

## ***Interactive comment on “Growth and production of the copepod community in the southern area of the Humboldt Current System” by R. Escribano et al.***

**R. Escribano et al.**

rescribano@udec.cl

Received and published: 26 April 2015

Response to Referee #2

We are grateful to this reviewer because of his (her) careful revision of our work and very helpful comments and suggestions. Our responses to specific comments are in capital cases and we are also attaching a revised version of the MS as marked text (as Supplement), so that our changes in according to comments from reviewers can be followed. This file also contains revised Tables and Figures.

Anonymous Referee #2 Received and published: 15 March 2015 The submitted work describes the spatial and temporal variation of copepod biomass in an upwelling and  
C1725

in further offshore areas in the southern Humboldt Current. Using environmental temperature as the main predictor for copepod production and hitherto largely unpublished data on growth rates of some copepod species occurring in the area, the authors compute the annual production of copepods with a large focus on a fixed station in the upwelling area. Results show that biomass and production is not related to environmental variables and that production is largely determined by copepod biomass which might be controlled by advection processes. Although very interesting, I find the submitted manuscript in its present state only preliminary as indicated by the large number of questions and remarks related to methods, procedures and interpretation. Of these, lacking detail in the description of the estimation of growth rate and the lacking inclusion of food conditions in the spatio-temporal analysis is my major concern. The growth rates used in this study to estimate production are largely unpublished, but central to the understanding of the study. I miss, therefore, detail on the conditions and methods used to determine these. Moreover, the estimates are largely for calanoid copepods while cyclopids and other small copepods were not included although they partly form an important part of the copepod assemblages. Although explicitly stated that the growth rate  $g$  was estimated at variable food conditions, no data is provided and apparently not included in the estimates of production although food conditions were much more variable than any other environmental factor. Because of this, the study contributes only little to the discussion whether temperature alone or in combination with other factors determines copepod production – a major question raised in the introduction. Apart from these fundamental issues, there are many other smaller issues that need improved before the quality of the study could completely assessed.

R: THERE ARE SEVERAL ISSUES RAISED BY THE REVIEWER, BUT SOME OF THEM APPEAR RELATED TO CONFUSION OR DIFFICULTIES TO UNDERSTAND OUR ANALYSIS AND INTERPRETATION. CERTAINLY, THESE DIFFICULTIES CAN BE ATTRIBUTED TO LITTLE CLARITY IN THE DESCRIPTION OF OUR METHODS AND PROCEDURES. IN THAT SENSE AND CONSIDERING THE SPECIFIC COMMENTS, WE HAVE MADE SEVERAL CHANGES IN THE TEXT TO IMPROVE

C1726

CLARITY. WE WANT TO MAKE CLEAR THAT WE HAD NO INTENTION TO PREDICT GROWTH AND PRODUCTION FROM OUR TEMPERATURE DATA. AFTER MANY YEARS OF STUDY IN THIS REGION, WE KNOW THAT BECAUSE OF LITTLE VARIATION, TEMPERATURE CAN HARDLY EXPLAIN SO MUCH VARIABILITY IN ZOOPLANKTON GROWTH AND PRODUCTION. INDEED, WE TESTED G AGAINST TEMPERATURE JUST TO SHOW HOW WEAK THAT CORRELATION WAS. NOW, OUR MAIN GOAL WAS ESTIMATING COPEPOD PRODUCTION AND THEREAFTER LOOKING INSIGHTS ON WHICH FACTORS COULD AFFECT PRODUCTION AND BIOMASS. IN THE SAME CONTEXT, WE MUST STRESS THAT NO MANY ESTIMATES OF COMMUNITY PRODUCTION OF ZOOPLANKTON ARE AVAILABLE IN THE WORLD OCEAN. THIS IS CRITICAL ISSUE, ESPECIALLY FOR EASTERN BOUNDARY CURRENT ECOSYSTEMS, AND FOR BIOGEOCHEMICAL MODELERS WHO ARE TRYING TO GUESS HOW MUCH OF THE PHYTOPLANKTON C CAN GO TO ZOOPLANKTON BIOMASS. HERE, WE PROVIDE FIRST ESTIMATES FOR THE HUMBOLDT CURRENT. FUTURE WORK IS CERTAINLY NEEDED, BUT WE ARE HERE PROVIDING A BASIS.

REGARDING A BETTER DESCRIPTION ON PROCEDURES FOR G ESTIMATES, WE HAVE INTRODUCED SEVERAL CHANGES IN METHODS TO FULLY DESCRIBE OUR APPROACHES. WE ALSO CLARIFIED THIS IN THE ABSTRACT AND IN THE LAST PARAGRAPH OF THE INTRODUCTION. TO ESTIMATE COPEPOD PRODUCTION FOR EACH SPECIES, WE USED G FROM PREVIOUS STUDIES OF THE SAME REGION MOST OF THEM ALREADY PUBLISHED AND A FEW UNPUBLISHED DATA FROM OUR TEAM USING SAME METHODS. THE COMPILATION OF G DATA IS NOW FULLY DESCRIBED IN THE NEW TABLE 1, INDICATING THE AREA (NORTHERN OR SOUTHERN CHILE), THE SPECIES AND STAGES, SIZE AND THE TEMPERATURE AT WHICH G WAS ESTIMATED. WITH ALL THESE CHANGES READERS COULD EASILY FOLLOW OUR PROCEDURE AND DATA ORIGINS. CONDITIONS FOR ESTIMATING G ARE PROVIDED IN EACH ONE OF THE REFERENCES, BUT WE NOTE THAT THERE WAS A VARIETY OF CONDITIONS UNDER

C1727

WHICH G WAS ESTIMATED, AND THAT IS EXACTLY WHAT WE NEED TO BETTER REFLECT AN IN SITU G. WE AGREE WITH THE REVIEWER THAT SMALL CYCLOPOID AND POECILOSTOMATOID COPEPODS ARE ABUNDANT AND SHOULD BE INCLUDED. IN ALL CALCULATIONS OF COPEPOD BIOMASS AND PRODUCTION THEY WERE INDEED INCLUDED. WE DID NOT INCLUDE THEM IN TABLE 1 AND IN OUR ANALYSIS FOR ESTABLISHING A RELATIONSHIP WITH TEMPERATURE AND BODY SIZE, BECAUSE NO DATA ON G WERE AVAILABLE FOR THESE SPECIES, BUT FOR THEM WE USED A MEAN VALUE OF  $G=0.27$  1/D TO CALCULATE CP. WE HAVE NOW MADE CLEAR THIS ISSUE IN THE METHODS. FOOD CONDITIONS, BOTH IN TERMS OF QUANTITY AND QUALITY, WERE CONSIDERED AND NOW ATTENDING THE COMMENT FROM THE REVIEWER WE HAVE EMPHASIZED THE DISCUSSION ON THIS ISSUE. DURING THE SPATIAL CRUISES AND ALSO AT THE TIME SERIES, CHLA WAS USED AS PROXY FOR FOOD AVAILABILITY. OTHER STUDIES ASSESSED THE COMPOSITION OF NANO- AND MICROPLANKTON FRACTIONS AS COPEPOD FOOD FROM THE SAME CRUISES AND THE TIME SERIES. WE USED THESE REFERENCES AND OUR DATA TO DISCUSS THE ISSUE OF FOOD CONDITIONS AND CONCLUDED THE LACK OF FOOD SHORTAGE FOR CP IN THIS AREA. SEVERAL REFERENCES SUPPORT THIS VIEW. IN THE CONTEXT OF ESTABLISHING WHAT DETERMINES COPEPOD PRODUCTION, WE SHOULD MENTION THAT ATTEMPTS TO DEVELOP RELATIVELY SIMPLE RELATIONSHIPS BETWEEN GROWTH AND AMBIENT VARIABLES, SUCH AS TEMPERATURE, FOOD OR OTHERS, HAVE NOT BEEN VERY SUCCESSFUL, OR A LARGE PART OF THE VARIATION REMAINS UNEXPLAINED BY THEORETICAL (E.G. LIN ET AL., 2013) OR EMPIRICAL (E.G. HIRST AND BUNKER, 2003) MODELS. THEREFORE, WE STRESS AGAIN THAT INSTEAD WE AIMED AT HAVING MORE DIRECT ESTIMATES OF CP AND UNDERSTANDING ITS SPATIAL AND TIME VARIATION, BUT NOT RELYING ON ANY FACTOR AS PREDICTOR.

Introduction: The introduction would benefit from a more explicit description of state- f

C1728

the art or results which are generally obtained: (see for instance remarks p 3059, line 11) p 3059, line 1: 'not' instead of 'no'; 'making it: : : ' instead of 'making: : : ' (Spelling should be checked throughout the MS)

OK: SPELLING CHECKED AND THE PARAGRAPH WAS EXTENDED TO BETTER SPECIFY RESULTS OBTAINED BY OTHER AUTHORS

p 3059, line 11: ': : :different results obtained: : ': Please specify what is meant here; do comparative studies provide evidence that results depend on the method applied. How large is the variation?

PARAGRAPH ALREADY CORRECTED, AND WE JUST STATE THAT SIGNIFICANT DIFFERENCES CAN OCCUR, ALTHOUGH NO ORDERS OF MAGNITUDE.

p 3059, line 14: Mitra et al is missing in the references

OK: REFERENCE WAS REMOVED FROM TEXT BECAUSE IT IS NOT NECESSARY

p 3059, line 29: Please specify what is meant by 'specific approaches should be adopted: : : ' I am not sure if the authors mean that methods specific for an area should be developed (although there are plenty: : :) or if a general method should be sought that could integrate the effects of T, body size and food conditions. p 3060, line 3: Please clarify: Do you argue here that methods applying to the needs of different groups of zooplankton in a specific area are required? Otherwise there is a contradiction between the statement that T is a general predictor for growth as described in the previous paragraph and the statement here that direct estimates of growth barely reflects this relationship.

THANKS FOR THIS COMMENT: WE AGREED THAT THESE STATEMENTS WERE A BIT CONFUSING AND WE HAVE NOW CORRECTED THE PARAGRAPHS. WE STRESS AGAIN THAT TEMPERATURE WAS NOT INTENDED AS A PRIMARY PREDICTOR IN OUR WORK (AS MENTIONED ABOVE). IN ANY CASE, WE THINK THAT UNTIL NOW THERE IS NO AGREEMENT ON WHICH METHOD (EMPIRICAL OR

C1729

THEORETICAL) APPEARS AS SUITABLE FOR ANY REGION OR COMMUNITY, AND THAT'S WHY MORE DIRECT ESTIMATES OR PRODUCTION SEEM RECOMMENDABLE. THAT IS WHAT WE DID.

p 3061, line 11: Were different food conditions not tested?

WE MODIFIED ALL THIS PARAGRAPH TO MAKE CLEAR THAT G WAS ONLY ESTIMATED FROM PREVIOUS STUDIES (NOT FROM THIS ONE) AND THUS WE DID NOT TEST ANY FOOD EFFECT, BUT JUST TEMPERATURE UNDER WHICH G WAS ESTIMATED AND THEN ASSUMED THAT FOOD WAS NOT A LIMITING FACTOR FOR G. THIS ISSUES HAS FULLY BEEN DISCUSSED IN THE WORK (ALSO SEE COMMENT ABOVE).

Material & Methods p 3061, line 23: I find Table 1 a bit redundant as it repeats much information given already in the text. The period and seasonal condition could be easily accommodated into the text.

WE AGREED, AND WE HAVE NOW REMOVED THIS TABLE AND THE INFORMATION INCLUDED IN THE TEXT IN THE FIRST PARAGRAPH OF METHODS.

p 3061, p 3062: I wonder why wind data and upwelling index is important information for the assessment of growth and production. This information might be available elsewhere and thus referred to if necessary.

AGREED. THIS INFORMATION HAS NOW BEEN COMBINED WITH FIG. 13 IN THE DISCUSSION

p 3062, line 19: I miss some information on how vertical heterogeneous data for T and Chla was treated to comparison to the integrating zooplankton samples to establish those environmental factors used in growth and production estimates. A few sentences on how the zooplankton abundance was estimated would be helpful, too.

WE HAVE NOW PROVIDED MORE DETAILS ON ZOOPLANKTON SAMPLING. ALSO WE HAVE ADDED A PARAGRAPH TO SPECIFY WHICH VALUES OF TEMPERA-

C1730

TURE AND CHLA WERE USED TO RELATE WITH CB AND CP. AGAIN, WE DID NOT USE OUR FIELD DATA TO ASSOCIATE WITH PREVIOUS ESTIMATED G'S.

p 3062 line 23: With the length-weight regressions at hand, I wonder why the authors did not cumulated the biomass from each stage because using the mean length is much more inaccurate. From which environment do the length weight regressions come from with regarding the effect of environmental conditions on length – comparable to the conditions in the present study? Table 2 does not provide the mean body size as indicated in the text.

THANKS FOR THIS COMMENTS. IDEALLY ONE COULD DO SO. HOWEVER ACCUMULATING STAGE-BIOMASSES MEANS HAVING ALL STAGES COUNTED PER SPECIES AND EVEN HAVING THEIR SIZES. WE HAVE BEEN ABLE TO ANALYZE JUST A COUPLE OF SPECIES BY STAGES FROM FIELD SAMPLES, BUT MOST OF THEM ARE COUNTED AS TOTAL COPEPODIDS WHICH INCLUDE ADULTS AND MAINLY LATE STAGES (C4-C5). HOWEVER EARLY STAGES OF SEVERAL SPECIES ARE VERY DIFFICULT TO IDENTIFY, BECAUSE COPEPOD TAXONOMY IS BASED ON ADULTS AND TOO FEW DESCRIPTION OF STAGES ARE AVAILABLE. SINCE THERE IS A CHANCE FOR STABLE AND NON-STABLE AGE DISTRIBUTION DEPENDING ON SPECIES OR OCCASION WE THINK THAT MEAN COPEPOD SIZE MAY BETTER ACCOUNT FOR THESE CHANCES AND THAT IS AN ASSUMPTION ON WHICH WE BASED OUR RESULTS. WE AGREED THIS COULD BE A SHORTCOMING AND NOW WE HAVE DISCUSSED THIS ISSUE IN THE DISCUSSION.

p 3063 line 6: In the introduction, the authors state that the first goal of the study was to assess growth rates in relation to environmental conditions. Here, however, they state that growth was estimated from the application of published growth rates, which – except for one species – have been determined for one T condition.

WE HOPE THIS ISSUE HAS BEEN CLARIFIED FROM COMMENTS ABOVE

C1731

Later on learns that especially the coastal zone is partly dominated by cyclopoids and poecilostomatoids for which no data is provided here (which also could give rise to a lacking relationship of copepod C-specific growth and size).. How can the effect of size and T on the Cspecific growth rate be tested for environmental conditions with variable food and T conditions (<12 - >16), then? This does not make sense to me. What about food conditions in the published estimates? This is more important because food conditions are much more variable together with DO than temperature on a spatial scale. Moreover, since much of the data is unpublished, more information on the methods of which 'most applied the molting rate method' should be provided.

WE THINK THAT ALL THESE ISSUES HAVE ALREADY BEEN CLARIFIED IN PREVIOUS COMMENTS. AS STATED ALSO THE TEXT HAS BEEN MODIFIED IN THE INTRODUCTION, METHODS AND DISCUSSION TO TOUCH THESE ISSUES AS WELL.

p 3063 line 22: Please provide information on the amplitude of seasonal variation of T and food at the time series station.

OK AGREED. RANGES ARE NOW SHOWN IN RESULTS

p 3064 line 5: May be I missed the point, but how can the relationship between g and temperature and body size be tested when a) g is not estimated in relation to the environmental variability in the area but taken from the literature and when b) the underlying estimate of g originates from a fixed T? As a results production is expected to be driven by biomass. In addition, it remains largely unclear how the effect of body size is tested here.

AS DESCRIBED ABOVE, WE DID NOT TEST G AGAINST OUR IN SITU DATA, SO OUR APPROACHES SHOULD BE CLEAR NOW FROM ABOVE COMMENTS

Results: p 3064 line 23: The isolines in Fig 3 are very difficult to read. Why are DO conditions described in detail here, when they are of no relevance for interpretation of

C1732

growth/production estimates?

AGREED. CORRECTED NOW

p 3065 lines 11-24: Similarly, results on upwelling could be condensed to the necessary.

WE HAVE REMOVED THE DETAILED DESCRIPTION OF WIND UPWELLING DATA AND RESULTS, ALTHOUGH KEPT OCEANOGRAPHIC DESCRIPTION UPON UPWELLING CONDITIONS, BECAUSE THESE ARE CRITICAL TO RELATE WITH COPEPOD ABUNDANCE AND PRODUCTION.

p 3066 line 16: According to Table 2, g has been studied at fixed T conditions, while the food conditions are not defined and body sizes are likely given for the different developmental stages. According to the text, however, g has been studied at variable T and food conditions. As most of the data is unpublished, Table 2 should provide g for the variable conditions. This is also necessary to calculate g and production over the seasonal/spatial scales.

PREVIOUS COMMENTS SHOULD BE SUFFICIENT TO CLARIFY THESE ISSUES

Moreover, length of copepods (especially those present the whole year round) will vary according to T and food conditions. Is this irrelevant for the estimates of growth and production? Please indicate also which studies are those which are those indicated as 'most' simulating the growth in the laboratory and for which species. Finally, - as already mentioned earlier - it is quite evident from the table that only 50% of the species present in the area are represented by the species listed in Table 2, of which none belong to cyclopoids or other smaller groups.. One species is listed which apparently is not a dominant species in the area (E. inermis).

AS ABOVE CLARIFIED ALL SPECIES WERE INCLUDED IN CALCULATING CB AND CP AND TABLE 2 INCLUDES ONLY SPP FOR WHICH G WAS AVAILABLE. WE HAVE NO EVIDENCE OF CLEAR SEASONAL PATTERNS OF BODY SIZES FOR

C1733

THIS TIME SERIES (SEE ESCRIBANO ET AL. 2007 PROGR. OCEANOGR.) ANYWAY WE HAVE ADDED THIS POINT IN THE DISCUSSION.

p 3066 lines 17: This figure is confusing. First of all, is the data used here from the laboratory experiments indicated in Table 2? This is not clear as it is stated in legend of Fig 6 for 'copepods from the upwelling zone'. Were food conditions saturating or irrelevant because they are ignored? However, the text states (line 13) that the studies simulated a variety of temperature and food conditions in the field. Why is the size of adult females basis for the estimate? Are the growth estimates in Tab 2 also based on egg production measurements? I also wonder if any allometric relationship should be tested with body mass rather body length. This all needs clarification in the Material and Methods.

WE THINK THAT ALL THESE ISSUES HAVE BEEN NOW CLARIFIED. WE NOW PROVIDE MORE DETAILS IN THE LEGEND OF THIS FIGURE.

p 3066 line 21: But seasonal data shows that T is much less variable than for instance food conditions (see Figure 5), so why is T thought to be main variable determining growth? I am again confused: g was estimated in the laboratory, so how can the 'influence of in situ temperature be tested'? This would be possible if field data to estimate g is used, but what about food conditions then? This should be clarified in the Material and Methods. Fig 6b shows quite a big variability regarding the estimates of growth for one species at a given temperature (by a factor of 8, which is very high), is this because variable food conditions have been included?

AGAIN WE HAVE CLARIFIED THAT IN SITU TEMPERATURE WAS NOT TESTED. IN THIS PARAGRAPH WE HAVE MADE SOME CHANGES TO ALSO STATE THAT TEMPERATURE HAS BEEN SUGGESTED AS A PREDICTOR, BUT IT IS NOT OUR SUGGESTION. VARIABILITY OF G SHOULD REFLECT SPECIES, STAGES AND CONDITION DURING WHICH EXPERIMENTS WERE CONDUCTED, THOUGH NOT NECESSARILY FOOD CONDITIONS (ISSUE ALREADY DISCUSSED).

C1734

p 3067 line 4: The calculation of annual means is unclear: Cruises in Nov-Dec were used as the basis for the calculation of spatial variability. How are annual means produced from this data? And I wonder why any spatial trends is removed by this procedure which could give more, interesting insights into upwelling vs off shore differences in the control of production. Moreover, the time series offers the opportunity to describe the temporal evolution of production in relation to the environmental variability described in such a great detail in the earlier results.

AGREED. WE DID NOT CORRECTLY DESCRIBE THIS TABLE (NOW TABLE 2). WE HAVE NOW STATED THAT ANNUAL MEANS ARE FROM MONTHLY SAMPLINGS AT THE TIME SERIES AND MEAN VALUES FROM THE SPATIAL SURVEYS REPRESENT MEANS FROM ALL THE SAMPLING STATIONS DURING EACH CRUISE. NO SPATIAL OR TEMPORAL TRENDS HAVE BEEN REMOVED. THESE MEAN VALUES ONLY ILLUSTRATE THE MAGNITUDES FOR N, CB AND CP, BUT FULL VARIABILITY IS ACCOUNTED FOR THE ANALYSES OF CB AND CP IN THE FOLLOWING GRAPHS, STATISTICAL ANALYSES AND RESULT DESCRIPTIONS. CERTAINLY, CB AND CP BETWEEN THE UPWELLING ZONE (NARROW BAND) AND OFFSHORE IS THE MOST IMPORTANT FEATURE IN TERMS OF SPATIAL VARIABILITY, AND THAT'S WHY OUR KEY FINDINGS RELATE CB AND CP AS BEING LOST FROM THIS REGION.

p 3067 line 8: That copepod biomass is the main driver of production is not surprising considering the low variation in T and that in principle the grand mean of estimates of g is used to calculate production. However, the coastal upwelling zone is characterized by large temporal fluctuations in food concentrations. Is this irrelevant?

IN GENERAL TERMS WE AGREE WITH THIS COMMENT. HOWEVER, HAVING CB AS CONTROLLING CP IS AN IMPORTANT FINDING, BECAUSE CB IS NOT A CONSERVATIVE VARIABLE AND EASIER TO MEASURE THAN G FOR EXAMPLE WHICH (FROM OUR ANALYSIS) SEEMS A MORE CONSERVATIVE VARIABLE ACROSS COPEPOD SPECIES AND STAGES. T IS VARIABLE, THOUGH IN A NAR-

C1735

ROW RANGE, PERHAPS NOT ENOUGH TO SUBSTANTIALLY AFFECT GROWTH. FOOD CAN ALSO BE VERY VARIABLE, IF WE JUST CONSIDER CHLA AS FOOD, BUT THEN WE ARGUED THAT CHLA MAY NOT BE A SUITABLE FOOD INDICATORS WHEN MOST COPEPODS ARE OMNIVOROUS.

p 3067 line 8: Zooplankton sampling was integrating depths from 0-200 m, but apparently surface environmental conditions have been used to calculate growth and production. This needs to be justified.

WE DID NOT KNOW THE EXACT DISTRIBUTION OF ZOOPLANKTON OVER THE VERTICAL AXIS AND PRESUME THAT MOST COPEPODS CONCENTRATE IN THE UPPER 50 M LAYER. HOWEVER A FEW CAN HAVE DIEL MIGRATION (EUCALANUS INERMIS FOR EXAMPLE) AND THIS DISTRIBUTION COULD ALSO CHANGE DEPENDING ON SAMPLING STATION(INSHORE-OFFSHORE) IN THE CASE THAT DEPTH OF THE OMZ COULD AFFECT DISTRIBUTION. SAMPLING STATIONS INCLUDED DAYTIME AND NIGHTTIME CONDITIONS AS WELL AS INSHORE-OFFSHORE, ALTHOUGH WE ASSUME THAT CONDITIONS OF THE MIXED LAYER MAY ACCOUNT FOR THE MAIN COPEPOD HABITAT IN THIS REGIONS. SEVERAL PREVIOUS STUDIES CAN SUPPORT THIS. IN ANY CASE WE NOW CONSIDER THIS ISSUE IN THE DISCUSSION.

p 3067 line 8: Again, potentially interesting spatial trends in the size composition of the copepods are removed.

THIS SPATIAL PATTERN CAN BE ACCOUNTED BY SIZE CATEGORIES OF THE SPECIES, AS WE DID. WE RECOGNIZE HOWEVER THAT NO INTRA-SPECIFIC VARIATION HAS BEEN ASSESSED BECAUSE OF DIFFERENTIAL STAGE DISTRIBUTION COULD BE FOUND, BUT STAGE-ANALYSIS WAS NOT PERFORMED FOR REASONS MENTIONED PREVIOUSLY.

p 3067 line 21: If I understood correctly, not integrated annual production, but average production was determined.

C1736

WE OBTAINED ANNUAL INTEGRATED PRODUCTION FROM DAILY ESTIMATES, NOT AVERAGE. INTEGRATION WAS OBTAINED USING THE TRAPEZOIDAL METHOD. THIS HAS BEEN NOW BETTER DESCRIBED IN METHODS.

p 3067 line 24: What is the difference of annual and daily P/B ratios and how can there be a difference of one order of magnitude? Since they are averages, shouldn't they have a similar magnitude?

DAILY P/B RATIOS REPRESENT AN INSTANTANEOUS (SHORT-TERM) ESTIMATE OF HOW MUCH CAN A CERTAIN BIOMASS REPRODUCE ITSELF. ANNUAL P/B CONSTITUTES AND INTEGRATED PRODUCTION OVER THE ANNUAL CYCLE AND ITS ESTIMATE DEPEND ON TOTAL PRODUCTION THROUGHOUT THE YEAR AND A AVERAGE BIOMASS DURING THE SAME CYCLE. THEREFORE IT COULD BE SAID THAT ANNUAL P/B REPRESENTS A BIOMASS YIELD FOR A YEAR CYCLE. WE HOPE THIS DIFFERENCE SHOULD BE CLEAR NOW; WE HAVE DESCRIBED IN MORE DETAIL THE PROCEDURE FOR CALCULATIONS

p 3068 line 2: The procedures of the stepwise linear regression need to be explained in the material and methods. The rationale behind this procedure need to be specified, especially because neither Chla as food nor dissolved oxygen were variables in the estimation of environmental factors on growth!

IN THE LAST PARAGRAPH OF METHODS WE HAVE NOW PROVIDED THE RATIONALE FOR GLM AND STEPWISE REGRESSION ANALYSIS. IN SITU CHLA AND DO WERE NOT USED TO TEST THEIR EFFECTS ON GROWTH DIRECTLY BUT JUST ON CB AND CP. HOWEVER, CB AND CP AREN'T SUPPOSED TO REPRESENT AND INTEGRATE OF COPEPOD GROWTH IN THE FIELD? Discussion: p 3068 line 22: This description would benefit from less general, but more specific summary of the species distribution because production is driven by species. Which are the dominating species in the respective areas/zones? The used methods need to be critically evaluated as well: 200  $\mu$ m nets largely underestimate the biomass of small cyclopoids and

C1737

poecilostomatoida (Oithona, Corycaeus, Oncaea) as well as that of the smaller copepodit stages of calanoid copepods. This can introduce a large error into production estimates.

WE HAVE ADDED MORE INFORMATION ON SPECIES DISTRIBUTION IN THE DISCUSSION. WE AGREE THAT SOME SHORTCOMINGS AND POTENTIAL UNDERESTIMATES CAN BE INTRODUCED FROM OUR SAMPLING GEAR, ANALYSES AND METHODS UPON LACK OF CONSIDERATION OF EARLY COPEPODIDS AND ALSO NAUPLII. WE HAVE ADDED A PARAGRAPH IN THE DISCUSSION TO CONSIDER THESE SOURCES OF ERRORS. HOWEVER, WE DO NOT AGREE THESE LIMITATIONS CAN INTRODUCE LARGE ERRORS, FOR REASONS NOW DETAILED IN THE DISCUSSION.

p 3069 line 1: For me it is largely unclear how food conditions are reflected in production estimates because food is – based on the present description of methods – not a factor in the calculation of production although it is the most variable factor. Food conditions offshore also vary by a factor of 20 (0.2 - > 4 mg Chla/m<sup>3</sup> and I wonder if this has no effect on production estimates.

THIS ISSUE HAS BEEN LARGELY DISCUSSED NOW AND WE PROPOSE THAT FOOD SHORTAGE IS NOT A RULE IN UPWELLING SYSTEMS DOMINATED BY OMNIVOROUS COPEPODS, AND PERHAPS THE RULE IS THE OTHER WAY AROUND.

p 3069 line 1: Actually, it is correct that production is the highest in the upwelling zone; however, this production is driven by biomass partially at very low food concentrations. Is this realistic? Moreover, the spatial study has been performed during 1-2 months only. So very little can be said about maxima and the variability occurring offshore..

WE ADDED A PARAGRAPH IN THE DISCUSSION TO TOUCH THIS POINT AND STATING THAT CHLA CAN CERTAINLY BECOME VERY LOW EVEN IN THE UPWELLING ZONE AT TIME, BUT THEN CHLA ALONE IS NOT A GOOD DESCRIPTOR FOR COPEPOD FOOD. THEY ARE OMNIVOROUS AND CAN USE OTHER FOOD

C1738

THAN JUST CHLA.

p 3069 line 13: The time series data on CP does not show any relation to Chla which contrasts with the statements here; I wonder also whether this statement is correct as annual means (based on sampling in one month) were apparently used to establish the relationship. Please specify in more detail those processes by which oxygen and OMZ could affect productivity and potentially explain the lacking correlation with Chla.

WE DID NOT USE ANNUAL MEANS TO ASSESS CORRELATION BETWEEN CP AND CHLA OR ANY OTHER VARIABLE. FULL MONTHLY VARIABILITY IS ACCOUNTED BY GLM AND STEPWISE REGRESSION. THIS SHOULD BE CLEAR WHEN DESCRIBING OUR ANALYSES IN METHODS. WE ALSO INCLUDE A DISCUSSION ON WHY WE THINK THAT DO AND OMZ DEPTH CAN CORRELATE TO CB AND CP. INDEED, WE DO NOT RECALL ANY CAUSAL RELATIONSHIP BETWEEN CP AND OMZ OR DO, BUT JUST CONCLUDE THAT ANY SIGNIFICANT ASSOCIATION ORIGINATES FROM SPATIAL COINCIDENCE.

p 3069 line 20: Here, the method to estimate production should be critically evaluated especially with regard to serious underestimation of small copepod biomass and lacking estimates of  $g$  representing this group.

THIS ISSUE HAS ALREADY BEEN DISCUSSED ABOVE AND IN THE DISCUSSION

p 3070 line 10: Food showed a much more pronounced seasonal, spatial and interannual variation: Why is this factor ignored although there is evidence that food conditions could have an influence on growth and production as stated in the introduction.

WE DID NOT IGNORE THIS FACTOR, BUT INSTEAD WE CONCLUDE IT IS NOT THE KEY FACTOR IN ACCORDING TO OUR WORK AND SUPPORTED BY PREVIOUS STUDIES IN THE SAME REGION AND EVEN DURING THE SAME TIME PERIOD. OTHER AUTHORS HAVE SUGGESTED FOOD EFFECTS UNDER OTHER CIRCUMSTANCES, AND WE HAVE TO RECALL THEM. PERHAPS THESE DIS-

C1739

CREPANCIES AGAIN RECOMMEND HAVING OUR OWN APPROACHES FOR A PARTICULAR SYSTEM AS WE SUGGEST.

p 3070 line 13: Adult copepods have been apparently used in estimates of growth (at least from table 2). How was this done?

NOT JUST ADULTS, BUT ALL COPEPODID STAGES ALTHOUGH WITH SOME BIAS TO LATE STAGES AND THIS IS NOW DISCUSSED IN THE SENSE THAT YOUNG STAGES (E.G. NAUPLII AND C1-C3) ARE LESS CONSIDERED IN THE CALCULATIONS BECAUSE THEY WERE NOT ASSESSED. MEAN COPEPODID SIZE AND THEIR CORRESPONDING BIOMASSES WITH THEIR  $G$ 'S ARE THE BASIS FOR ESTIMATING CP.

p 3071 line 1: Although it is appealing to attribute the variation in production to dilution of the biomass, the lacking relationship of biomass to any of the studied environmental variables needs explanation.

WE PROVIDE A THROUGH FULLY DISCUSSION ON POTENTIAL CAUSES OF A NEGATIVE TREND IN CB AND CP AND REMARK THE LACK OF ASSOCIATION WITH T, FOOD OR OTHER ENVIRONMENTAL VARIABLE, BUT UPWELLING PERSISTENCE. THEREFORE, THERE IS INDEED A RELATIONSHIP WITH THE ENVIRONMENT AND THIS WAS UPWELLING, WHICH HAS BEEN WIDELY SHOWN TO BE A KEY PROCESS INFLUENCING COPEPOD DYNAMICS IN MANY SYSTEMS. THE EXISTENCE OF THE SO-CALLED LATERAL TRANSPORT OF CARBON (KEISTER ET AL., 2009 CITED IN REF.) IS NOT NEW, BUT WE HAVE BEEN ABLE TO DEMONSTRATE THIS AS A KEY DENSITY-INDEPENDENT PROCESS INFLUENCING COPEPOD DYNAMICS IN UPWELLING SYSTEMS.

Figure 13 needs more explanation

IN THE DISCUSSION THIS FIGURE (NOW FIGURE 12) HAS BEEN NOW DESCRIBED IN FULL.

C1740



GENERAL COMMENT FROM AUTHORS:

THE TEXT HAS BEEN FULLY REVISED AND ALSO THE FIGURES TO IMPROVE  
THE WORK IN ALL ASPECTS.

Please also note the supplement to this comment:

<http://www.biogeosciences-discuss.net/12/C1725/2015/bgd-12-C1725-2015-supplement.pdf>

---

Interactive comment on Biogeosciences Discuss., 12, 3057, 2015.

C1741