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REVIEW

Zooplankton secondary production: main methods, overview and perspectives from Brazilian studies

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Abstract Since zooplankton is the main route of biomass transfer between producers and consumers, zooplankton secondary production is an important measure to evaluate the flow of matter through the trophic levels in aquatic food chains. Secondary production measures may be employed to characterize the zooplankton functional role and to assess the impacts on ecosystem processes and services. The objectives of this study were: 1- to review the main methods to quantify zooplankton secondary production and 2- to carry out a survey of the studies made in Brazil, identifying their gaps, potentialities and perspectives. We conducted a search of publications using secondary production measures in Brazilian aquatic environments in different databases ("Web of Science", "Scopus" and "Scielo"). We found that secondary production measures are based on three main approaches: physiological, enzymatic and population dynamics. The main measures of zooplankton secondary production used in freshwater environments are based on recruitment and biomass increase methods while in transitional and marine environments predominate measures based on growth rate. We found 60 publications among scientific articles, thesis and book chapters developed in Brazil. The studies on zooplankton secondary production have grown in recent years, however most publications were carried out in the southeast region, especially in reservoirs with descriptive approaches. Since there is still a lack of basic information on tropical species and environments, it is important to develop new studies focusing on more complex issues, such as aquatic ecosystems functioning, the effects of environmental changes and anthropic impacts on ecosystem processes and the aquatic environments contribution to biogeochemical global cycles.

Keywords Productivity . Food chains . Energy flow . Matter cycling

Introduction

The importance of production measures has been recognized since the last century due to the increasing concern to quantify ecosystem dynamics and functioning (Edmondson and Winberg 1971; Waters 1977). From the ecosystem functioning perspective, production is the mean by which energy is provided from one trophic level to the next (Waters 1977). However, it can also be understood as the set of processes by which heterotrophic organisms sustain and propagate themselves (Lehman 1988). It can also express the population or community fitness over time (Dolbeth et al. 2012).

The secondary production of a system corresponds to the production of organic matter by heterotrophic organisms, which can be quantified by measuring the increase in biomass resulting from food assimilation per unit of time (Edmondson and Winberg 1971). It is the final step of all processes involved in consumption and matter transformation (Santos-Wisniewski and Rocha 2007), life history patterns and survival strategies (Lehman 1988) and energy storage rates of consumers (Odum 1983). The idea behind the studies that measure secondary production is that the ecological units are analyzed as bioenergetic systems whose

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balance between matter input and output is related to productivity (Petrusewicz and Macfadyen 1970). Since secondary production is a measure of the fresh matter formed, its quantification allows measuring the amount of biomass renewed per unit of time (Lampert and Sommer 1997).

According to Downing (1984) the use of secondary production measures is related to four different objectives: 1 - Comprehension of the transfer mechanisms of matter and energy; 2 - Management of water resources; 3 - Detection and evaluation of pollutants and 4 - Formulation and testing of biological productivity theories. Secondary production is a measure that has great advantages over others because it incorporates the population performance and integrates the biotic interactions among community members. The main advantages are: characterization of the species or community functional role; better assessment of the impacts of natural or anthropic disturbances on ecosystem processes and load capacity for a given resource (Dolbeth et al. 2012).

The first study of zooplankton secondary production was performed by Lindeman (1942), serving as a basis for further studies and establishing important information on the dissipative processes of excretion and respiration. Since then, the number of studies on secondary production has grown, especially in the 1970s after the publication of the International Biological Program (IBP) Handbook N17 (Edmondson & Winberg 1971 - 1st ed., Rigler and Downing 1984 - 2nd ed.). The IBP Handbook N17 establishes the main methods of secondary production measurement and is still one of the main references for aquatic production studies. With the increase of environmental changes, studies on secondary production, metabolism (respiration, excretion, feeding rates, etc.) and zooplankton trophic role represent priority research lines for ecologists around the world (Lopes 2007). However, although more than 30 years have passed since the publication of IBP Handbook N17, studies on secondary production are still scarce, especially in neotropics, despite their recognized importance (Abra 2012). The objective of this study was to review the main methods for quantifying zooplankton secondary production, their advantages and difficulties, as well as to evaluate the studies carried out in Brazil with this type of approach. Through an extensive review of the specialized literature, we have detailed procedures for calculating secondary production for different groups and types of environments, especially for freshwater environments that have been the most studied. We also identified the main gaps in studies using secondary production and the main perspectives for future research.

Measures of zooplankton secondary production

Zooplankton is characterized by species with short life cycles and high reproductive rates. Parameters such as density or biomass alone do not reflect all the responses of these organisms to ecological interactions and environmental factors (Edmondson 1974). Therefore, from an ecosystem approach, secondary production measures have particular importance (Melão and Rocha 2006 ; Dolbeth et al. 2012). In addition, because of their recognized role in energy transfer from producers to consumers in higher trophic levels, zooplankton secondary production provides valuable information for studies about trophic chains (Brito et al. 2016).

The secondary production can be evaluated from three main methods: physiological measures, population dynamics analysis or, more recently, enzymatic measures (Melão 1999 ; Avila et al. 2012). Physiological methods are those that consider the rates of assimilation, respiration and/or organisms' excretion. Methods based on population dynamics quantify cohort variations by the sum of increments among development phases or even by the product between growth rates and biomass (Melão 1999). The enzymatic method is based on the concentration in the water of enzymes related to the crustacean ecdysis process and, therefore, to its growth and biomass increase (Sastri and Dower 2009). For all methods, individual biomass, fecundity, development rates, predation, organism age, food availability and ecological interactions are important intrinsic factors that may affect the zooplankton production. In addition, climatic, hydrologic variations as well as disturbances also influence zooplankton secondary production (Melão and Rocha 2004).

Among the groups that make up the zooplankton, rotifers and microcrustaceans (copepods and cladocerans) are the most important. Despite their reduced size and lower biomass expression, when compared to other groups, the secondary production of rotifers may acquire special importance in certain types of environments where this group is abundant (Dias et al. 2014). Their consumption capacities restricted to a certain type of food (small algae and detritus) and high reproductive rates result in an important conversion of organic matter through the secondary production (Winberg 1971; Peláez-Rodrigues and Matsumura-Tundisi 2002 ; Dias et al. 2014). Thus, in terms of ecosystem processes, analysis of rotifers secondary production represents a more realistic measure of the community's energy and mass contribution than density or abundance (Peláez-Rodríguez and Matsumura-Tundisi 2002). For rotifers, the commonly used measure is the recruitment-based method described by Elster (1954; also found in Edmondson 1965; Edmondson and Winberg 1971; Rigler and Downing 1984). In this method, the difference in size between the newly hatched individual and the adult is irrelevant. Therefore, the finite birth rate is calculated in accordance with the following formula:

$$B=E/Te$$

Where:
B = finite birth rate
E = number of eggs/female ratio
Te = egg development time

The values for the embryo development time of the egg can be obtained by experiments conducted in the laboratory, continuous sampling in field, by equations that consider the environment temperature values (see Bottrell et al. 1976) or in specific literature (for Brazilian continental aquatic environments see: Peláez-Rodrigues and Matsumura-Tundisi 2002; Negreiros 2010; Negreiros 2014). Once the values of the finite birth rate are obtained, the recruitment of the community is calculated as the number of individuals added to the population by the formula:

$$Pn=Nf*B$$

Where:
Pn = recruitment of new individuals
Nf = number of females
B = finite birth rate

The secondary production (organic matter weight) is obtained by multiplying the population recruitment value by the average individual weight in the equation:

$$P=Pn*W$$

Where:
P = secondary production
Pn = recruitment of new individuals
W = average individual weight

The weights of the rotifers can be obtained by direct weighting on a microanalytical precision balance or from their biovolumes obtained by the formulas provided by Ruttner-Kolisko (1977).

In freshwater environments several studies have found a great contribution of cladocerans to plankton productivity (Melão 1999; Brito 2010), while in marine environments the copepods contribution is more significant (Ara 2004; Ara 2008). Regardless of the type of environment, the most used secondary production measure for both groups of microcrustaceans is the biomass increase method proposed by Winberg et al. (1965) (also found in Edmondson & Winberg 1971). The population production will be the sum of the increments in weight, for each stage of development, age or size class. For cladocerans, which usually present continuous growth, it is more appropriate to consider size classes (neonates, young and adults). Thus, the simplified formula for secondary production is:

$$Pd=\frac{Ne*(Wn-We)}{Te}+\frac{Nn*(Wy-Wn)}{Tn}+\frac{Ny*(Wa-Wy)}{Ty}$$

Where:
Pd = Production in a unit of time
e = egg

W = dry weight
N = number of individuals
T = duration of each stage of development

n=neonate
y=young
a=adult

The secondary production calculation for copepods is done following the same procedure applied to cladocerans. As adults do not show growth, we consider the different phases of development (nauplii, copepodite and adult), development time and biomass of each phase (Winberg et al. 1965). Thus, the formula is:

$$Pd=\frac{Ne*(Wn-We)}{Te}+\frac{Nn*(Wc_{1-2}-Wn)}{Tn}+\frac{Nc_{1-2}*(Wc_{3-4}-Wc_{1-2})}{Tc_{1-3}}+\frac{Nc_{3-4}*(Wa-Wc_{3-4})}{Tc_{3-4}}$$

Where:
Pd = Secondary Production in a unit of time
W = dry weight
N = number of individuals
T = duration of each development stage
A = adult

e=egg
n=nauplii
c_{1-2} = copepodite phase 1 to 2
c_{3-4} = copepodite phase 3 to 4

The post-embryonic development time for each phase for both groups of microcrustaceans can be obtained through laboratory cultures or in the literature (see Bottrell et al. 1976; Espíndola 1994; Rietzler 1995; Santos-Wisniewski and Rocha 2007; Santos et al. 2010). The weight can also be obtained directly by weighting on precision balance or indirectly calculated from weight-length regressions (See Botrell et al. 1976, for regressions of Brazilian species from lakes, floodplain lakes and reservoirs see Maia-Barbosa and Bozelli 2005; González et al. 2008; Azevedo et al. 2012; Brito et al. 2013). However, for most species this information has not yet been established. For marine species, this information is even more scarce (see Chisholm and Roff 1990 for weight-length regressions for tropical marine species).

Due to difficulties in obtaining the biomass increment values of the different development phases for different species, other secondary production measures may be employed. An alternative calculation is the product between biomass and birth rate (Hart 1987). This type of estimate is most found in marine studies. First, the finite birth rate is estimated by the formula:

$$\beta = E / N*Te$$

Where:
β = finite birth rate
E = density of eggs
N = adult population density
Te = time of embryonic development

Then, secondary production is estimated by the product of the finite birth rate and individual biomass:

$$P= \beta * B$$

Where:
P = secondary production
B = biomass
β = finite birth rate

Many studies in marine environments still use other methods to estimate secondary production. These estimates are made by equations similar to those proposed by Hart (1987), but instead of considering the product between biomass and finite birth rate, the models consider the product of biomass by the rate of growth and are called production by instantaneous growth. Some studies propose the following equation

(Rigler and Downing 1984; Avila et al. 2012):

$$P= N*B*G$$

Where:
P = secondary production
N = abundance or density
B = individual biomass
G = growth rate

In turn, growth rates can be calculated based in models that consider, at different levels, the influence of temperature, food availability and organism size. The most common models are those proposed by (1) Huntley and Lopez (1992), (2) Hirst and Sheader (1997), (3) Hirst and Lampitt (1998) e (4) Hirst and Bunker (2003), whose equations are:

$$(1)\ G=0{,}445e^{0{,}111*T}$$

$$(2)\ Log_{10}.G=0{,}0246*T - 0{,}2962*Log_{10}.C - 1{,}1355$$

$$(3)\ Log_{10}.G=0{,}0208*T - 0{,}3221*Log_{10}.C - 1{,}1408$$

$$(4)\ Log_{10}.G= a*T - b*Log_{10}C - c*Log_{10}Chlo\text{-}a + d$$

Where:
G = growth rate
T = temperature
C = biomass in carbon content
Chlo-a = concentration of chlorophyll
a, b, c and d = coefficients for each development stage and spawning strategy (for more details see Hirst and Bunker 2003).

More recently, methods based on the relationship between the enzyme activities involved in ecdysis, mainly the enzyme quitobiase, and the growth of crustaceans has been developed. In this estimation, the method proposed by Sastri and Dower (2009) is the most widely used in studies in freshwater and marine environments. This method is based on the balance over time between the activity generated due to the enzyme released and the natural enzyme degradation, where there is a positive correlation between the quitobiase activity and the size and biomass of the microcrustaceans. However, this method may be inaccessible due to the complex chemical analyzes. It also may overestimate secondary production values due to interference from other non-planktonic organisms (e.g. benthic crustaceans) or enzyme releases by organism's death and predation and not actually by increment or production.

All methods listed here have some limitations and difficulties. The great problems in the zooplankton secondary production measures are the validation of global growth models, accurate estimates of biomass and development time, especially for tropical species. Most equations available in the literature were elaborated based on temperate and freshwater species and the few estimates available for the tropical ones do not contemplate all species diversity. In addition, some problems listed by Melão (1999) are still present, such as: difficulties in the analysis of samples; definition of developmental stages or size classes; maintenance of laboratory cultures for determination of life cycle and problems in obtaining dry weight values. A large number of individuals of the same species and size class is required to reach a detectable level, even on high precision balances.

Despite its recognized importance, the entire procedure for obtaining the zooplankton secondary production is quite complex and laborious, especially during the sample analysis. It requires a long time for the individual's measurement and/or weighting and/or cultivation. All these steps require a certain expertise, dedication, planning and full attention in the species identification or measurement. Because the microscopic size of the zooplankton, many errors and inaccuracies can occur during the sample analysis. All these difficulties make the studies with secondary production unattractive and/or infeasible, resulting in the low number of studies carried out in neotropical countries, such as Brazil, as detailed below.

Studies with secondary production in Brazil: a case study

Studies carried out over the past decade have already pointed to the incipience of secondary production studies in tropical regions when comparing the amount of information produced for temperate environments (Lopes 2007; Santos-Wisniewski and Rocha 2007). To quantify the number of studies carried out in Brazil using zooplankton secondary production and have an updated scenario of these studies, we searched for publications in the “Web of Science”, “Scopus” and “Scielo” databases. We used different combinations of the following keywords: 1- “Production” and “Zooplankton” and “Brazil”; 2- “Secondary production” and “Zooplankton” and “Brazil”; 3- “Productivity” and “Zooplankton” and “Brazil”. Searches with the same words in Portuguese were also performed. We also considered book chapters, doctoral thesis, master’s dissertations and publications that were not found in the initial searches in the databases, but which were cited in other publications. For publications whose access was not possible, we obtained the information from the abstract, keywords and title or from other publications that referred them. We considered publications made up to 2019.

We extracted the following information from the publications: year, type of publication, type of environment, type of ecosystem, region where the study was carried out, ecological approach according to Downing (1984), study group, biological organization level, secondary production measure and values of secondary production found in each study. All information and respective categories extracted from the publications are detailed in Table 1. Review studies that did not present original data on secondary production were not included.

A total of 60 studies were developed in Brazil on zooplankton secondary production during the period from 1984 to 2019 (Table 2, Figure 1). Among these studies, 34 or 56.66 % are articles published in

Table 1 Data extracted from 60 studies on zooplankton secondary production published from 1984 to 2019 in Brazil. *two or more ecosystem; **studies on zooplankton culture or experiments were classified among of the type of environment (marine, freshwater or transitional) according to the origin of the species used.

	Category	Sub-category
Year of publication	-	-
Type of publication	Article	-
	Thesis/Dissertation	
	Book chapter	
	Scientific Meeting abstract	
Type of environment and ecosystem	Freshwater	Reservoir
		Floodplain lake
		Lake
		Coastal lagoon
	Marine	Continental shelf
		Coral reef
		Estuary
	Transitional	Mangrove/Estuary
		Lagoon/Estuary
		Various*
		Culture/Experiment**
Region	North	-
	Northeast	
	Central-western,	
	Southeast	
	South	
Ecological approach	Matter and energy transfer mechanisms	
	Management of water resources	
	Detection and evaluation of pollution agents	
	Hypothesis testing about productivity	
	Methodological	
Study group	Mesozooplankton	
	Copepods	
	Cladocerans	
	Rotifers	
	Two or more groups	
Biological organization level	Population	
	Community	
Secondary production measure	-	-
Secondary production values	Minimum	mgDW m^{-3} day^{-1}
		mgC m^{-3} day^{-1}
	Maximum	
		mgDW m^{-3} day^{-1}
		mgC m^{-3} day^{-1}

Table 2 List of Secondary Production studies published in Brazil from 1984 to 2019 and respective information. References in bold were not accessed directly and, when possible, the information was obtained from abstract, keywords, title or in other studies. Ecological Approach: 1 – Elucidation of energy or material transfers within communities and ecosystems; 2 – Rational management of aquatic resources; 3 – Detection of the effects of pollution; 4 – Formation of general theories of biological productivity; 5 – Methodological; Max SP – Maximum Secondary production; Min SP – Minimum secondary production; R – Rotifera; Cla – Cladocera; Cop – Copepoda; *Approximated values extracted from graphics; **Values to each enzymatic methods respectively; ***Values obtained from Melão, M.G.G , 1999 and/or Santos-Wisniewski, M.J & Rocha, O. 2007; ****Values obtained from abstract. NA – information not available.

Authors	Year	Type	Environment	Ecosystem	Region	Approach	Biodiversity level	Study group	Measure	Species	Max SP (mgDWm ^{3}day^{-1})	Mim SP (mgDWm ^{3}day^{-1})	Max SP (mgCm^{-3}day^{-1})	Min SP (mgCm^{-3}day^{-1})
Rocha, O. & Matsumura-Tundisi, T.	1984	Paper	Freshwater	Reservoir	Southeast	4	Population	Copepoda	Not informed	1	NA	NA	45.15	<1.0*
Matsumura-Tundisi, T. & Tundisi, J.G.	**1986**	**Congress abstracts / annals**	**Freshwater**	**Lake**	**Southeast**	**4**	**NA**	**NA**	**NA**	**NA**	**NA**	**NA**	**NA**	**NA**
Araújo, M.A. & Pinto-Coelho, R.M.	1988	Paper	Freshwater	Reservoir	Southeast	1	Community	Mesozoop.	Pourriot & Champ,1982	>3	NA	NA	160.29	55.31
Okano, Y.W.	**1994**	**Thesis**	**Freshwater**	**Reservoir**	**Southeast**	**4**	**Population**	**Rotifera**	**NA**	**NA**	**NA**	**NA**	**0.036*****	**NA**
Araujo, M.A.; Coelho, R.M.P.	1995	Thesis	Freshwater	Reservoir	Southeast	1	Community	Mesozoop.	Winberg et al., 1965	>3	NA	NA	212.5	22.8
Tundisi, J.G. & Matsumura-Tundisi,T.	**1995**	**Book chapter**	**Freshwater**	**Reservoir**	**Southeast**	**4**	**Population**	**Copepoda**	**NA**	**1**	**NA**	**NA**	**6.26*****	**NA**
Melão, M.G.G.	**1997**	**Thesis**	**Freshwater**	**Reservoir**	**Southeast**	**4**	**NA**	**NA**	**NA**	**NA**	**NA**	**NA**	**NA**	**NA**
Rodriguez, M.P.	**1997**	**Thesis**	**Freshwater**	**Reservoir**	**Southeast**	**4**	**Population**	**Rotifera**	**NA**	**2**	**NA**	**NA**	**0.054*****	**NA**
Ara, K.; Tommasi, L.R.³	**1998**	**Thesis**	**Transitional**	**Lagoon /Estuary**	**Southeast**	**4**	**Community**	**Copepoda**	**NA**	**>3**	**NA**	**NA**	**NA**	**NA**
Santos-Wisniewski, M.J.; Rocha, O.	1998	Thesis	Freshwater	Reservoir	Southeast	4	Community	Copepoda /Cladocera /Rotifera	NA	NA	NA	NA	NA	NA
Melão, M.G.G , 1999	1999	Book chapter	Freshwater	Reservoir	Southeast	4	Community	Copepoda /Cladocera /Rotifera	Emondson, 1965 Winberg et al., 1965	>3	3.64	0.31	NA	NA
Castilho-Noll, M.S.M & Arcifa, M.S.	2000	Paper	Freshwater	Coastal lagoon	Southeast	4	Population	Rotifera	Rigler & Downing, 1984	1	152	8	NA	NA
Maia-Barbosa, P. M.	2000	Thesis	Freshwater	Lake	North	4	Community	Cladocera	Hart, 1987	5	7.48	2.72	NA	NA
Melão, M.G.G. & Rocha, O.	2000	Paper	Freshwater	Reservoir	Southeast	4	Community	Copepoda /Cladocera /Rotifera	Edmondson, 1965; Winberg et al., 1965	>3	9.6	0.2	NA	NA
Ara, K.	2001	Paper	Transitional	Mangrove /Estuary	Southeast	4	Population	Copepoda	Huntley & Lopez, 1992 Hirst & Sheader, 1997	1	<12.0*	<0.1*	<0.6*	<0.1*
Ara, K.	2001	Paper	Transitional	Mangrove /Estuary	Southeast	4	Population	Copepoda	Huntley & Lopez, 1992 Hirst & Sheader, 1997	1	<10.0*	<0.5*	5.354	0.357
Ara, K.	2002	Paper	Transitional	Mangrove /Estuary	Southeast	4	Population	Copepoda	Hirst & Sheader, 1997	1	<2.0*	<0.1*	1.115	0.0002

Table 2 continued

Authors	Year	Type	Environment	Ecosystem	Region	Approach	Biodiversity level	Study group	Measure	Species	Max SP (mgDWm ^{3}day^{-1})	Mim SP (mgDWm ^{3}day^{-1})	Max SP (mgCm^{-3}day^{-1})	Min SP (mgCm^{-3}day^{-1})
Peláez-Rodríguez, M. & Matsumura-Tundisi, T.	2002	Paper	Freshwater	Reservoir	Southeast	4	Population	Rotifera	NA	2	0.1914	<0.01*	NA	NA
Santos-Wisniewski, M.J.; Matsumura-Tundisi, T. & Rocha, O.	**2002**	**Congress abstracts /annals**	**Freshwater**	**Reservoir**	**Southeast**	**4**	**NA**	**NA**	**NA**	**NA**	**NA**	**NA**	**NA**	**NA**
Rocha, G.R.A.; Rossi-Wongtschowski, C.L.D.B.; Pires-Vanin, A.M.S. & Jarre-Teichmann, A.J.	2003	Paper	Marine	Continental shelf	Southeast	1	Community	Copepoda /Cladocera /Rotifera	Cole et al., 1988	>3	NA	NA	88.2	39.7
Ara, K.	2004	Paper	Transitional	Mangrove /Estuary	Southeast	4	Community	Mesozoop.	Hisrt & Lampitt, 1998	>3	6.183	24.156	11.106	2.819
Melão, M.G.G. & Rocha, O.	2004	Paper	Freshwater	Reservoir	Southeast	4	Population	Copepoda	Winberg et al., 1965	2	12.5	0.01	NA	NA
Panarelli, E.A.; Henry, R.[2]	**2004**	**Thesis**	**Freshwater**	**Reservoir**	**Southeast**	**4**	**Community**	**Cladocera**	**NA**	**NA**	**NA**	**NA**	**NA**	**NA**
Rietzler, A.C., Rocha, O. & Espindola, E.L.G.	2004	Book chapter	Freshwater	Reservoir	Southeast	4	Community	Copepoda /Cladocera /Rotifera	Edmondson, 1965; Winberg et al., 1965	>3	R-0.93/ Cla-108.00/ Cop-82.70	R-0.02/ Cla-11.30/ Cop-19.30	NA	NA
Casanova, S.M.C.; Henry, R.[2]	**2005**	**Thesis**	**Freshwater**	**Reservoir**	**Southeast**	**4**	**Community**	**Rotifera**	**NA**	**NA**	**NA**	**NA**	**NA**	**NA**
Melão, M.G.G. & Rocha, O.	2006	Paper	Freshwater	Reservoir	Southeast	4	Population	Cladocera	Winberg et al., 1965	1	5.08	0.24	NA	NA
Santos, M.A.P.F.; Melão, M.G.G. & Lombardi, A.T.	2006	Paper	Freshwater	Cultive /Experiment	Southeast	4	Population	Cladocera	Rigler & Downing, 1984	1	1.3 (ug.DW. Female^{-1})	0.6 (ug.DW. Female^{-1})	NA	NA
Santos-Wisniewski, M.J & Rocha, O.	2007	Paper	Freshwater	Reservoir	Southeast	4	Community	Copepoda	Winberg et al., 1965	>3	23.61	14	NA	NA
Casanova, S.M.C.;Panarelli, E.A & Henry, R.	2009	Paper	Freshwater	Floodplain lake	Southeast	4	Community	Rotifera	Edmondson & Winberg, 1971	>3	9.36	0.047	NA	NA
Melo-Junior, M, de; Lopes, R.M.	2009	Thesis	Marine	Continental shelf	Southeast	4	Community	Copepoda	Hirst & Bunker, 2003	>3	NA	NA	6.48	0.01
Miyashita, L.K; Melo-Junior, M. de & Lopes, R.M.	2009	Paper	Marine	Continental shelf	Southeast	4	Community	Copepoda	Huntley & Lopez, 1992 Hirst & Lampitt, 1998	>3	NA	NA	14.3	0.19
Brito, S.L.; Maia-Barbosa, P.M.	2010	Thesis	Freshwater	Reservoir	Southeast	4	Community	Copepoda /Cladocera	Hart, 1987	>3	5.82	0.01	NA	NA
Negreiros, N.F.; Rocha, O.	2010	Thesis	Freshwater	Reservoir	Southeast	4	Community	Rotifera	Edmondson & Winberg, 1971	>3	0.0321	0.0143	NA	NA
Panarelli, E. A.; Casanova, S. M.C; Henry, R.	2010	Paper	Freshwater	Floodplain lake	Southeast	4	Community	Cladocera	Winberg 1971	>3	33.466	0.0175	NA	NA

national and international journals, 22 or 36.66 % are PhD theses and master's dissertations, 2 are book chapters and 2 are abstracts of scientific meetings, making up together about 7 % of publications. The first publications on secondary production occurred in the 80's and after a period without any publication (between 1989 and 1992), there is an increase in the number of publications up to 2019 (Figure 1). Most studies were conducted in freshwater environments or with species from these environments (Figure 1). The first publication for transitional environments occurred in 1998 and in a marine environment only in 2003. In a review of marine zooplankton studies from Brazil, Lopes (2007) already pointed out the small number of publications and the necessity to investigate the process and mechanisms that govern the trophic interactions. He also pointed out the lack of studies on zooplankton production in relation to abiotic factors (Lopes 2007). However, the increase in number of publications was small for all types of environments.

Given the species loss scenario and environmental degradation, the discrete increase in the number of publications is a result of researchers' concern to quantify the relationship between productivity and ecosystem services. Recent estimates reinforce the importance of biodiversity for biomass accumulation and resource use within different trophic levels, with important implications for ecosystem services such as fishery, food production and water purification (Duffy et al. 2017). Caliman et al. (2010) found that ecologists are already recognizing the potential of aquatic environments to increase the knowledge on ecosystem functioning. Therefore, the use of zooplankton secondary production measures may be an essential tool for understanding the mechanisms that govern the functioning of aquatic environments.

When considered the region of Brazil where the studies were developed, the results showed a predominance of the Southeast region, with 44 studies or 73.33 % of all publications, followed by the South region, with 10 publications or 16.66 %. In the North region only 4 publications were found (6.66%) and for the Northeast region only 2 (3.33%) (Table 2, Figure 2). No publication was found for the Central-Western region of Brazil. The predominance of studies in the Southeast region is expected since the most part of universities and research centers are concentrated in this region and, consequently, most of the research groups on aquatic ecology. This fact is a result of the historical process of Brazilian development, where the Southeast region concentrates not only the largest populations, but also the most important economic centers. Brazil is a country of continental dimensions and the difficulty of covering larger areas is a great challenge in terms of economic and human resources.

The lack of studies in the North and Central-Western regions is surprising since they have the world's most important river basins in terms of area and volume (Amazonian basin in North) and the largest wetland

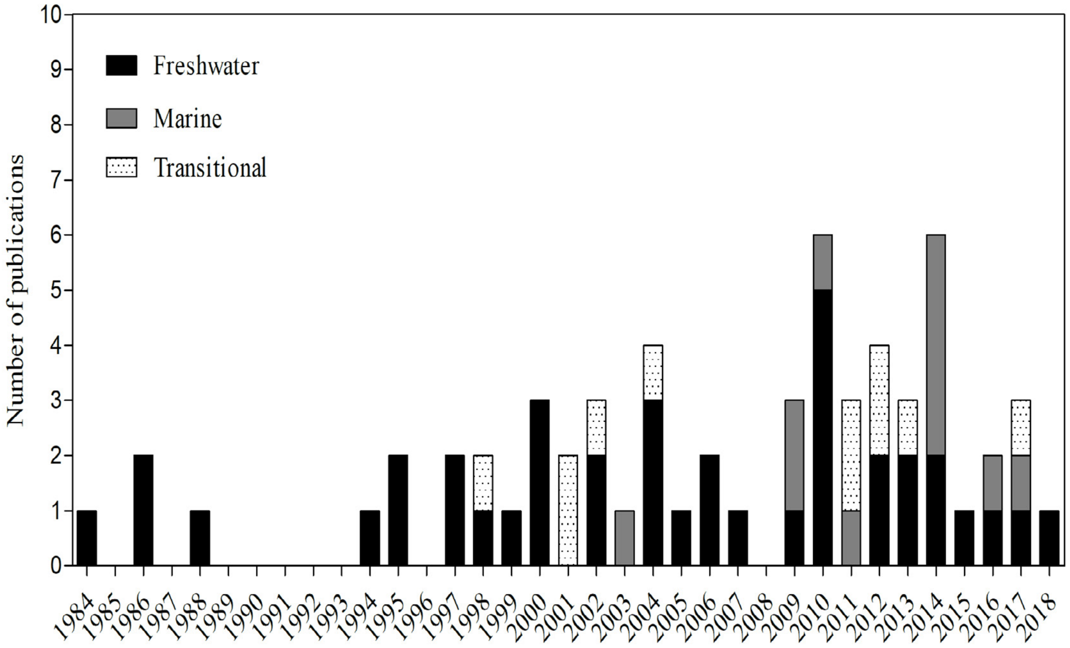

Fig. 1 Number of publications on zooplankton secondary production in Brazil from 1984 until 2019 divided by type of environment.

(Pantanal in Central-Western). For marine environments the pattern is the same, the studies are concentrated on the Southeast region. However, Southeast region corresponds only to 1,650 km of the total 7,367 km of the Brazilian coast (IBGE, 2011). Considering the importance of zooplankton to matter transfer in marine trophic chains and fishery production, the absence of studies on secondary production in other regions of Brazil is equally surprising. Our results illustrated that even today there is a lack of knowledge about aquatic productivity in Brazil. Since this information is practically nonexistent, the development of studies investigating the mechanisms that govern the productivity on these environments is urgent.

We found studies in 9 different types of aquatic ecosystems, studies carried out in more than one ecosystem and experimental studies in laboratory (Table 2). Reservoir was the most studied ecosystem, with 24 publications on zooplankton secondary production or 40 % of the total. Mangrove/estuary, floodplain lakes and continental shelf were the second most studied ecosystems with 6 publications or 10% each (Figure 2). Pioneering studies on secondary production were carried out in reservoirs and only from the 2000s onwards occurred a real diversification of the types of environments as a consequence of the increase in the number of studies. Until now studies on secondary production in reservoirs continues to be a common research area (Brito et al. 2016). This predominance is related to several objectives, such as the assessment of the potential of energy production, evaluation of multiple uses, pollution effects, potential for the discharge of sanitary sewage and water quality control (Peláez-Rodrigues and Matsumura-Tundisi 2002; Brito 2010; Viti et al. 2013). Reservoirs can also be used for leisure activities, water consumption and aquiculture. Therefore, understanding the trophic relationships and matter transfer through secondary production measures is an important management tool for these environments.

The few studies carried out on ecosystems such as coastal lagoons, temporary environments and coral reefs illustrate how these environments are still neglected in relation to their productivity. Although they are recognized for their high contribution to biogeochemical cycles, trophic webs and productivity at global levels (Esteves et al. 2008; Figueirêdo 2014; Calhoun et al. 2017), little is known about such information in Brazilian environments.

Regarding the level of biological organization, most studies considered the secondary production at community level (more than three species). However, the number of studies evaluating only one or few

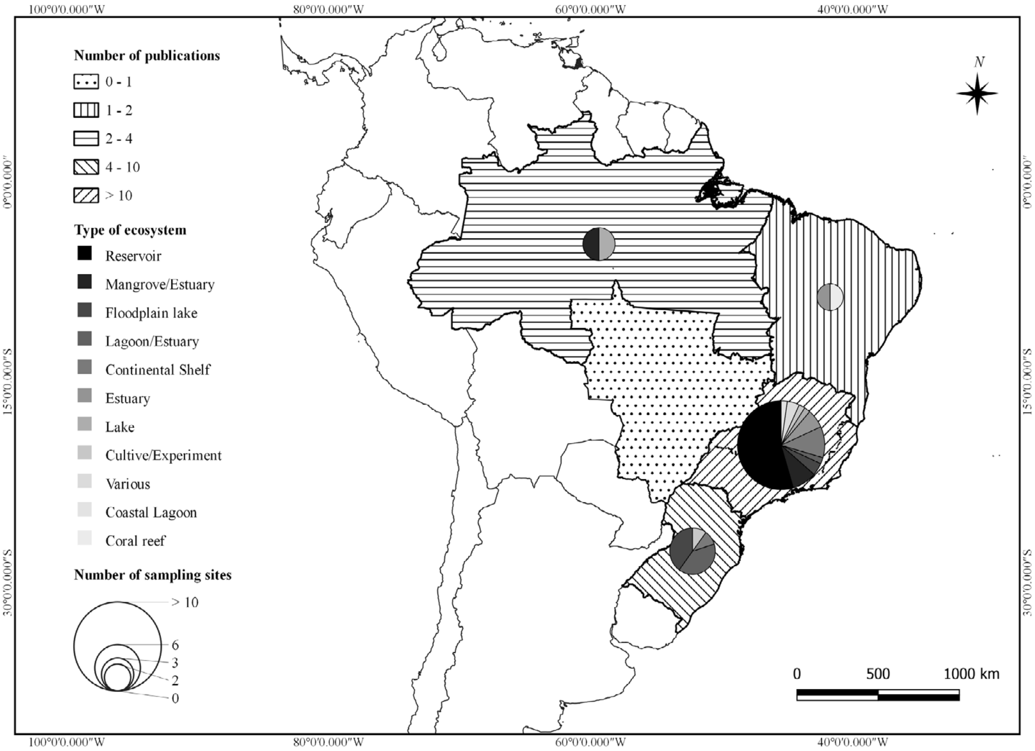

Fig. 2 Number of publications on zooplankton secondary production in Brazilian regions among different ecosystem types and sampling sites.

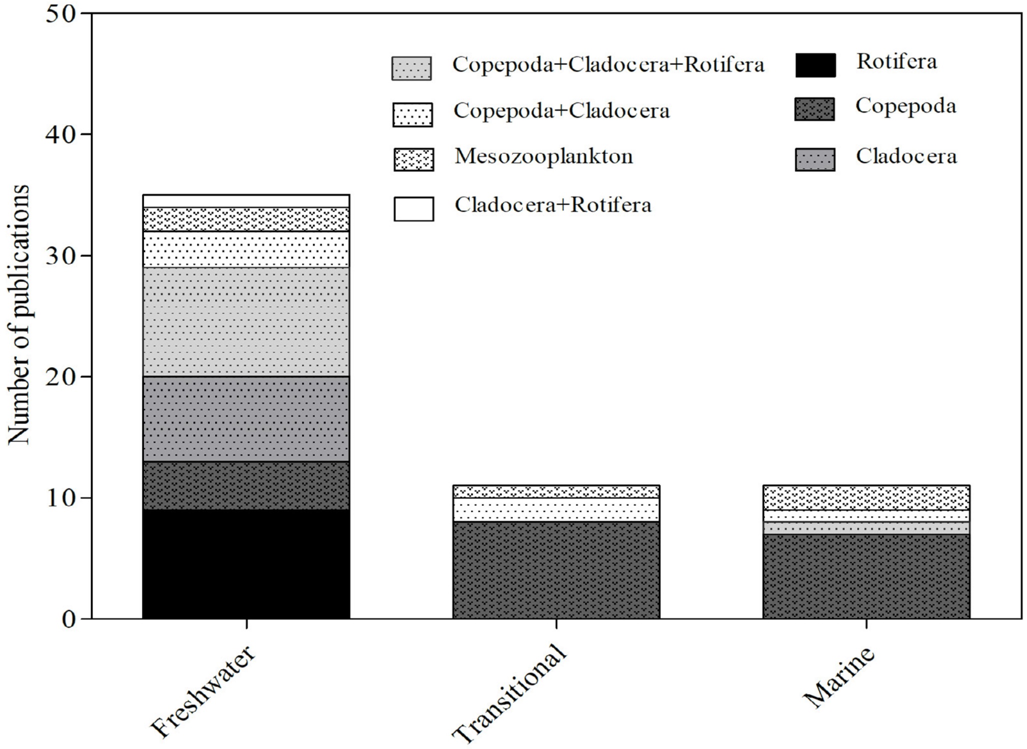

Fig. 3 Number of publications on zooplankton secondary production divided by environment type and study group

species was quite expressive (Table 2). Many authors choose to evaluate few species or only a group of organisms due to the difficulties in evaluating the secondary production for all groups, as previously explained. In this sense, studies considering only the secondary production of copepods were the majority, with 19 publications, whereas studies with all three main groups (copepods, cladocerans and rotifers) were only 10 (Table 2, Figure 3). In marine and freshwater environments copepods can account for most of the zooplankton biomass, but the predominance of studies evaluating this group is related to the facility to manipulate larger specimens and the easy identification of the developmental stages (nauplii, copepodites and adults). However, an integrated view of all groups allows a more accurate evaluation of zooplankton secondary production. For example, for freshwater environments, studies have shown that microzooplankton, rotifers and cladocerans may present greater importance than expected by their biomass (Panarelli et al. 2010; Dias et al. 2014)

Most of the publications had as their main ecological approach the hypothesis testing about productivity (sense Downing, 1984). Most of which correspond to studies describing seasonal or spatial patterns of zooplankton production (Table 2). Research on zooplankton secondary production has been primarily descriptive, with most studies focusing on community structure analysis (Lopes 2007). The lack of studies evaluating food webs and energy transfer through trophic levels, as well as the correlation of secondary production with broader ecosystem patterns and processes, illustrates how this field of knowledge in Brazil is recent. The compilation of basic information on Brazilian ecosystem's productivity is still necessary for the characterization of these environments and, consequently, for the understanding of its functioning and management of its resources and services.

Mangroves were characterized as the most productive ecosystems, reaching values higher than 1000 mg DW m^{-3} day^{-1} (Figure 4). Similarly, a study in mangroves located in India found zooplankton secondary production values around 850 mg C m^{-3} day^{-1} (Nayar et al. 1999). These environments are widely recognized for their high productivity since there is a large amount of carbon available for secondary production from decomposing organic matter (Odum and Heald 1975 ; Komiyama et al. 2008). The high levels of mangrove productivity have been associated mainly with hydrological conditions, such as salinity levels, and the concentration and composition of organic detritus from the mangrove forest (Magalhães et al. 2011). Zooplankton production in these environments contributes significantly to carbon transfer to higher trophic levels (Magalhães et al. 2016) and consequently to fishery production (Rakhesh et al. 2008). However, the number of studies investigating the productivity of Brazilian mangroves is still incipient, considering the relevance of these environments in both economic and conservation terms.

Even with few studies, continental lakes were the second most productive environment, followed by reservoirs (Figure 4). Continental aquatic environments have also been recognized for their high productivity (Esteves et al. 2008) with values often overcoming surrounding terrestrial environments (Hunter et al. 2017). Although globally they only contribute with 6 % of the planetary surface coverage, continental aquatic environments play a key role in biogeochemical cycles, they are sources and sinks of carbon and important buffers of the landscape hydrological variation (Junk et al. 2013). Lakes can have a disproportionate contribution in relation to their areas (Biggs et al. 2017, Calhoun et al. 2017). Globally, estimates have shown that inland aquatic environments can process twice as much carbon content annually than that calculated as the contribution of large rivers and oceans (Downing 2010). Despite their importance, productivity estimates for Brazilian continental aquatic environments are practically nonexistent (Bozelli et al. 2018).

Continental shelf showed the highest values of secondary production among marine environments with maximum value of 163.2 mg C m^{-3} day^{-1} (Figure 4). The high productivity of the Brazilian continental shelf is associated with the great abundance of species and small climatic seasonality (Lopes 2007; Dias et al. 2015). Some studies indicate that this region of the Atlantic Ocean has the highest production values on the planet, exceeding global average (Ara 2001; Miyashita et al. 2009; Duarte et al. 2014). The large biomass production on the continental shelf is associated with mechanisms of fertilization such as the discharge of nutrients by large rivers and the upwelling of deep water (Lopes 2007; Duarte et al. 2014; Dias et al. 2015). The high zooplanktonic production on the continental shelf is very important for fishery production in Brazil (Duarte et al. 2014). However, studies are still incipient and scarce, mainly in the north Brazilian neritic section (Lopes 2007).

Surprisingly, estuaries and coral reefs, environments traditionally considered as the most productive in the world (Crossland et al. 1991), presented low values of secondary production with a maximum value of 0.1 mg C m^{-3} day^{-1} (Figure 4). For example, a study conducted in coral reefs of the coast of Malaysia found average values ranging from 0.93 to 1.83 mg C m^{-3} day^{-1} (Nakajima et al. 2014). In an estuary located in Portugal, the average of zooplankton secondary production ranged from 0.03 to 0.13 mg C m^{-3} day^{-1} (Gonçalves et al. 2015). Coral reefs and estuaries cover a small surface area in global terms, but may account for more than 10 % of the world's fishery production (Pauly et al. 2002). The low values

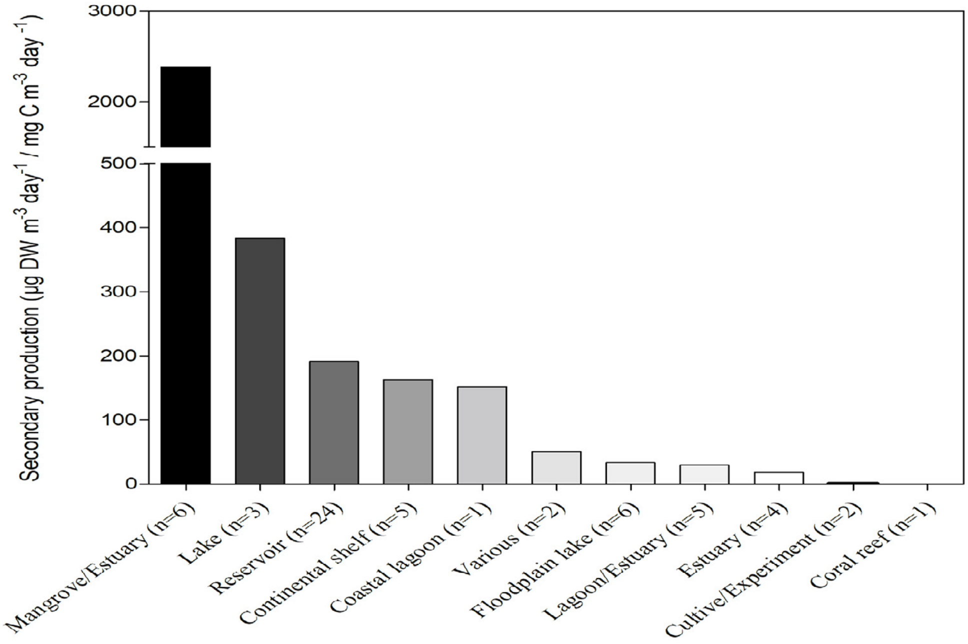

Fig. 4 Zooplankton secondary production range variation among different aquatic ecosystems.

found for the Brazilian environments may be associated with the small number of studies, resulting in low temporal and spatial variability. Therefore, it is crucial to establish estimates of production rates at different seasons and sampling sites for a real understanding of the ecological mechanisms that sustain the marine food webs (Nakajima et al. 2014). In this sense, it is necessary to expand the studies developed in Brazil mainly because the great variety, extension and complexity of the estuarine and reef environments along the Brazilian coast.

Conclusions, recommendations and perspectives

The studies with zooplankton secondary production in Brazil have grown in recent years, however there is a concentration of studies carried out in the southeast region, especially in reservoirs with descriptive approaches. The methods used in the measurement of secondary production are diversified and there is no standard method, but measures based on recruitment and biomass increment are the most used in freshwater environments. In transitional and marine environments measures based on growth rates are largely applied.

Considering the importance of zooplankton secondary production for the real understanding of the mechanisms of matter and energy transfer in trophic chains and their use in the management of aquatic environments, we suggest that efforts should be made to increase the number of studies. Special attention should be paid to environments that are historically neglected or at risk of degradation, such as small wetlands and coral reefs. There is also a wide variety of aquatic environments in which this type of study has not yet been performed and, in the face of a scenario of global changes and anthropic impacts (Caliman et al. 2010; Junk et al. 2013; Hunter 2017), studies on the functioning of these ecosystems are paramount. We suggest that further studies be carried out mainly in small ponds, marshes and coastal lagoons in central, north and northeast of Brazil and in the continental shelf, estuaries and coral reefs along the entire coast. However, efforts for the entire national territory for all types of environment must be considered since the total number of studies is very low.

In general, we recommend that measures of secondary production be carried out for the whole zooplankton community, allowing a more realistic view of the organism's functional role. Both abundant and rare species must be considered, since some studies have shown that the removal of species with less than 10% of the community biomass, can cause disproportionate effects on the upper trophic levels (Bracken and Low 2012). In addition, studies that use secondary production measures as indicators of ecosystem processes coupled with measures of community functional diversity can allow us the appropriate measurement of the biodiversity effects on ecosystem functioning (McGill et al. 2006).

There is still a lack of basic information on tropical environments. In this sense, basic studies on the biology of organisms can be done addressing more complex issues, such as the effects of environmental changes and human impacts on ecosystem productivity and the real contributions of aquatic environments to biogeochemical global cycles.

Competing interests The authors declare that they have no competing interests.

Authors' contributions RBS conceived of the study, participated in its design, helped to draft the manuscript, collected the data presented and wrote the manuscript. RAN contributed to the data acquisition and made the graphics. RLB contributed to the data acquisition and reviewed the manuscript. All authors read and approved final manuscript.

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