following on the success of the practical workshop on "Production methodologies and measurements for *in situ* zooplankton", which was co-hosted by PICES Working Group 37 and Yokohama National University, we propose a second practical workshop that focuses on biochemical methods. PICES Working Group 37, Ocean Networks Canada and the Hakai Institute will jointly host this second workshop.

The goal of the second workshop is to provide a "hands-on" practicum on the two most widely used biochemical methods for measuring zooplankton production rates. The first method is Aminoacyl-tRNA-synthetases activity. The second method is Chitobiase activity. In addition, lectures would be given by Hakai and UBC scientists detailing other phytoplankton and zooplankton collection methods.

We suggest that a 3-day workshop is run at the Hakai Institute's Quadra Island field station preceding the PICES 2019 Annual Meeting that is taking place in Victoria, Canada. Tentative dates are October 14 to 16, 2019. Quadra Island is located about 4 hours north of Victoria by car and ferry. Once at the Hakai Institute's Quadra Island field station, participants will have access to boats for sample collection, laboratory space for learning and practicing and biochemical methods, and meeting space for dedicated lectures and discussions. In addition, accommodation and food provided by the Hakai Institute means that attendees can stay on site and focus on outcome of the workshop.

We estimate that there will be 10 international participants at this workshop (3 to 4 lecturers and 6 early career attendees). We estimate the following in kind support from ONC and the Hakai Institute:

- Transport from Victoria to Quadra Island (funded by ONC) ~$750.
- Accommodation, field and lab support, and food on Quadra Island (funded by Hakai Institute at $200 per person per day) ~$6000.

There are several anticipated deliverables of this workshop:

- About 10 Canadian and international scientists will be exposed to Hakai Institute's Quadra Island field station where new zooplankton production techniques will be taught and learned.
- This workshop is a partial fulfillment of one of Working Group 37's terms of reference.

This would enhance collaborative opportunities, particularly between ONC and Hakai.

WG 37 Endnote 5

Proposal for a Workshop on
"*PICES/ICES collaborative research initiative: Toward regional to global measurements and comparisons of zooplankton production using existing data sets*" at PICES-2019

Duration: 1 day

Convenors: Toru Kobari (Japan), Akash Sastri (Canada), Lidia Yebra (ICES/Spain)

Suggested Invited Speakers: TBD

Material and energy transfer in the lower food web are integrated through zooplankton communities. The standing stock and productivity of this group represent a proxy for the functional response of marine ecosystems to regional and global climate change. A variety of methods and information on zooplankton production rates have been assembled over the past half century, however, we are still struggling in our evaluation of zooplankton productivity and its driving forces. This workshop will discuss prospective tasks and collaborative research activities in an effort improve and standardize zooplankton field (and laboratory) methods from both PICES and ICES nations. We encourage presentations and discussion on novel applications of traditional and biochemical methodologies and/or new approaches for evaluating zooplankton productivity in the field.

WG 37 Practical Workshop on “*Production methodologies and measurements for in situ zooplankton: Phase 2*”

October 11–14, 2019, Quadra Island, British Columbia

Scope

Zooplankton production represents a quantitative proxy for the functional response of marine ecosystems to regional and global climate change, because material and energy scattering in the lower food web is integrated by zooplankton communities. In the last half century, many methodologies for measuring zooplankton production have been developed as described in the ICES Zooplankton Methodology Manual (published in 2000). Unfortunately, conventional field methods for measuring zooplankton population and community growth and production rates have practical limitations. This practical workshop will provide participants with both the theoretical background and hands-on experience needed to estimate zooplankton production rates using contemporary biochemical methodologies. The workshop is also intended as a forum for encouraging international collaboration on zooplankton production measurements among young scientists and students in the PICES region.

Sponsors

Hakai Institute, PICES, Working Group 37

Organizers

Toru Kobari (WG 37)
Akash Sastri (WG 37, BIO)

Local Organizing Committee (LOC)

Akash Sastri (Institute of Ocean Sciences)
Jennifer Jackson (Hakai Institute)

Dates

October 12th–13th, 2019 (Friday to Monday, just before the PICES 2019 Annual Meeting). Note travel dates to and from the workshop on Quadra Island are October 11th and 14th.

Venue

Hakai Institute, Quadra Island, British Columbia, Canada (https://www.hakai.org/)

Maximum number of participants

10 young scientists and students

Practical Workshop Schedule

October 11 (Friday)

13:00 Meeting at Victoria Conference Center (at Douglas Street)

13:00–17:00 Transportation to Hakai Institute

17:00–18:00 Opening ceremony

- Welcome address (Dr. Eric Peterson, chief of Hakai Institute)
- Description on background, objectives and schedule (Dr. Sastri, chair of LOC)
- Orientation for Hakai (Dr. Jennifer Jackson, LOC)

18:00–20:00 Ice breaker (dinner with beer and wine)
Self-introduction (all participants)
Name, Institute/University, Academic interests and others

October 12 (Saturday)

07:00–08:00 Breakfast

- Breakfast is available at meeting house, where all lectures are held.

08:00–09:30 Lecture on Chitobiase Activity for Zooplankton Productivity (Dr. Sastri)
Principle, advantages/disadvantages and recommendations

09:30–12:00 Onboard sampling with Dr. Yebra (Group A)/Lecture on procedure with Dr. Sastri (Group B)

- After Group A comes back from onboard sampling, Group B goes to onboard sampling.
- Participants for onboard sampling move to the port by Hakai van.

12:00–13:00 Lunch

- Lunch is available at meeting house.

13:00–18:00 Laboratory work (Dr. Sastri)
Biochemical reactions
Fluorescence measurements

  - Laboratory work is conducted at main laboratory house.
  - A methods manual will be provided for all participants.

18:00–19:00 Dinner

- Dinner is available at meeting house where lecture on data analysis is conducted.

19:00–20:30 Data analysis (Dr. Sastri)

October 13 (Sunday)

07:00–08:00 Breakfast

- Breakfast is available at meeting house, where all lectures are held.

08:00–09:30 Lecture on AARS Activity for Zooplankton Productivity (Dr. Yebra)
Principle, advantages/disadvantages and recommendations

09:30–12:00 Onboard sampling with Dr. Sastri (Group A)/Lecture on procedure with Dr. Yebra (Group B)

- After Group A comes back from onboard sampling, Group B goes to onboard sampling.
- Participants for onboard sampling move to the port by Hakai van.

12:00–13:00 Lunch

- Lunch is available at meeting house.

13:00-18:00 Laboratory work (Dr. Yebra)
  Biochemical reactions
  Spectrophotometer measurements
    - Laboratory work is conducted at main laboratory house.
    - A methods manual will be provided for all participants.

18:00–19:00 Dinner
  - Dinner is available at meeting house where lecture on data analysis is conducted.

19:00–20:30 Data analysis (Dr. Yebra)

October 14 (Tuesday)

07:00-08:00 Breakfast
  - Breakfast is available at meeting house, where closing ceremony is held.

08:00–08:30 Wrap-up

08:30–09:00 Closing ceremony
  Closing address (Dr. Eric Peterson, chief of Hakai Institute)
  Some notes (Drs. Sastri and Jackson)
  Take group-photo

09:00–13:00 Transportation to Victoria downtown

13:00 Break up

PICES-2019
October 16–27, 2019, Victoria, Canada

Excerpted from:

Summary of Scientific Sessions and Workshops at PICES-2019

BIO Workshop (W10)
PICES/ICES collaborative research initiative: Toward regional to global measurements and comparisons of zooplankton production using existing data sets

Convenors: *Toru Kobari (Japan), Akash Sastri (Canada), Lidia Yebra (Spain)*

Invited Speaker:
Shin-ichi Uye (Hiroshima University, Japan)

Background

Material and energy transfer in the lower food web are integrated through zooplankton communities. The standing stock and productivity of this group represent a proxy for the functional response of marine ecosystems to regional and global climate change. A variety of methods and information on zooplankton production rates have been assembled over the past half century, however, we still struggle to evaluate zooplankton productivity and its driving forces. Presentations and discussion on novel applications of traditional and biochemical methodologies and/or new approaches for evaluating zooplankton productivity in the field were encouraged.

Summary of presentations

The 1-day workshop was convened on October 16, 2019 to discuss aspects of the assessment of standing stock and productivity of zooplankton communities. In particular, talks focused on i) application and synthesis of zooplankton production rate measurements in the field; ii) modeling and laboratory validation studies; and iii) regional assessments of the performance/utility of empirical models for estimating zooplankton production rates using biomass time series. Much of the group discussion centered on how to take best advantage of online resources which can be used to derive broad-scale secondary production rate measurements using empirical models of zooplankton growth rates. The workshop was intended to focus on a number of issues relevant to the Working Group 37 (Zooplankton Production Methodologies, Applications and Measurements in PICES Regions). There were a total of 9 talks with 18 participants from 6 countries: Canada, Chile, Chinese Taipei, Japan, Spain, and USA. The 3 poster presenters also highlighted the major results of their studies as part of the afternoon session.

The afternoon discussion focused on three areas relevant to WG 37’s terms of reference. Our first discussion item centered around collaborative activities for zooplankton production measurements and methodologies with the ICES Working Group on Zooplankton Ecology. Dr. Lidia Yebra emphasized the importance of networking and regional to global collaboration as major achievements of the collaboration between ICES WGZE and PICES WG 37, and that there was a general agreement on pursuing further collaborations between PICES and ICES members. Dr. Yebra also noted that we should be aware of a large community of zooplankton production scientists from the Mediterranean and southern hemisphere. A representative example of similar efforts by the global community is the International Group for Marine Ecological Time Series (IGMETS) initiative. The second discussion topic approached a WG 37 terms of reference related to comparing secondary production time series based on conversion of biomass time series using empirical growth rate models. Several existing collaborations were noted and a general concern about how to choose the best model for times series' comparisons was raised. Drawing on the experience of participants, the most important issue is not to choose a single common production empirical model but rather, to select a model that accurately describes production at a particular site. This could take the form of choosing region-specific species models or providing a range of production estimates based on several global models. The ultimate goal is to develop comparable time series of zooplankton production rates. Finally, we discussed novel approaches for advancing zooplankton production measurements in the field. Participants noted that existing empirical models were developed 15–30 years ago. Thus, it was agreed that efforts to compile new data not included in those models would be an excellent option for updating current models prior to application to produce zooplankton production time series.

In brief, our invited speaker, Prof. Shin-ichi Uye (Japan) presented how to go from individual-based to population- and community-based production estimations and stressed the need for more direct measurements of species-specific growth rates before we can advance towards a community-level assessment of zooplankton production in the field. He also presented new information on the importance of tertiary production, using a chaetognath as example. In this sense, Dr. Pei-Chi Ho (Chinese Taipei) showed how specific growth rates estimated from relatively short artificial cohort incubations were used to test the importance of the predator/prey stoichiometry on zooplankton production in the field. Apart from direct measurements, indirect approaches were also presented such as models and enzymatic methods to facilitate the assessment of growth at the individual and community level. Prof. Hui Liu (USA) showed a new IBM model that allows the *in silico* development of natural and artificial cohorts to estimate field production rates of jellyfish, *Aurelia aurita*. Dr. Kazuaki Tadokoro (Japan) presented examples of a physiological model of zooplankton growth rates applied to existing zooplankton biomass time series data. Dr. Karyn Suchy (Canada) presented and compared crustacean production rates estimated from a variety of empirical models and applied to the West Coast of Vancouver Island and the Strait of Georgia, BC, Canada. Also, Dr. Akash Sastri (Canada) and Ms. Megu Iwazono (Japan) showed the importance of biomass in determining copepod production rates from chitobiase and AARS activity in the laboratory. Prof. John. Dower (Canada) presented a major decline in crustacean zooplankton production rates (estimated with the chitobiase method) and increases in gelatinous plankton biomass along the west coast Vancouver Island, since 2015. Finally, Dr. Lidia Yebra (Spain) presented online options through the COPEPOD website (https://www.st.nmfs.noaa.gov/copepod/) to move towards a global estimation and mapping of zooplankton field production using existing time series data. To close, the poster presentations by Ms. Megu Iwanzono (Japan), Mr. Fukutaro Karu (Japan), and Mr. Takeru Kanayama (Japan) highlighted their studies on zooplankton growth and feeding rates in the laboratory and field.

Workshop 10 participants in the entrance of the Victoria Conference Center, Victoria, Canada. Back row, from left: Sei-ichi Uye, Samantha Zeman, Julie Keister, Karyn Suchy, Akash Sastri, Lidia Yebra. Front row, from left: Hui Liu, Kazuaki Tadokoro, Kim Corporon Jacobson, David Kimmel, Pei-Chi Ho, Megu Iwazono, Takeru Kanayama.

List of papers

Oral presentations

Zooplankton production in temperate coastal waters: from individual to community level (Invited)
Shin-ichi Uye

Prey stoichiometry, primary production, and plankton composition influence production of marine zooplankton
Pei-Chi Ho, Esther Wong, Fan-Sian Lin, Akash R. Sastri, Carmen García-Comas, Noboru Okuda, Fuh-Kwo Shiah, Gwo-Ching Gong, Rita S.W. Yam and Chih-hao Hsieh

What have we learned from 13 years of chitobiase-based measurements of crustacean zooplankton productivity along Canada's west coast?
John F. Dower, Theresa A. Venello, Karyn D. Suchy and Akash R. Sastri

Seasonal population dynamics, biomass, production, and feeding of the chaetognath *Aidanosagitta crassa* in a temperate eutrophic inlet
Shin-ichi Uye and Liang Dong

A simulation model for estimating the growth and production of jellyfish (*Aurelia aurita*)
Hui Liu

Chitobiase-based estimates of developing biomass, growth rate, biomass production rate for a synchronous cohort of *Pseudodiaptomus inopinus* in culture
Akash Sastri, John Dower, Alex Clancy, Yuichiro Yamada, Tomonari Kotani, Toru Kobari and Yuka Matsuura

Application of the physiological model to the existing data sets for estimating zooplankton production rates
Toru Kobari, Kazuaki Tadokoro, Megu Iwazono and Debbie Steinberg

Biomass production rates of copepod communities along the West Coast of Vancouver Island and in the Strait of Georgia, BC, Canada: An application of multiple empirical growth rate models
Akash R. Sastri, Karyn D. Suchy, Lian E. Kwong, and Moira Galbraith

A global collaboration for the worldwide mapping of marine zooplankton biomass and production
Lidia Yebra and Todd D. O'Brien

Poster presentations

Trophic sources and feeding impacts of microzooplankton on phytoplankton community in the Kuroshio
Takeru Kanayama, Toru Kobari, Fukutaro Karu, Koji Suzuki, Naoki Yoshie and Gen Kume

Energy sources and feeding impacts of mesozooplankton community in the Kuroshio
Fukutaro Karu, Toru Kobari, Koji Suzuki, Naoki Yoshie, Taiga Honma, Takeru Kanayama and Gen Kume

Evaluation of protein synthetases activity as a proxy for zooplankton biomass and production rate using cultured copepod population, *Pseudodiaptomus inopinus*
Toru Kobari, Yuka Matsuura, Akash Sastri, Yuichiro Yamada, Megu Iwazono and Tomonari Kotani

Report of Working Group 37 on *Zooplankton Production Methodologies, Applications and Measurements in PICES Regions*

The third meeting of the Working Group on *Zooplankton Production Methodologies, Applications and Measurements in PICES Regions* (WG 37) was held on October 20, 2019 from 14:00 to 18:00 h in Victoria, Canada, under the chairmanship of Dr. Toru Kobari (Japan) and Dr. Akash Sastri (Canada). Sixteen participants including national representatives and observers attended the meeting (***WG 37 Endnote 1***). Several members who could not attend the meeting reported progress on their inter-sessional activities (see ***WG 37 Endnote 2***) and/or provided comments through the E-mail communication.

AGENDA ITEM 1
Activities in 2019

Drs. Kobari and Sastri reported the following WG activities achieved in 2019.

- Drs. Sastri, Jennifer Jackson (Hakai Institute), Lidia Yebra and Kobari organized a Practical Workshop Phase 2 during October 11 to 14, 2019 (just before the PICES-2019) at the Hakai Institute, Quadra Island, British Columbia, Canada (see pp. 12–13, 17 in PICES Press, 2020, Vol. 28, No. 1). Eight students and 6 scientists participated. Onboard sampling, laboratory work and lectures on how to measure chitobiase activity and aminoacyl tRNA synthetases activity for zooplankton were conducted.
- The Co-Chairs and Dr. Lidia Yebra (*ex-officio* member representing ICES, Spain) convened a Workshop (W10) on "*PICES/ICES collaborative research initiative*" on October 16, 2019 at PICES-2019 in Victoria. Eighteen people attended, and 9 talks and 3 posters were presented.
- Drs. Sastri and Yebra reviewed the outcomes of the practical and 1-day workshops held on October 12–14, 2019 and October 16, respectively, with the WG.
- Dr. Yebra summarized the "Discussion" section of W10 in detail (Dr. Sastri presented the slides from the introduction of the workshop).

AGENDA ITEM 2
Plans to promote terms of references

Dr. Kobari described the WG 37 work plan and progress on terms of references after which participants provided comments and suggestions. The Co-Chairs asked members to confirm that they could meet the new deadline of each task owing to the 1-year extension given to the WG for summarizing the WG 37 final report.

1. *Review papers on traditional and biochemical methodologies (ToR1)*
    - A review paper on traditional methodologies by the WG members (T. Kobari, A. Sastri, L. Yebra, H. Liu and R. Hopcroft) was submitted to a Special Issue (Dr. Bill Peterson Commemorative Issue) of *Progress in Oceanography* by the end of April 2019. Following comments and suggestions provided by two reviewers, a revised manuscript was resubmitted to the journal in mid-July, accepted in late July and published online in August 2019: (https://doi.org/10.1016/j.pocean.2019.102137).

2. *Guidelines and recommendations (procedures/protocols) of traditional and biochemical methodologies (ToR2)*
    - Dr. Yebra will make a draft based on the review paper on biochemical methodologies by Yebra *et al*., (2017, https://doi.org/10.1016/bs.amb.2016.09.001).
    - Similar guidelines for traditional methodologies are being developed by the WG members and colleagues. At the PICES-2018 meeting, Co-Chairs had asked for guidelines on the following: molting rate by Dr. Hopcroft (US member; T. Kobari will also provide), artificial cohort by H. Liu (US member), egg production by Dr. Shinji Shimode (materials for Practical Workshop Phase 1), empirical models by Dr. Koichi Ara (materials for Practical Workshop Phase 1), and physiological model (to be provided by T. Kobari).
    - Dr. Kobari asked all corresponding authors to send the guidelines and recommendations to him by the end November 2019. These will be posted on the PICES website in January 2020 and will be included in the WG 37 final report.
    - Dr. Kobari clarified that the procedures are detailed step-by-step.
    - WG members agreed that the level of understanding/experience for the procedures would be aimed at undergraduate or graduate student readers.

3. *Develop practical models for estimating zooplankton production to time-series (ToR3)*
    - At the PICES-2018 workshop (W6, *Regional evaluation of secondary production observations and application of methodology in the North* Pacific) and WG 37 business meeting, the Ikeda-Motoda was judged to be a suitable model that could be applied to zooplankton time-series due to the wide coverage of various taxonomic groups, locations and situations, minimum requirements of variables only for temperature and animal body weight, and high temporal and spatial resolutions.
    - Drs. Kazuaki Tadokoro and Kobari demonstrated the applications of the Ikeda-Motoda model to some Japanese zooplankton data sets. They had already demonstrated the applications to zooplankton data sets in the Inland Sea of Japan and on the Canadian coast at W6 during PICES-2018. These results will be included in the WG 37 final report (expected to be completed by the end of February 2020).
    - Dr. Kobari has contacted Dr. Kym Jacobson (NOAA Newport Zooplankton Program) requesting zooplankton time-series results along the Oregon coast.

4. *Build a platform of information exchange on zooplankton production measurements through an interactive website for regional and/or global mapping (ToR4)*
    - The following zooplankton data sets will be run with the Ikeda-Motoda model in order to make regional-to-basin-scale comparisons of zooplankton production rates:
        - Station P and Line P in the subarctic North Pacific (I. Perry, A. Sastri, Canada)
        - Newport Line in the western US coast (K. Jacobson, USA)
        - Tsushima Strait (T. Kobari, Japan)
        - Kuroshio in the East China Sea (T. Kobari, Japan)
        - A-Line in the western North Pacific (T. Tadokoro, Japan)
        - Inland Sea of Japan (K. Tadokoro, Japan)
        - Strait of Georgia (I. Perry, A. Sastri, K. Suchy, Canada)
        - CalCOFI and HOT time series (will be included if permission is obtained from the data owners).
    - Prof. Uye suggested including a general picture (*i.e.*, spatial or temporal patterns); members agreed to include temporal or spatial averages based on the zooplankton time series. Ultimately,

these comparisons will be to depict similar maps of phytoplankton biomass and primary production even if using different methodologies, which Dr. Liu pointed out.

- The WG will compare zooplankton production within each time series as a first step. However, there is a difficulty in comparing biomass data collected with different mesh sizes. A comparison of trends or anomalies rather than direct data was suggested as possibility to overcome dissimilarities between time series.

5. *Build a network of scientists and laboratories measuring zooplankton production among PICES and ICES nations as well as developing countries (ToR5)*
    - Information on scientists and laboratories (*e.g.*, name, institute, email, methodology used, selected publications) was reviewed by WG 37. WG members were requested during PICES-2019 to email any more information on scientists and laboratories measuring zooplankton production for entry into tables. Dr. Yebra provided a list of laboratories from ICES Working Group on Zooplankton Ecology and MedZoo. The completed list will be posted on the WG 37 website by the end of November 2019.

6. *Promote international collaborations among zooplankton production researchers through international organizations such as PICES, ICES and IMBeR (ToR6)*
    - A joint AP-NPCOOS/WG 37 PICES Spring School on “Coastal Ocean Observatory Science” will be held in early March 2020 in Kagoshima, Japan. The theme is “What is the Deep Scattering Layer (DSL) in the coastal region?”.
    - *In situ* and laboratory experiments for comparing traditional methodologies have been conducted by Drs. Kobari and Sastri and the preliminary results were presented at PICES-2017. Further results were shown at PICES-2019. These results will be included in the WG 37 final report.
    - WG 37, including *ex-officio* member, Dr. Yebra (Chair of ICES WGZE), will contribute a session or workshop at the 7th Zooplankton Production Symposium (Hobart, Australia, 2022).
    - WG 37 submitted a proposal for a workshop at PICES-2020 (***WG 37 Endnote 3***).

7. *Publish a final report summarizing results (ToR7)*
    - Dr. Kobari presented a tentative plan for contents, and authors responsible for the final report, referring to previous reports of past working groups as examples (see ***WG 37 Endnote 4***).

AGENDA ITEM 3

Bibliography for zooplankton production methodology and measurements in the PICES region

Published papers for Korean and Japanese waters have been added to a zooplankton production methodology and measurements bibliography. The Co-Chairs will contact national representatives to collect more published papers, in particular papers from the China and Russian regions. The bibliography will be included to the WG final report (as Appendix 5) and will be uploaded to the WG 37 website.

AGENDA ITEM 4

Report of the Practical Workshop Phase 2 on Quadra Island

Dr. Sastri showed members a draft article that will be submitted to the PICES Secretariat by the end of November 2019 for publication in PICES Press [since published in PICES Press, 2020, Vol. 28, No. 1, pp. 12-13, 17].

AGENDA ITEM 5

Report of Workshop W10 at PICES-2019

Dr. Yebra presented a draft article that will be submitted to the PICES Secretariat by the end of November 2019 for publication in PICES Press [since published in PICES Press, 2020, Vol. 28, No. 1, pp. 22–23, 26] .

Attendees at the WG 37 meeting on October 20 at PICES-2019, Victoria, Canada. Back row, from left: Fukutaro Karu, Toru Kobari, Hui Liu, Russ Hopcroft, Shin-ichi Uye, Kazuaki Tadokoro, Akash Sastri. Front row, from left, Takeru Kanayama, Megu Iwazono, Naoki Yoshie, Karyn Suchy, Lidia Yerba, Pei-Chi Ho, Hyunjin Yoon.

WG 37 members (left photo, from left) Lidia Yebra, Russell Hopcroft, Hui Liu and Karyn Suchy and (right photo, at front) Akashi Sastri and Se-Jong Ju enjoying a collegial dinner together with other PICES members (from left) Taewon Kim, Julie Keister and Lisa Eisner.

WG 37 Endnote 1

WG 37 participation list

Members

Toru Kobari (Co-Chair, Japan)
Akash Sastri (Co-Chair, Canada)
Russell Hopcroft (USA)
Se-Jong Ju (Korea)
Hui Liu (USA)
Karyn Suchy (Canada)
Kazuaki Tadokoro (Japan)
Lidia Yebra (Spain, *ex officio* member representing ICES)

Observers

Megu Iwazono (Japan)
Takeru Kanayama (Japan)
Fukutaro Karu (Japan)
Wongyu Park (Korea)
Pei-Chi Ho (Chinese Taipei)
Shin-ichi Uye (Japan)
Hyunjin Yoon (Korea)
Naoki Yoshie (Japan)

Members unable to attend

China: Qing Yang
Korea: Min-Chul Jang, Hyung-Ku Kang, Jung-Hoon Kang
Russia: Vladimir Napazakov
USA: Todd O'Brien

WG 37 Endnote 2

WG 37 meeting agenda

1. Activities in 2019
   - Practical Workshop Phase 2
   - Workshop W10 in the PICES 2019 Annual Meeting
2. Plans to promote terms of references
   1) Review papers on traditional and biochemical methodologies (ToR1).
   2) Guidelines and recommendations of traditional and biochemical methodologies (ToR2).
   3) Develop practical models for estimating zooplankton production to time-series (ToR3).
   4) Build a platform of information exchange on zooplankton production measurements through an interactive website for regional and/or global mapping (ToR4).
   5) Build a network of scientists and laboratories measuring zooplankton production among PICES and ICES nations as well as developing countries (ToR5).
   6) Promote international collaborations among zooplankton production researchers through international organizations such as PICES, ICES and IMBER (ToR6).
   7) Publish a final report summarizing results (ToR7).
3. Bibliography for zooplankton production methodology and measurements in the PICES region
4. Report of Practical Workshop Phase 2
5. Report of Workshop at PICES-2019

WG 37 Endnote 3

Proposal for a Workshop on
"Can we link zooplankton production to fisheries recruitment?"
at PICES-2020

Convenors: Hui Liu (USA), Toru Kobari (Japan), Karyn Suchy (Canada), Russ Hopcroft (USA)

Duration: 1 day

Invited speaker: Xianshi Jin (China)

Sustainability of fisheries requires a better understanding of stock dynamics and resilience to environmental and anthropogenic forcing. Zooplankton play a vital nexus between primary producers and higher level consumers and are thus highly relevant to fisheries production and ecosystem functions. Understanding the impact of trophic relationships on the nutrition of larvae and foraging fishes is a critical step needed to forecast the stock response and resilience to environmental changes. However, limited attention has been paid to the role of zooplankton in sustaining fisheries production, which is largely because routine measurements of secondary production remain rare. This workshop will discuss prospective ways for understanding functional and structural roles of secondary production on fisheries dynamics and production. In particular, we encourage presentations and discussions on research using experimental, observational and modeling approaches linking zooplankton productivity and fish larvae and foraging fishes.

WG 37 Endnote 4

Report of Working Group 37
Table of Contents

In Memoriam (T. Kobari and A. Sastri): almost done

Executive Summary (A. Sastri and L. Yebra): write after completed all information and circulate among all members

1. Introduction
    1.1. Background (T. Kobari): almost done
    (WG to explain that target was meso to macrozooplankton in this final report and microzooplankton should be target as future prospects.)
    1.2. Rationale: almost done
    1.3. Working Group Timeline: almost done
2. Principle, Advantages/Disadvantages and Recommendations
    2.1. Introduction (T. Kobari): almost done
    2.2. Traditional Methodologies (from review paper: T. Kobari)
        2.2.1. Natural Cohort: partially done
        2.2.2. Artificial Cohort: partially done
        2.2.3. Molting Rate: partially done
        2.2.4. Egg Production: partially done
        2.2.5. Empirical Models: partially done

- 2.3. Biochemical Approaches (from review paper: L. Yebra)
  - 2.3.1. Nucleic Acid Indices: not yet
  - 2.3.2. Chitobiase Activity: not yet
  - 2.3.3. Aminoacyl tRNA Synthetases Activity: not yet

  (These sections would be described and summarized using the tables for traditional and biochemical approaches rather than repeating the review papers.)

3. Zooplankton Production Measurements in Regional Seas (R.R. Hopcroft)
   - 3.1. Introduction
   - 3.2. Zooplankton Production Measurements
     - 3.2.1. Gulf of Alaska (R.R. Hopcroft and H. Liu): not yet
     - 3.2.2. Canadian waters and Bering Sea (from PICES 2018 workshop: A. Sastri and K. Suchy): not yet
     - 3.2.3. Okhotsk Sea (Russian members?): not yet
     - 3.2.4. Japanese waters (from PICES 2018 workshop: T. Kobari): not yet
     - 3.2.5. Korean waters (Hyung-Ku Kang and Jung-Hoon Kang): almost done
     - 3.2.6. East China Sea (Chinese members?): not yet

     (These sections are described using the bibliography as described below.)
4. Application of Production Models to Zooplankton Data Sets in PICES region
   - 4.1. Introduction (T. Kobari): almost done
   - 4.2. Station Papa (A. Sastri, K. Suchy, and L. Kwong): not yet
   - 4.3. Strait of Georgia (K. Suchy and A. Sastri): not yet
   - 4.4. West coast of Vancouver Island (A. Sastri, K. Suchy, L. Kwong)
   - 4.5. Northern Gulf of Alaska (R. Hopcroft): not yet
   - 4.6. Chukchi Sea (R. Hopcroft): not yet
   - 4.7. Inland Sea of Japan (K. Tadokoro): not yet
   - 4.8. Other Japanese waters (T. Kobari): not yet
5. Comparisons of Zooplankton Production among Methodologies
   - 5.1. Introduction (T. Kobari): almost done
   - 5.2. Copepod Culture (T. Kobari): almost done
   - 5.3. Natural Cohort and Modified Natural Cohort (T. Kobari): almost done
   - 5.4. AARS activity and Natural Cohort (T. Kobari and Megu Iwazono): almost done
   - 5.5. Chitobiase Activity and Natural Cohort (A. Sastri): not yet
   - 5.6. AARS activity and Physiological Model (Megu Iwazono and T. Kobari): not yet
   - 5.7. AARS activity and Chitobiase Activity (A. Sastri and T. Kobari): not yet
6. Concluding Remarks (T. Kobari, A. Sastri and L. Yebra)
   - 6.1. Recommendations (T. Kobari, A. Sastri and L. Yebra): not yet
   - 6.2. Future Prospects (T. Kobari, A. Sastri and L. Yebra): not yet

(WG describe that target was meso to macrozooplankton in this final report and microzooplankton should be target as future prospects.)

7. Acknowledgements (T. Kobari): almost done
8. References: not yet
9. Supplemented Information

   Appendix 1 WG 37 Terms of References: will be provided by the Secretariat

- Appendix 2 WG 37 Membership: will be provided by the Secretariat
- Appendix 3 Business Meeting Reports from Past PICES Annual Meetings: will be provided by the Secretariat
- Appendix 4 Session/Workshop Summaries of International Conference Related to WG37 (T. Kobari): not yet
- Appendix 5 Bibliography (T. Kobari): partially done
- Appendix 6 Information on Laboratories Working on Zooplankton Production (T. Kobari): partially done
- Appendix 7 Guidelines and procedures for traditional and biochemical methodologies: not yet
    - Appendix 7.1. Traditional methodologies
        - Append.7.1.1. Artificial Cohort (Russ Hopcroft): not yet
        - Append.7.1.2. Molting Rate (T. Kobari): almost done
        - Append.7.1.3. Egg Production (Shinji Shimode and T. Kobari): almost done from Workshop Phase 1
        - Append.7.1.4. Empirical Models (Koichi Ara and T. Kobari): not yet
        - Append.7.1.5. Physiological Models (T. Kobari): not yet
    - Appendix 7.2. Biochemical methodologies
        - Append.7.2.1. Nucleic Acid Indices (L. Yebra): needs formatting from published version prior to posting at the PICES website
        - Append.7.1.2. Chitobiase Activity (A. Sastri): needs formatting from published version prior to posting at the PICES website
        - Append.7.1.3. Aminoacyl tRNA Synthetases Activity (L. Yebra): needs formatting from published version prior to posting at the PICES website

Proposed deadlines:
Section 3: April 1, 2020
Section 4: end of November 2019
Section 5: end of November 2019
Practical Workshop Report Phase 2 and PICES workshop W10: end of November, 2019

PICES-2020
October 13–15, 2020, Virtual Annual Meeting

Report of Working Group 37 on *Zooplankton Production Methodologies, Applications and Measurements in PICES Regions*

The Working Group on *Zooplankton Production Methodologies, Applications and Measurements in PICES Regions* (WG 37) annual meeting was held at online (Zoom) on October 1, 2020 from 14:00 to 17:00 (Pacific standard time, +UTC-8), under the chairmanship of Dr. Toru Kobari (Japan) and Dr. Akash Sastri (Canada) (see *WG 37 Endnote 1*). Ten participants including national representatives and observers attended and participated in the meeting (*WG 37 Endnote 2*).

AGENDA ITEM 1
Activities done in 2020

Dr. Kobari reported on the following WG activities planned for 2020.

2020 PICES Spring School

Drs. T. Kobari, Naoki Yoshie (Ehime University) and Gen Kume (Kagoshima University) organized a 2020 PICES Spring School on "Coastal Ocean Observatory Science" planned for March 4 to 8, 2020 and hosted by Kagoshima University, Kagoshima, Japan. This Spring School was sponsored by PICES, AP-NPCOOS, Japan Society for the Promotion of Science, and Kagoshima University. This Spring School participation included 25 early career scientists from 9 countries, 3 lecturers from Japan, and 5 supporting staff. We scheduled onboard sampling, laboratory work, and lectures on monitoring of coastal environments and ecosystems using the latest instruments (*e.g.*, CTD, ADCP, scientific sonar) and analyses. Unfortunately, due to the severe COVID-19 situation, the organizers cancelled this Spring School in late February 2020.

Workshop at the PICES 2020 Annual Meeting

Drs. Hui Liu, T. Kobari, K. Suchy, and R. Hopcroft, planned to convene a workshop (*Can we link zooplankton production to fisheries recruitment?*) for the PICES 2020 Annual Meeting. Potential speakers were as follows.

- ✓ Wim Kimmerer (Zooplankton production and its consequences)
- ✓ Xianshi Jin (Fish production in the Yellow Sea, invited)
- ✓ Dave McKinnon (Zooplankton production and its consequences)
- ✓ Anthony Richardson
- ✓ Gen Kume (Gut contents analysis of fish larvae in the Kuroshio)
- ✓ A. Sastri (Zooplankton production in the eastern Pacific)
- ✓ Evgeny Pakhomov (Zooplankton size spectrum to estimate production, Canada)

Due to COVID-19, the PICES 2020 Annual Meeting was changed to an online format and most of sessions and workshops were cancelled or postponed. After discussion, WG members decided to postpone the in-person workshop until PICES-2021 in China. Depending on the situations of COVID-

19, it is likely necessary to re-consider whether the workshop should be held online or cancelled in next year.

AGENDA ITEM 2

Terms of references

After Dr. Kobari described the working plans and progress toward the terms of references (ToR), all participants discussed progress of each ToR in turn. Particularly, the Co-Chairs asked all participants to confirm the deadline for summarizing the WG 37 final report (mid-December).

1. *Review papers on traditional and biochemical methodologies (ToR1)*

   The two papers on zooplankton production methodologies have been already published.

2. *Guidelines and recommendations (procedures/protocols) of traditional and biochemical methodologies (ToR2)*

   Guidelines for several of the traditional methodologies have been made by the WG members and colleagues. These materials will be included as supplemented information on the final report. It is expected that the responsible authors submit the guidelines for the artificial cohort method by the end of October. The deadline will not be extended further.

3. *Develop practical models for estimating zooplankton production to time-series (ToR3)*

   Drs. Kazuaki Tadokoro and Kobari demonstrated the applications of the Ikeda-Motoda model as applied to some Japanese zooplankton data sets. Dr. Sastri will provide similar results using Canadian data sets. These results have been included in the WG 37 final report.

4. *Build a platform of information exchange on zooplankton production measurements through an interactive website for regional and/or global mapping (ToR4)*

   Following the discussions during the WG meeting, the zooplankton production estimates for several time series (Canadian time series, Oyashio time series, and BATS) or data sets (Inland Sea of Japan and Kuroshio) were available from the WG final report. However, we have no available platform for “information exchange” on zooplankton production measurements through “an interactive website”. Drs. Kobari and Yebra will seek such platform or alternative way within a year (the extended term of the WG 37 to October 2021 has been requested to BIO).

5. *Build a network of scientists and laboratories measuring zooplankton production among PICES and ICES nations as well as developing countries (ToR5)*

   The information on scientists and laboratories measuring zooplankton production among PICES and ICES member countries will be included as supplemental information for the WG final report and made available through the PICES website.

6. *Promote international collaborations among zooplankton production researchers through international organizations such as PICES, ICES, and IMBeR (ToR6)*

   WG 37 organized two PICES Practical Workshops (Japan and Canada) and one PICES Spring School (Japan). While the Spring School was cancelled, WG 37 promoted international collaborations by organizing several workshops at PICES Annual Meetings and thematic sessions (Zooplankton Production Symposium and Ocean Sciences meeting) at international meetings.

7. *Publish a final report summarizing results (ToR7)*

The timeline is scheduled as follows. WG 37 will submit the final report by the end of December 2020. Note that the blank sections will be deleted if these are not submitted by mid November.
November 15: Deadline for submission of all responsible sections
December 15: Deadline for editing all sections by Co-Chairs and Dr. Yebra
Late December: Submit the WG final report to BIO for review

AGENDA ITEM 3

Bibliography for zooplankton production methodology and measurements in the PICES region

The bibliography is included in the WG final report and will be demonstrated at the PICES website.

AGENDA ITEM 4

Term of WG 37

All participants discussed the possibilities whether the WG 37 term should be extended until 2021 or closed 2020 because all scientific activities have been cancelled or extended since the last spring when COVID-19 was under severe situations. Through the extensive discussions, all participants agreed to the following points:

- ✓ Final report of WG 37 to be submitted to BIO for review by the end of December.
- ✓ WG 37 to convene the PICES workshop (*Can we link zooplankton production to fisheries recruitment?*) postponed to the 2021 PICES Annual Meeting.
- ✓ Co-Chairs request an extension of the WG 37 term to October 2021.

WG 37 Endnote 1

WG 37 participation list

Members

Toru Kobari (Co-Chair, Japan)
Akash Sastri (Co-Chair, Canada)
Kazuaki Tadokoro (Japan)
Lidia Yebra (*ex officio* member, representing ICES)
Se-Jong Ju (Korea)
Karyn Suchy (Canada)
Jung-Hoon Kang (Korea)
Russell Hopcroft (USA)
Hui Liu (USA)

Members unable to attend

China: Qing Yang
Korea: Min-Chul Jang, Hyung-Ku Kang
Russia: Vladimir Napazakov
USA: Todd O’Brien

Observer

Harold (Hal) Batchelder (PICES)

WG 37 Endnote 2

WG 37 meeting agenda

1. Activities done in 2020
   - Spring School
   - Workshop at the PICES 2020 Annual Meeting
2. Plans to complete terms of references
   - Review papers on traditional and biochemical methodologies (ToR1)
   - Guidelines and recommendations of traditional and biochemical methodologies (ToR2)
   - Develop practical models for estimating zooplankton production to time-series (ToR3)
   - Build a platform of information exchange on zooplankton production measurements through an interactive website for regional and/or global mapping (ToR4)
   - Build a network of scientists and laboratories measuring zooplankton production among PICES and ICES nations as well as developing countries (ToR5)
   - Promote international collaborations among zooplankton production researchers through international organizations such as PICES, ICES and IMBER (ToR6)
   - Publish a final report summarizing results (ToR7)
3. Others
   - Bibliography for zooplankton production methodology and measurements in the PICES region

PICES-2021
October 18–22, 2021, Virtual Annual Meeting

Excerpted from:

Summary of Scientific Sessions and Workshops at PICES-2021

BIO/FIS Workshop (W1)
Can we link zooplankton production to fisheries recruitment?

Convenors:
Toru Kobari (Japan), Hui Liu (USA), Karyn Suchy (Canada)

Background

Sustainability of fisheries requires a better understanding of stock dynamics and resilience to environmental and anthropogenic forcing. Zooplankton play a vital nexus between primary producers and higher level consumers and are thus highly relevant to fisheries production and ecosystem functions. Understanding the impact of trophic relationships on the nutrition of larvae and foraging fishes is a critical step needed to forecast the stock response and resilience to environmental changes. However, limited attention has been paid to the role of zooplankton in sustaining fisheries production, which is largely because routine measurements of secondary production remain rare. This workshop will discuss prospective ways for understanding functional and structural roles of secondary production on fisheries dynamics and production. In particular, we encourage presentations and discussions on research using experimental, observational and modelling approaches linking zooplankton productivity and fish larvae and foraging fishes.

Summary

The 1-day workshop was convened to discuss aspects of the linkage of zooplankton production to fisheries recruitment. The workshop objective was to understand functional and structural roles of secondary production on fisheries dynamics and production. This workshop was virtual using Zoom and thus all topics were presented using pre-recorded MS PowerPoint or video files. It held the following 11 presentations and 37 attendees from four countries: Canada, USA, Japan, and Russia.

1. Community structure of fish larvae associated with advections of the Kuroshio and its neighboring waters. Yusuke Manako
2. Comparison of plankton community structure, standing stocks and productivity along the Kuroshio at the Tokara Strait. Toru Kobari
3. Distribution, feeding habits, and growth of chub mackerel, *Scomber japonicus*, larvae during a highstock period in the northern Satsunan area, southern Japan. Gen Kume
4. Evaluating pathways of environmental association with mesozooplankton and fisheries production. Lian Kwong
5. How to adapt growth and productivity of fish larvae to the Kuroshio. Tomoko Kusano
6. Importance of gelatinous zooplankton on plankton food web in the Kuroshio based on metabarcoding analysis. Yusuke Tokumo
7. Model-based spatiotemporal variability in mesozooplankton productivity in the Salish Sea. Karyn D. Suchy

8. Promising perceptions of linking zooplankton production to fisheries dynamics. Hui Liu
9. Source of coastal waters advected to the Kuroshio using particle-tracking experiments on high-resolution coastal ocean model. Shin Kazuno
10. The Tortoise and the Hare: distinct early growth strategies in a nearshore groundfish persist in the seasonally variable Northern California Current. Megan N. Wilson
11. The effect of zooplankton community composition on variability of trophic transfer efficiency in the NE Pacific. Theresa A. Venello

To stimulate discussions on each presentation among the participants and to focus workshop objectives during the limited discussion time (1 hour), co-convenors prepared another platform (Google Drive) before this workshop that all presentation files were uploaded and any attendees could post their questions, comments and suggestions on them. This platform might be useful for non-native speakers to understand their questions, comments and suggestions and to provide their answers to them.

The workshop discussions were focused on the two questions, Q1) “what are necessary for zooplankton to evaluate fishery dynamics and production?” and Q2) “what are advantages/disadvantages for current zooplankton production methodologies and measurements to be linked with fishery dynamics and production?”. To achieve effective and efficient discussions, co-conveners asked all presenters to provide their ideas to these questions before workshop. Main points of their ideas were summarized as follows.

Q1: What are necessary for zooplankton to evaluate fishery dynamics and production?
For evaluating fishery dynamics and production, we need spaciotemporal data sets

- ✓ with application to monitoring activities for accumulating production data sets in time and space,
- ✓ with high spatiotemporal resolution using ecological modelling on ocean dynamics.

We also need taxon-based data sets

- ✓ breaking down to taxonomic levels as a proxy of food availability for fishes,
- ✓ expanding to non-crustacean groups or major functional groups for differential prey preference,
- ✓ to focus specific taxonomic groups having significantly trophodynamics hub among various trophic pathways.

After sharing these ideas from presenters, many comments and suggestions were provided from attendees to this workshop. As a major issue for this workshop question, our discussions were focused on the availability of zooplankton production rates for fish recruitments and stock assessments based on time-series data sets. While zooplankton production rates are rare among the time-series currently available in the PICES region, all attendees shared that direct measurements of zooplankton rate process are crucial for understanding mechanistic link of fish recruitments and stock assessments to lower trophic levels. As these issues were associated with the second question, we moved to the next discussion.

Main points of the ideas to the second question from presenters were summarized as follows.

Q2: What are advantages/disadvantages for current zooplankton production methodologies and measurements to be linked to fishery dynamics and production?
As advantages, zooplankton production data sets

- ✓ are directly comparable to fish population dynamics or fishery stocks through larval growth and survival,

- ✓ provide information to understand biological mechanisms,
- ✓ are representative of carrying capacity for fish populations.

As disadvantages,

- ✓ zooplankton production data sets are still low resolution in time, space and taxa,
- ✓ measurement methodologies are tedious and time-consuming for operation and not practical to generate time-series.

As described above, direct measurements on zooplankton production rates are always desired for stock assessments of various fishes since these rates are representative of biological mechanisms. However, many attendees felt that these disadvantages made data accumulation and utilization difficult. Co-chairs of PICES Working Group 37 introduced the two practical approaches based on the WG scientific reports, zooplankton production rates estimated with the empirical and physiological models applicable to time-series and direct measurements with biochemical approaches like enzyme activities in time-series.

Given the extensive discussions, the co-conveners mentioned that the continuous scientific activities are needed to link zooplankton production to fish recruitment and/or stock assessment through some approaches in future. As one of them, all attendees were informed on a 1-day session proposed for the PICES 2022 Annual Meeting in Korea.

Fig. 1. Attendees of Workshop 1 during the PICES 2021 Annual Meeting

2021 Report of Working Group 37 on *Zooplankton Production Methodologies, Applications and Measurements in PICES Regions*

The Working Group on *Zooplankton Production Methodologies, Applications and Measurements in PICES Regions* (WG 37) annual business meeting was held at online (Zoom) on September 21, 2021 from 14:00 to 17:00 h (Pacific Standard Time, UTC-8), under the chairmanship of Dr. Toru Kobari (Japan) and Dr. Akash Sastri (Canada) (see *WG 37 Endnote 1*). Six participants including national representatives and 1 observer attended and participated in the meeting (*WG 37 Endnote 2*).

WG 37 virtual meeting participants during PICES-2021.

Agenda Item 1
Activities in 2021

Dr. Kobari reported on the following WG activities in 2021.

Workshop at the PICES 2021 Annual Meeting
The workshop (W1) on "*Can we link zooplankton production to fisheries recruitment?*" was convened October 18, 2021 during PICES-2021. Co-Convenors were Toru Kobari, Russ Hopcroft, Hui Liu and Karyn Suchy. The workshop was virtual with topics presented using pre-recorded MS PowerPoint File. Discussion was conducted using Zoom. Presenters included 6 from Japan, 3 from Canada and 2 from USA:

- Toru Kobari (Comparison of plankton community structure, standing stocks and productivity along the Kuroshio at the Tokara Strait)

- Gen Kume (Distribution, feeding habits, and growth of chub mackerel, *Scomber japonicus*, larvae during a high-stock period in the northern Satsunan area, southern Japan)
- Yusuke Manako (Community structure of fish larvae associated with advections of the Kuroshio and its neighboring waters)
- Yusuke Tokumo (Importance of gelatinous zooplankton on plankton food web in the Kuroshio based on metabarcoding analysis)
- Tomoko Kusano (How to adapt growth and productivity of fish larvae to the Kuroshio)
- Karyn D. Suchy (Model-based spatiotemporal variability in mesozooplankton productivity in the Salish Sea)
- Shin Kazuno (Source of coastal waters advected to the Kuroshio using particle-tracking experiments on high-resolution coastal ocean model)
- Lian Kwong (Evaluating pathways of environmental association with mesozooplankton and fisheries production)
- Hui Liu (Promising perceptions of linking zooplankton production to fisheries dynamics)
- Megan N. Wilson (The Tortoise and the Hare: distinct early growth strategies in a nearshore groundfish persist in the seasonally variable Northern California Current)
- Theresa A. Venello (The effect of zooplankton community composition on spatiotemporal variability of trophic transfer efficiency in the subarctic NE Pacific)

Due to the limited time for discussions among workshop participants, the following approaches were proposed by Dr. Kobari prior to the meeting.

1. *For efficient and effective discussions*

Under the format of PICES workshops during the Annual Meeting, it would have been difficult to have a productive discussion on workshop objectives (How can we link zooplankton production to fisheries recruitment?) and to compile them without any direct implications or contributions. Therefore, the Chair of the workshop conveners (T. Kobari) first, encouraged all participants to add the implications of their topics to the workshop objectives. Second, to promote efficient and effective discussions within short discussion duration, the participants were asked to indicate some points to be discussed as follows: 1) What is necessary for zooplankton production to evaluate fishery dynamics and production? 2) What are advantages/disadvantages for current zooplankton production methodologies and measurements to link fishery dynamics and production? All participants were requested to present their ideas and solutions as slide presentations.

2. *Create an online platform for discussion*

As an example, Dr. Kobari created a folder in Google Drive to upload the presentation files. (Some files were uploaded in early October.) The files were open for anyone wishing to post comments. Working Group members were encouraged to use this folder for a platform of open discussions for all participants before the PICES-organized “discussion hour”.

Agenda Item 2

Plans to complete terms of reference

- **Term of reference 4**
  Build a platform of information exchange on zooplankton production measurements through an interactive website for regional and/or global mapping

  WG 37 has no available platform for information "exchange" on zooplankton production measurements through an interactive website. As alternative platform, "figshare" was proposed for exchanging production data sets. Dr. Kobari asked contributing authors to provide production data sets for the WG final report but unfortunately, some data owners have not permitted their data sets to be used because figshare is a public platform. The other data sets have been uploaded successfully to https://figshare.com/.

- **Term of reference 7**
  Publish a final report summarizing results

  After positive comments and suggestions by two BIO committee reviewers, the report co-editors and section co-authors made revisions and sent the revised version to BIO committee by the end of September. The final revised report was recommended for publication by BIO committee (October 4, 2021, following the WG 37 business meeting), and subsequently approved for publication by Science Board and Governing Council at their respective meetings.

WG 37 Endnote 1

WG 37 meeting agenda

1. Activities done in 2021
2. Plans to complete terms of references
    - Build a platform of information exchange on zooplankton production measurements through an interactive website for regional and/or global mapping (ToR4).
    - Publish a final report summarizing results (ToR7).
3. Others

WG 37 Endnote 2

WG 37 participation list

<u>Members</u>

Toru Kobari (Co-Chair, Japan)
Akash Sastri (Co-Chair, Canada)
Karyn Suchy (Canada)
Kazuaki Tadokoro (Japan)
Hui Liu (USA)
Lidia Yebra (*ex officio* member, representing ICES)

<u>Members unable to attend</u>

China: Qing Yang
Korea: Se-Jong Ju, Jung-Hoon Kang
Russia: Vladimir Napazakov
USA: Russell Hopcroft

<u>Observer</u>

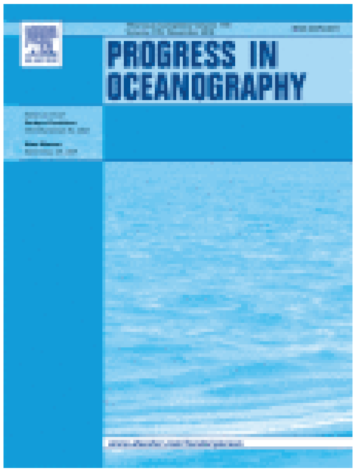
Minju Kim (Korea, representing Se-Jong Ju)

Appendix 6

WG 37 Publications

A book chapter titled “Advances in Biochemical Indices of Zooplankton Production” (Authors: L. Yebra, T. Kobari, A.R. Sastri, F. Gusmão, and S. Hernández-León) was published in Advances in Marine Biology, 2017, Volume 76, pp. 157–240. Members of PICES Working Group 37 (Zooplankton Production Methodologies, Applications and Measurements in PICES Regions) contributed and co-authored this review publication.

https://doi.org/10.1016/bs.amb.2016.09.001



A review article titled “Evaluation of trade-offs in traditional methodologies for measuring metazooplankton growth rates: Assumptions, advantages and disadvantages for field applications” (Authors: Toru Kobari, Akash R. Sastri, Lidia Yebra, Hui Liu, and Russell R. Hopcroft) was published in Progress in Oceanography, 2019, Volume 178, 102137. Members of PICES Working Group 37 (Zooplankton Production Methodologies, Applications and Measurements in PICES Regions) contributed and co-authored this review publication.

https://www.sciencedirect.com/science/article/abs/pii/S0079661119301020X

PICES/ICES Workshop on "*ICES/PICES cooperative research initiative – Towards a global measurement of zooplankton production*"

by Toru Kobari and Lidia Yebra

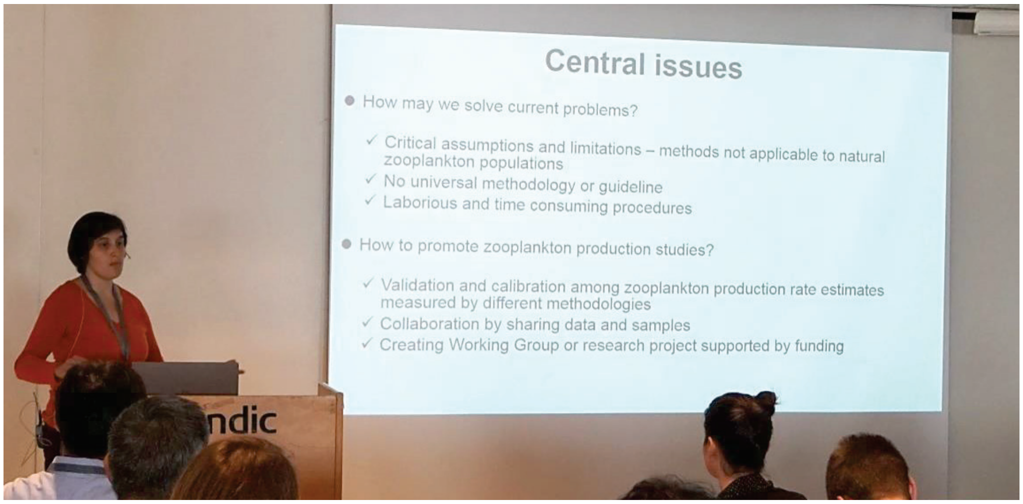
Approximately 20 zooplankton ecologists met March 11, 2016, to discuss zooplankton production methodologies and measurements at a half-day workshop during the ICES/PICES-sponsored 6th International Zooplankton Production Symposium in Bergen, Norway. We briefly summarize the presentations (one invited) and subsequent discussions of this workshop (W2) in this report. The workshop focused on contemporary methodologies and advances in estimating zooplankton production, with a goal of eventually providing a global assessment of zooplankton production. Workshop presentations included direct estimates of growth, empirical models and indirect biochemical indices of zooplankton production.

Dr. Lutz Postel presented an invited talk on estimating zooplankton production by applying P:B ratio to multiple times series data of biomass and abundance. He mentioned that empirical models of growth rates provide useful information on zooplankton productivity and proposed that empirical models on P:B ratio would give good estimates of zooplankton production. Dr. Koichi Ara estimated mesozooplankton production in Japanese coastal waters using abundances from microscopic counts, biomass indirectly estimated from length–weight equations and growth rates computed from an empirical model (*i.e.*, coupling different traditional methodologies). Alejandro Marrero, presented a poster that tested three zooplankton production models against direct measurements of growth in the marine mysid *Leptomysis lingvura* (Mysidacea, Crustacea). In her presentation, Dr. Karyn Suchy showed crustacean production estimates using chitobiase activity in Canadian coastal waters. She emphasized that this biochemical approach would overcome some disadvantages of traditional methods and provide high temporal and spatial data resolution using simple procedures and rapid measurements compared to traditional methods. Posters displayed by Dr. Toru Kobari and Dr. Lidia Yebra showed the application of biochemical methods like aminoacyl-tRNA synthetases (AARS) activity to estimate production of the zooplankton community in the field.

There were additional contributions demonstrating the utility of other direct and indirect methods to estimate zooplankton production. Unfortunately, due to the economic situation in Brazil, some authors could not attend and present their work at the workshop.

Before discussion, the major problems for zooplankton production assessment were summarized as follows:

- *How do we solve current problems?*
  - ✓ Critical assumptions and limitations: Methods not applicable to natural zooplankton,
  - ✓ No universal methodology or guideline,
  - ✓ Laborious and time consuming procedures.
- *How do we promote zooplankton production studies?*
  - ✓ Validation and calibration among zooplankton production rate estimates measured by different methodologies,
  - ✓ Collaboration by sharing data and samples,
  - ✓ Creating a Working Group or research project supported by funding.



Central issues

- How may we solve current problems?
  - ✓ Critical assumptions and limitations – methods not applicable to natural zooplankton populations
  - ✓ No universal methodology or guideline
  - ✓ Laborious and time consuming procedures
- How to promote zooplankton production studies?
  - ✓ Validation and calibration among zooplankton production rate estimates measured by different methodologies
  - ✓ Collaboration by sharing data and samples
  - ✓ Creating Working Group or research project supported by funding

Workshop 2 Co-Chair, Dr. Lidia Yebra, summarizing the central issues for zooplankton production assessment.

Since a previous PICES workshop on zooplankton production at the 2012 PICES Annual Meeting (see pp. 51–54 in Session Summaries-2012), some progress has been made by colleagues from ICES and PICES nations. Principal among these achievements is the organization of this workshop at the 6th International Zooplankton Production Symposium and the preparation of a review paper on biochemical methodologies for zooplankton production estimation for submission to a peer-reviewed journal.

It should be noted that these achievements had been accomplished without financial support, and therefore, progress towards a global measurement and assessment of zooplankton production has been slower than hoped for. We discussed different approaches that might be necessary for achieving more effective advances in the measurement and intercalibration of zooplankton production. For example, we discussed using multiple but small funding sources for our working group activities, rather than continuing unsuccessfully to approach major international science organizations like SCOR or EUROCEANS for greater resources. Collaborative research opportunities alongside summer schools that could include training courses on zooplankton ecology, and especially target the measurement of secondary production by zooplankton, could be an alternative approach.

During the workshop, we discussed the advantages and disadvantages of the current methodologies that are used to estimate zooplankton production of natural zooplankton populations or communities. More direct measurements on body mass would be recommended for those who use the traditional methods, such as incubations to estimate the "molt rate". These incubation methods are laborious and time-consuming and need special care to eliminate artifacts. Most biochemical approaches have relatively simple protocols and quick measurements, but they need to be calibrated against the direct rates they approximate. As confirmed at the earlier PICES workshop on zooplankton production, all participants realize that little attention and effort is being directed to community-based zooplankton production. Indeed, it is uncommon to propose sessions and workshops on zooplankton production methodologies and measurements even at the Zooplankton Production Symposium. Since zooplankton have key structural and functional roles in complex food webs, zooplankton production might be considered an integrated response of biogeochemical cycles and trophodynamics in marine ecosystems. Throughout the discussion, we confirmed that more quantitative evaluations like zooplankton production estimates are essential for understanding the response of marine ecosystems and trophic pathways in oceans that are rapidly changing. This is an issue of concern worldwide, and of particular focus for ICES and PICES in the North Atlantic and North Pacific, respectively.

A main outcome of W2 was the initiation of an international network of plankton ecologists interested or already involved in developing a cooperative research initiative with a goal to achieving a global assessment of zooplankton production. The prospective activities to be carried out by the group include:

1. Proposing a PICES Working Group on Zooplankton Production;
2. Producing reviews and guidance on the advantages and disadvantages of traditional and biochemical approaches for estimating zooplankton production;
3. Organizing international workshops and/or summer schools for intercomparison of zooplankton production methodologies and measurements using multiple small funding sources;
4. Expanding the cooperative network among ICES, PICES and southern hemisphere nations.

Dr. Toru Kobari is an Associate Professor on the Faculty of Fisheries of Kagoshima University, Kagoshima, Japan. His research focuses on the population dynamics, life cycles and feeding dynamics of marine copepods in the waters of the Northwest Pacific. He was a member of the PICES Oceanic Ecodynamics COmparison in the Subarctic Pacific (OECOS) project to compare the oceanic Gulf of Alaska in the eastern subarctic Pacific to the Oyashio region off Northern Japan in the western subarctic Pacific. Toru convened the Workshop on "Secondary production: Measurement methodology and its application on natural zooplankton community" at PICES-2012 in Hiroshima, Japan and co-convened W2 at the ICES/PICES 6th International Zooplankton Production Symposium. He is a chair-invited member of the ICES Working Group on Zooplankton Ecology.

Dr. Lidia Yebra is a researcher at the Spanish Institute of Oceanography in Málaga, Spain. Her interests include zooplankton physiology and ecology, and she developed methodologies to estimate production rates using biochemical approaches, such as the activity of the enzymes aminoacyl-tRNA synthetases (AARS). She was an invited speaker at the Workshop on "Secondary Production: Measurement methodology and its application on natural zooplankton community" at PICES-2012 in Hiroshima, Japan. She is a member of the ICES Working Group on Zooplankton Ecology and contributes to the ICES Zooplankton Status Report. She is also a member of the Scientific Steering Committee of the ICES/PICES 6th International Zooplankton Production Symposium, and co-convened W2.

Working Group 37 organizes a Practical Workshop on "*Production methodologies and measurements for in situ zooplankton: Phase 1*" in Manazuru, Japan

by Toru Kobari and Akash Sastri

Zooplankton production represents a quantitative proxy for the functional response of marine ecosystems to regional and global climate change. In the last half century, many methodologies for measuring zooplankton production have been developed and reviewed in the ICES Zooplankton Methodology Manual. Unfortunately, the applications to the zooplankton population and community in nature remain limited due to the specific expertise required for these methodologies.

This past fall, the Working Group on *Zooplankton Production Methodologies, Applications and Measurements in PICES Regions* (WG 37) held a 3-day training workshop to introduce early career scientists and students to information on several traditional methodologies used for estimating zooplankton production and to share the practical tricks for doing so. Drs. Shinji Shimode (Yokohama National University), Koichi Ara (Nihon University) and Toru Kobari (WG 37 Co-Chair) organized a Practical Workshop titled "*Production methodologies and measurements for in situ zooplankton: Phase 1*" which took place October 22 to 24 at the Manazuru Marine Center for Environmental Research and Education (Yokohama National University), just prior to PICES-2018. The Center was located about a 90-minute drive southwest of Yokohama. The workshop was aimed at early arrivals to the Annual Meeting, and was envisioned as the first of two workshops (Phase 2 to take place immediately prior to PICES-2019).

Eleven participants (4 males and 7 females) from 5 PICES member countries (China, Japan, Korea, Canada, USA) registered for this event. The organizers had originally planned for a minimum number of participants, as advertised in the announcement, but due to the exceptional interest the workshop generated, the organizers were able to make arrangements to accommodate twice the number! On the evening of the first day, after a welcome address and description of the workshop by the organizers, all participants introduced themselves during an ice breaker. On the morning of the second day, all participants collected zooplankton samples on board the T/S *Tachibana*, and after lunch listened to lectures on egg production by Dr. Shimode and on empirical models by Dr. Ara. This was immediately followed by laboratory work on identifying, counting and sorting the target species and eggs, and computing their measured data which continued into the morning of the third day.

Participants and two of the organizers, back row: Dr. Shinji Shimode (second from left) and Dr. Koichi Ara (fifth from left) at the ice-breaker.

Sorting adult females of target species for the egg production experiments lectured by Dr. Shimode.

Dr. Ara giving a lecture on sensitivity analysis of zooplankton production estimations among several empirical models.

Dinner and night session on the second day, with everyone enjoying Japanese soul food, "Okonomi-yaki", which was kindly made by Japanese support staff.

Group shot of all participants at the gate of the Manazuru Marine Center for Environmental Research and Education, Yokohama.

Prior to the closing ceremony on Day 3, all participants were asked to complete a questionnaire to evaluate and give their impressions of the workshop. Overwhelmingly, everyone enjoyed the laboratory work, lectures and discussions regarding zooplankton production measurements and methodologies. Such a response indicates that this practical workshop is a good opportunity for making international collaborations and integrating information on zooplankton production measurements. WG 37 will conduct a Phase 2 Practical Workshop on biochemical approaches for measuring zooplankton production just before the PICES-2019 in Victoria, Canada. Stay tuned for a follow-up article in PICES Press.

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Dr. Akash Sastri (asastri@uvic.ca) is Ocean Networks Canada's staff scientist supporting interdisciplinary research in the "Plankton Dynamics and Biogeochemistry" research theme. He has a background in biological oceanography with a focus on the roles of marine plankton communities in changing environments. Akash completed his undergraduate studies and a M.Sc. in Zoology at the University of Guelph, Ontario. His Ph.D. (2007) thesis at the University of Victoria focused on the development and application of novel ways to measure zooplankton productivity routinely at sea. Within PICES he is a member of the Biological Oceanography Committee, Advisory Panel on North Pacific Coastal Ocean Observing Systems, and co-chairs the Working Group on Zooplankton Production Methodologies, Applications and Measurements in PICES Regions.

Working Group 37 organizes Phase 2 of a Practical Workshop on *"Production methodologies and measurements for in situ zooplankton"*

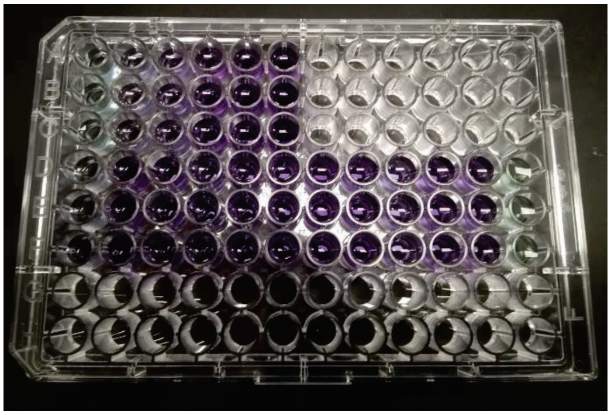
Akash Sastri, Jennifer Jackson, Karyn Suchy, Lidia Yebra and Toru Kobari

Zooplankton production represents a quantitative proxy for the functional response of marine ecosystems to regional and global climate change. Two practical workshops were organized by the Working Group on *Zooplankton Production Methodologies, Applications and Measurements in PICES Regions* (WG 37) with the objective of providing participants with the theoretical background and hands-on experience needed to estimate zooplankton production rates using traditional (Phase 1, 2018, Japan; PICES Press, Vol. 27, No. 1, pp. 29–30) and contemporary (Phase 2, 2019, Canada; this article) biochemical methodologies. These workshops were also intended as a forum for encouraging international collaboration on zooplankton production measurements in the PICES region among early career scientists and students.

In October 2019, the Hakai Institute at Quadra Island, British Columbia, Canada, hosted eight early career scientists from 5 countries which included Canada, Chile, China, Japan and Korea, for the Practical Workshop Phase 2: "*Production methodologies and measurements for in situ zooplankton*".

During this long-weekend workshop, hands-on activities, lectures, and field trips provided the participants with opportunities to learn about the physical and biological oceanographic properties of coastal British Columbia, to run enzymatic assays such as chitobiase and aminoacyl-tRNA synthetases (AARS) activity, to measure zooplankton protein content, and to learn how to analyze and interpret these metabolic measurements in the context of growth and production rates.

Chris Mackenzie and Brett Johnson (Hakai Institute) showing participants how to deploy Niskin bottles for water sampling.



Microplate showing color-based zooplankton protein content assay results during laboratory work.

Participants Lady Liliana Espinosa Leal (Chile, standing) and Megu Iwazono (Japan) loading a microplate for AARS enzyme activity assays.

On arrival at the Institute, participants and lecturers received a warm welcome from Hakai personnel, followed by a description of the facilities and the workshop agenda by the organizers, and an ice breaking reception and dinner during which participants introduced themselves.

During the following two days, local and invited experts lectured on oceanographic time-series and coastal oceanography (Dr. Jennifer Jackson, Hakai Institute), chitobiase activity (Drs. Akash Sastri, Fisheries and Oceans Canada, and Karyn Suchy, University of Victoria) and AARS activity (Dr. Lidia Yebra, Instituto Español de Oceanografia, Spain).

Workshop participants enjoyed the scenery from Quadra Center and the good weather during the workshop.

Several field trips onboard the Hakai Institute research vessel were organized to provide participants with hands-on experience in sampling coastal waters in the northern Strait of Georgia using standard sampling gear/techniques for characterization of physico-chemical water column properties as well as for collection and handling of sea water and zooplankton samples to conduct biochemical methods.

The busy weekend ended by celebrating Canadian Thanksgiving with dinner offered by the Hakai Institute at the local pub. Prior to returning to Victoria to attend the PICES Annual Meeting, the workshop participants had the opportunity to go kayaking around Quadra Island on a sunny morning. All participants enjoyed the laboratory works, lectures and discussions regarding zooplankton production measurements and methodologies.

WG 37 would like to thank the hosting partners: the Hakai Institute and PICES for helping to make the PICES Phase 2 workshop an outstanding success.

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Dr. Jennifer Jackson (jennifer.jackson@hakai.org) is a physical oceanographer at the Hakai Institute (funded by the Tula Foundation) in Victoria, British Columbia, Canada. She leads the Hakai Oceanography Program, which studies coastal waters along British Columbia's central coast. Her focus is on ocean climate including marine heatwaves, bio-physical interactions, and interactions between the open ocean and coastal waters. In PICES she is on the Physical Oceanography and Climate (POC) Committee.

Dr. Karyn Suchy (ksuchy@uvic.ca) is currently a Research Associate with the Pacific Salmon Foundation and the Department of Geography at the University of Victoria in British Columbia, Canada. Her broad research interests are in zooplankton ecology and biological oceanography. The main goal of her current work is to look at how seasonal patterns at the base of the food web (e.g. phytoplankton and zooplankton) are changing over time in the Salish Sea in response to different environmental drivers. In PICES, she is a member of the Working Group on Zooplankton Production Methodologies, Applications and Measurements in PICES Regions (WG 37).

Dr. Lidia Yebra (lidia.yebra@ieo.es) is a Research Scientist at the Spanish Institute of Oceanography in Málaga, Spain. Her interests include zooplankton physiology and ecology, and she developed methodologies to estimate production rates using biochemical approaches, such as the activity of the enzymes aminoacyl-tRNA synthetases (AARS). She is a member of the ICES Working Group on Zooplankton Ecology and contributes to the ICES Zooplankton Status Report. In PICES, she is an ex officio member, representing ICES, of Working Group on Zooplankton Production Methodologies, Applications and Measurements in PICES Regions (WG 37).

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PICES/ICES collaborative research initiative: Toward regional to global measurements and comparisons of zooplankton production using existing data sets

Lidia Yebra, Akash Sastri and Toru Kobari

Workshop 10 participants at PICES-2019, Victoria, Canada.

About 20 zooplankton ecologists met October 16, 2019, to discuss zooplankton production methodologies and measurements at a 1-day workshop during PICES-2019 in Victoria, Canada. The workshop focused on: i) the application and synthesis of zooplankton production rate measurements in the field; ii) modeling and laboratory validation studies; and iii) regional assessments of the performance/utility of empirical models for estimating zooplankton production rates using biomass time series. Much of the group discussion centered on how to take best advantage of online resources which can be used to derive broad-scale secondary production rate measurements using empirical models of zooplankton growth rates. The workshop was intended to focus on a number of issues relevant to PICES Working Group (WG 37) on *Zooplankton Production Methodologies, Applications and Measurements in PICES Regions* and ICES Working Group on *Zooplankton Ecology* (WGZE). Workshop presentations included direct estimates of growth, empirical models and indirect biochemical indices of zooplankton production.

Prof. Shin-ichi Uye (invited speaker, Japan) talked about how to go from individual-based to population and community-based production estimations and stressed the need for more direct measurements of species-specific growth rates before we can advance toward a community-level assessment of zooplankton production in the field. He also presented new information on the importance of tertiary production, using a chaetognath as an example. Next, Dr. Pei-Chi Ho (Chinese Taipei) showed how copepod-specific growth rates estimated from relatively short artificial cohort incubations were used to test the importance of the predator/prey stoichiometry on zooplankton production in the field. Apart from direct measurements, indirect approaches were also presented, such as models and enzymatic methods to facilitate the assessment of growth at the individual and community level. Prof. Hui Liu (USA) showed a new Individual-Based Model (IBM) that allows the *in silico* development of natural and artificial cohorts to estimate field production rates of the jellyfish, *Aurelia aurita*. Dr. Kazuaki Tadokoro (Japan) presented examples of a physiological model of zooplankton growth rates applied to existing zooplankton biomass time series data. Dr. Karyn Suchy (Canada) compared crustacean production rates estimated from a variety of empirical models and applied to the west coast of Vancouver Island and the Strait of Georgia, BC, Canada. Also, Dr. Akash Sastri (Canada) and Ms. Megu Iwazono (Japan) showed the importance of biomass in determining copepod production rates from chitobiase and aminoacyl-tRNA synthetases (AARS) activity in the laboratory. Prof. John. Dower (Canada) described a major decline in crustacean zooplankton production rates (estimated with the chitobiase method) and increases in gelatinous plankton biomass along the west coast Vancouver Island, since 2015. Finally, Dr. Lidia Yebra (Spain) looked at the COPEPOD website as a potential online tool which may be used to move towards a global estimation and mapping of zooplankton production rates using existing time series data. Additional contributions, as poster presentations, by Ms. Megu Iwanzono (Japan), Mr. Fukutaro Karu (Japan), and Mr. Takeru Kanayama (Japan) highlighted their studies on zooplankton growth and feeding rates in the laboratory and field.

The afternoon discussion focused on three areas relevant to WG 37's terms of reference. Our first discussion item centered around collaborative activities for zooplankton production measurements and methodologies with ICES WGZE. Dr. Yebra emphasized the importance of networking and regional to global collaboration as major achievements of the collaboration between ICES WGZE and PICES WG37, and that there was a general agreement on pursuing further collaborations between PICES and ICES members. Dr. Yebra also noted that we should be aware of a large community of zooplankton production scientists from the Mediterranean and southern hemisphere. A representative example of similar efforts by the global community is the International Group for Marine Ecological Time Series (IGMETS) initiative.

The second discussion topic approached a WG37 term of reference related to using existing biomass time series and empirical zooplankton growth rate relationships to compile and compare secondary production time series. Several existing collaborations were identified and a general concern about how to choose the best model for times series comparisons was raised. Drawing on the experience of participants, the most important issue is not to choose a single common empirical growth rate model, but rather to select a model which accurately describes growth/ production in a particular region. This could take the form of choosing region-specific species models or providing a range of production estimates based on several global models. The ultimate goal is to develop comparable time series of zooplankton production rates.

Finally, we discussed novel approaches for advancing zooplankton production measurements in the field. Participants noted that existing empirical models were developed 15 to 30 years ago. Thus, it was agreed that efforts to compile new data not included in those models would be an excellent option for updating existing models prior to their application for zooplankton production time series.

This workshop is the most recent in a series of international workshops organized to advance towards a global measurement and assessment of zooplankton production. Since the PICES-2012 workshop on "*Secondary production: Measurement methodology and its application on natural zooplankton community*" (Hiroshima, Japan, 2012) and the workshop on "*ICES/PICES cooperative research initiative: Towards a global measurement of zooplankton production*" at the ICES/PICES 6th International Zooplankton Production Symposium (Bergen, Norway, 2016), notable progress has been made by colleagues from PICES and ICES. Principal among these achievements is the establishment of PICES WG 37 (2017-2020,), and the publication of two review papers summarizing the recent advances in biochemical (Yebra *et al.*, 2017, *Advances in Marine Biology*, https://doi.org/10.1016/bs.amb.2016.09.001) and traditional (Kobari *et al.*, 2019, *Progress in Oceanography*, https://doi.org/10.1016/j.pocean.2019.102137) methodologies for zooplankton production estimation. To foster advances on these topics, additional workshops were organized by WG 37 during PICES Annual Meetings in 2017 ("*Advantages and limitations of traditional and biochemical methods of measuring zooplankton production*", Vladivostok, Russia), and in 2018 ("*Regional evaluation of secondary production observations and application of methodology in the North Pacific*", Yokohama, Japan), as well as a session at the 2018 Ocean Sciences Meeting ("*Zooplankton productivity as a function of trophodynamics in marine ecosystems*", Portland, USA). Also, two practical workshops (Manazuru, Japan, 2018 and Quadra Island, Canada, 2019) were recently organized and convened by WG 37 members to provide early career scientists with training on state-of-the-art methodologies for *in situ* zooplankton production measurement within an international context.

A main outcome of W10 was the expanding of international collaboration among plankton ecologists from the North Pacific and Atlantic. The prospective activities proposed for development during the workshop include a regional comparison of zooplankton production rates estimated from zooplankton biomass coastal time series in the Northeast Pacific, fostering the use of online databases, updating of current production empirical models with recent zooplankton growth rates, and promoting further international collaboration by pursuing new venues for discussion and knowledge exchange in form of workshops and summer schools.

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