Review of Marina et al 2023: New insights into the Weddell Sea ecosystem applying a quantitative network approach

In this paper, the authors apply a method for estimating interaction strength to a large dataset of the Weddell Sea food web structure. They then conduct network analysis to explore the sensitivity of the Weddell Sea food web stability to loss of species. Within the food web, they identify 13 species whose presence is destabilising and 2 species whose loss would be destabilising. They characterise the species with significant influence on stability according to their average interaction strengths, trophic level, trophic similarity, degree, and habitat association. They have discussed how their findings relate to other theoretical food web analyses to advance understanding of food web stability more generally.

The extreme environments of the Antarctic present major challenges to collecting sufficient data for constructing quantitative trophic networks, and consequently few (if any) studies have assessed stability of Antarctic ecosystems. I was therefore very pleased to read this paper which is an important first step in advancing understanding of ecological networks and stability in this environment. I found the paper interesting and generally well written. The authors have done well to identify methods that cater to the limitations of Antarctic data, although I found it needed additional methodological detail and discussion. Overall, once the minor corrections described below are addressed, I think this will be a valuable contribution to the journal, special issue and literature.

MAIN COMMENTS

My main comment is that the paper is lacking some necessary detail about the dataset and methods. As someone familiar with the topic area, but not these precise methods or data, I found myself having to refer the referenced papers for details that should be included here. The choice of methods, and the nature of the dataset, impose a number of assumptions about the underlying food web, and caveats on the findings. This is understandable given the challenges of collecting data in Antarctic ecosystems (the dataset is an impressive one), but readers need these additional details in order to put the findings into context. Here I've documented questions I had while reading the paper, which should help clarify what additional details are needed and possible implications of these for the conclusions drawn. Addressing these main comments mostly involves adding details to the methods, and extending the discussion to help the reader interpret the findings in the context of the data, methods and realities of the ecosystem in question. Some questions I posed below may not need to be explicitly answered – as long as enough detail is provided, readers would be able to answer some questions for themselves. To support these amendments, I've also included some specific suggestions in the attached document, in addition to some other specific comments.

1. The method for estimating interaction strength does not factor in temporal variability, yet the Weddell Sea is highly seasonal and stochastic, and the topology of the food web is also variable, depending on the scales and temporal resolution considered. For example, is *Arctocephalus gazella* present in the food web in winter? What are the consequences of assuming that all species are present all year round? E.g. is it valid for the mean IS of a temporary resident be weighted in the same way as year-round resident? What impact would weighting IS according to residence time have on your findings (i.e. what is the sensitivity of your results to the assumption that the food web is constant – would stability still be sensitive to *A. gazella*)? Other studies (e.g. Ushio et al., 2018) have shown that stability varies temporally, and while that can't be assessed with this dataset, it could

theoretically be possible to consider e.g. winter and summer versions of the food web separately, or to weight year-round residents interactions differently from migrants within the same network. The authors need to be explicit that the method and data are not temporally resolved, and that the conclusions may be different if the temporally variable nature of the system is taken into account.

2. More detailed description of the dataset is required. For example,
    - what is the temporal resolution and extent of the data? From Jacob et al, it looks like all trophic data collected since 1982 is amalgamated (i.e. the food web is assumed to be static) – if so, that should be stated. If there is evidence that the Weddell Sea food web has exhibited trends over that time (ie. is non-stationary), then that discrepancy should be indicated - results should be discussed in that context -
    - What are the trophic data? According to Jacob et al (2011), it looks like it is mostly stomach content analysis for larger animals, and stable isotope for lower trophic levels – this should be stated because different methods impose different limitations for identifying trophic interactions, which affects the topology of the resultant foodweb.
    - What spatial extent does it represent? (refer to and amend Figure 1 and its legend)
    - How are species that have ontogenetic shifts in size and diet treated? (referring to Jacob et al 2011, it looks like all species are assumed to be adult – do you adjust body size estimates to be the mean across all lifestages of a species [e.g. averaging across larval, juvenile and adult lifestages] or are they all adult body size estimates [i.e. averaging across body sizes of the adult population]? If your body size estimates are adult sizes, but you include trophic links that only occur in smaller size classes – how would that affect your findings?)
    - What uncertainties may still underly the dataset and therefore the analysis? (e.g. topological uncertainties due to methodological biases such as trophic interactions that can't be detected by stomach content analysis; uncertainties due to assuming stationarity of the food web – e.g. trophic interactions may have changed strength, been lost through phenological mismatches, or new interactions gained over the time period the dataset represents). Sufficient details about the dataset should be given for readers to understand the caveats they impose on the results.

3. There are many different types/dimensions of stability (e.g. Kéfi et al., 2019), and species can also be both stabilizing and destabilizing through their relative impacts on the different dimensions of stability (e.g. White et al., 2020). The type of stability being assessed here should be defined (some readers will not know what an eigenvalue is), and explained in terms of the ecology – e.g. what does it mean if the foodweb is unstable – what will happen? What is it unstable to? (e.g. press, pulse perturbations?) Then for the discussion – what do the stability results (taking the type of stability and the data and methodological caveats into account) mean for the real Weddell Sea ecosystem and how it will change or be vulnerable into the future?

As a general comment, it may help to consider some of the above points in terms of the types of uncertainty they represent – e.g. structural uncertainty, parameter uncertainty or predictive uncertainty (i.e. arising from the way the data are analysed). Conducting additional sensitivity analyses could make the study more robust, and enable greater clarification of uncertainties to inform how the results should be interpreted. This could include, as suggested in the comment

above, exploring the impact of removing multiple species at once – a situation which is not infeasible. Sensitivity analyses should be standard practice, but I would not strictly require it here so long as all the caveats, assumptions etc highlighted above (and their implication for the results) are made very clear and discussed. It would be interesting to know the authors expectations/thoughts about the likely relative sensitivity of the findings presented to different sources of uncertainty.

The discussion is very brief, and largely focuses on comparison with findings from other theoretical studies. Expanding the discussion to incorporate the above points, as well as considering the findings in the context of observed trends in the Weddell Sea will add value for readers, and better contribute to progressing understanding and management of the Weddell Sea ecosystem.

SPECIFIC COMMENTS

Introduction:

[L27] However a species interaction can be important stability just based on its presence (regardless of strength), e.g. by contributing to destabilizing feedbacks (e.g. Ward et al., 2022).

[L70-72] These two statements are contradictory. The first is correct, but the second must be an error. Jacob et al (2011) found that the system was more sensitive to loss of lower trophic levels, not to predators. i.e. this is contradictory, not consistent, to the findings of the other papers cited here.

[L74-76] This sentence is not clear – rephrasing to emphasise the key point would help. E.g. Predators with specific trait combinations (e.g. large swimming or flying predators which tend to have high predator-prey body ratios) are particularly important in this and other foodwebs because they generate weak interactions that…

Methods:

Figure 1. This figure should clearly indicate the extent of the case study area (dataset). – e.g. is it inclusive of all the polygons? Or just the area within the dashed oval (including land?)? This should be made clear in the map and the legend. The main text does refer to 74-78^{o}S [L86], but these high latitudes are not indicated on the map.

[L86-90] the strong seasonality and stochasticity of the system should be mentioned as a reminder for non-polar specialists.

[L92-97] Greater detail on the dataset is needed, as it is critical to the interpretation of the findings:

- temporal extent (and resolution?),
- spatial extent (referring to Figure 1),
- the nature of the trophic data (e.g. is it based on stomach contents for large things and stable isotope for lower trophic levels? Specify if any gaps filled based on other methods?);
- what are the body size estimates? - e.g. mean adult size or body size averaged across all size classes

- if/how ontogenetic shifts in diet are dealt with in terms of body size and trophic interactions. (e.g. are trophic interactions of larval life stages included as interactions for species with adult body size estimates? Or are those interactions excluded?)

[L98] Are closure terms or exports applied to any species (e.g. top predators) to represent other sources of mortality, as is common practice with other methodologies? (just wondering if this could be contributing factor to your finding that predators are destabilizing?)

[L101-110] At what scale is the dimensionality considered? E.g. at one scale a tiny benthic animal may seem to move in 2D space, but relative to its size may be moving a long way above the benthos. Is habitat complexity factored in? e.g. are animals moving on a flat mud surface and animals clambering around and over complex sponge gardens both considered 2D, or is the latter 3D? (this may be beyond the scope of this study to consider, but it would be interesting to know if/how these decisions influence the results).

[L115-118] The explanation of the method for estimating resource density is not very clear. You've said that resource density scales with resource mass, but haven't specified your calculation, or what the 2D/3D exponents are. It is also unclear how rare species are treated? (And if all species of common body size and dimension are treated the same – i.e. assumed to have the same resource mass – then this should be clarified as presumably it would alter IS estimates and impact on stability etc. (apologies if I've missed something here)

[L124] You should state how you selected the model. e.g. you selected the model with the lowest AIC (or however you made that decision)

[L128] "Unweighted properties are related to properties…" this is unclear because it sounds like you are comparing two vague undefined sets of properties → I think rearranging the sentence might help, e.g. Properties of the unweighted foodweb only describe the presence or absence…… These properties are commonly used in qualitative food web studies.

Figure 2. This is a helpful figure – very clear.

[L130] Again, a trophic interaction can also be important just by virtue of its presence (e.g. by contributing to feedbacks). So considering the interaction strengths (weighted properties) is capturing a different aspect of the importance of an interaction. I'd suggest rephrasing slightly.

[L132-133] Is averaging interaction strengths for a species standard practice? This should be justified or supported with a reference.

[L144-148] What specifically did you do with the species habitat affiliation data? It is not clear exactly how it was taken into account.

[L156] What stability means in the context of this study should be defined (e.g. Kéfi et al., 2019).

[L159-160] This the action of this sentence is unclear – you used the mean real part […] and the randomized Jacobians to do what? And can you define what a randomized Jacobian represents ecologically?

[L160-161] What does this mean ecologically – i.e. what is a more stable food web, by this measure?

[L162] "this difference" is unclear. What exactly is being compared? Should state exactly what is being tested, e.g. the difference between X and X…

[L162] Why was an Anderson-Darling test chosen?

[L164] in other words, *the presence* of this species makes the network less stable

[L168-170] How did you use these plots to identify species? What criteria were used to characterise species with greatest effect on stability? What metric/s was the basis for identifying the species, and were there cut-offs above/below which species were determined to have high impact on stability? Or were the species identified in the previous step, and then this sentence is explaining how the characteristics of these species were explored? This is unclear. Either way, greater explanation is needed to clarify how the plots were used (and any other basis for characterising them). (And if the species were identified in the previous step, then the beginning of the sentence needs to be modified so it doesn't sound like the plots are being used to identify the species)

Results

[L176] The key statistics should be stated here, and it would be helpful to indicate here what is in the supplementary table.

Figure 3. The gamma distribution should also be plotted on the same axes, e.g. as a line

Figure 4. "-value" is not needed after p. Just p= or p<

[L180-181] readers should be referred to the specific subplots of Figure 4 for evidence of each of these statements (as Fig. 4D is referred to in L185)

Figure 5: It should be made clear what each point represents – ie. is each point the mean stability difference across all the random Jacobians? Can uncertainty/confidence intervals be represented either here somehow (possibly in a different format) or as a supplementary figure?

Table 2. This is referred to in L190 and L194 but is not included in the manuscript.

Discussion:

[L206-207] These statements are unclear, and seem unnecessary here. The sentence can be deleted.

[L221-222] This orphan sentence doesn't provide much – it needs further support to make a clear point. E.g. what do you mean by the "quality of interactions". How do you see this statement is related to your own findings? Do you need to say anything about how this combination of information is assessed to determine species role in stability?

[L239-240] It is not entirely clear what "this" refers to. Also, the statement itself seems obvious – that non-pelagic parts of the ecosystem are also sensitive to perturbation. If you are intending to refer to your finding of the importance of land-based predators to stability – they are often pelagic or bentho-pelagic, so the point is not clear. The sentence may need to be rephrased.

[L241] An additional section should be added to discuss implications of the uncertainties, data and methodological constraints on the results, and how the findings should be interpreted in the context of that and the realities of the (highly variable) Weddell Sea environment and ecosystem (i.e. based on main comments at the top to put the findings into context). For example, non-stationarity of the system – do the trophic data collected in 1982 still

represent current interactions? What are the uncertainties, and how could these be refined in future studies?

A related gap to address: the discussion compares the findings to those of similar studies, but does not consider the findings in the context of changes currently being observed or predicted in the Weddell Sea. This feels like a considerable omission. For example, you found a few species with greater impact on stability - is there evidence that any of these species are particularly threatened? Are there other trends occurring in the system that have particular implications for your findings?

Some related comments/questions you could consider:

- Other studies (e.g. Kéfi et al., 2016) show that loss of species that perform multiple functions, including non-trophic interactions, can have outsized importance in terms of stability – e.g. are more likely to cause cascading extinctions. It would be interesting to hear the authors thoughts on how including other types of interactions e.g. interactions between habitat-forming benthos and their residents, would alter the results, - e.g. perhaps a larger importance of benthic species for stability than was found here.
- How is climate change affecting body mass, consumer search space, interaction strength and therefore stability? It would also be interesting to know if these types of climate change effects will alter the species with greatest impact on network stability (might be a future research question).

[L247-248] What information specifically should be incorporated into these efforts? Based on your findings, what specific recommendations would you make in the development of policies and management strategies? You should provide some tangible examples from your study. For example, have you identified species or parts of the foodweb that should be prioritised for protection? Have you identified critical knowledge gaps that need to be addressed as a priority? And if so, what are they?

Technical corrections:

[L72] grammar: “This findings” → “this finding” or “these findings”

[L123] missing word: “to” the IS distribution

[L166] typo: “ahs” → has

[L181] grammar: “Contrary,” → “in contrast” (or “to the contrary”)

[L182-183, L192] formatting: species Latin names should be italicized

[L189-190] delete “except for a few species (red points in figure 5)” from L189, and add reference to Fig 5 to parentheses on L190, i.e. “(red points in Figure 5; Table 2)”.

[L245] typos: “Futher” and “tha”

[L254] grammar: “all persons” → “everybody” or “all people”

[L254] gr: “enable” → “enabled”

Papers cited

Kéfi, S., Domínguez-García, V., Donohue, I., Fontaine, C., Thébault, E., & Dakos, V. (2019). Advancing our understanding of ecological stability. *Ecology Letters*, *22*(9), 1349–1356. https://doi.org/10.1111/ele.13340

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Ushio, M., Hsieh, C., Masuda, R., Deyle, E. R., Ye, H., Chang, C.-W., Sugihara, G., & Kondoh, M. (2018). Fluctuating interaction network and time-varying stability of a natural fish community. *Nature*, *554*(7692), 360–363. https://doi.org/10.1038/nature25504

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White, L., O'Connor, N. E., Yang, Q., Emmerson, M. C., & Donohue, I. (2020). Individual species provide multifaceted contributions to the stability of ecosystems. *Nature Ecology & Evolution*, *4*(12), 1594–1601. https://doi.org/10.1038/s41559-020-01315-w