



The place of chemosynthesis in marine food webs: towards a global perspective







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7th International Symposium on Chemosynthesis-Based Ecosystems – São Paulo, Brazil, 17/08/2023

Food webs

Food webs: networks formed by entirety of trophic interactions found in a given ecosystem.



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Trophic interactions are numerous and dynamic, leading to complex ecological networks

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Trophic interactions are numerous and dynamic, leading to complex ecological networks

Since food webs link all organisms living in a given ecosystem together, their structure conditions system functioning and reaction to environmental fluctuations (natural or anthropogenic)

They can act as vectors, through which ecological changes can propagate across ecosystem compartments, or even across ecosystems

Chemosynthesis



While initially depicted as a rather anecdotic carbon fixation pathway, chemosynthesis has proven to be a major mechanism supporting food webs in multiple marine ecosystems, including hydrothermal vents

Hügler M, Sievert SM. 2011. Annu. Rev. Mar. Sci. 3:261–89

Hydrothermal vent food webs



Decades of intensive research led to many discoveries regarding hydrothermal vent food webs...



Diagrams from Govenar 2012

Hydrothermal vent food webs



Decades of intensive research led to many discoveries regarding hydrothermal vent food webs...



Diagrams from Govenar 2012

... and yet, trophic ecology of deep-sea vents remain, by many aspects, in its infancy when compared with other systems. Many questions about food web structure, trophic interactions and how they condition vent ecosystem functioning remain open, and new ones keep arising!



Chemosynthetic habitats are not only, as initially thought, "oases within a barren deep ocean"

There is increasing evidence that they are strongly connected to surrounding ecosystems

Levin et al. 2016



Hydrothermally-sourced iron triggers massive phytoplankton blooms in shallower layers of the Southern Ocean Influence extending to hundreds of km



Chemosynthetic OM can be exported through particle advection + active movement of predators and scavengers



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Overall: >10% of deep-sea benthic carbon flux could be derived from chemosynthesis

Mostly cold seeps (less intense production than vents, but more widespread)

Levin et al. 2016



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Overall: >10% of deep-sea benthic carbon flux could be derived from chemosynthesis

Mostly cold seeps (less intense production than vents, but more widespread)

Many things about the nature, occurrence or intensity of those subsidies are still unadequately understood...

About me

2022 - Present: Assistant professor at University of Liège, Belgium

2017 - 2022: Research scientist at Ifremer Brittany, Brest, France



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2017 - 2022: Research scientist at Ifremer Brittany, Brest, France

Research interests:

- How do food web structure and trophic interactions influence marine ecosystem functioning and biodiversity?
- How do natural or anthropogenic environmental variations impact animal feeding?
- How does ecological plasticity mediates marine consumers' response to change?

I mostly tackle those issues by using polar and deep-sea benthic invertebrates as ecological models, and by developing approaches based on trophic markers, notably stable isotopes.



NOTES ON A MLAJOR OCEANOGRAPHIC FINID

Discovery of hydrothermal vents: 1977

by Robert D. Ballard

Oceanus Vol. 20, No. 3, Summer 1977

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616 Nature Vol. 293 22 Oct	484	Nature Vol. 289 5 February 198	21 NATURE VOL. 306 3 NOVEMBER 1983	ETTER
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For 4 decades, stable isotopes have been instrumental to many findings about vent ecology... And still have much potential to offer!

Stable isotopes: you are what you eat

Stable isotope ratios in animals can be used as integrative trophic markers (indirect info on animal diet)







Stable isotopes: you are what you eat

Stable isotope ratios in animals can be used as integrative trophic markers (indirect info on animal diet)







Mixing law: stable isotope composition of an animal is a proportional mix of its food sources' isotopic compositions

By measuring the isotopic compositions of an animal and those of its food sources, it is possible to estimate the contribution of each food source to the animal's diet













 δ^{13} C of marine producers is variable and mostly conserved throughout the food web

δ¹³C can be used to identify and quantify relative contributions of production mechanisms supporting animal populations in marine ecosystems

Nitrogen stable isotopes

Higher trophic position



Higher

Lower

Lower trophic position

Nitrogen stable isotopes

Higher trophic position



Lower trophic position

Producers using NH₄⁺



Nitrogen stable isotopes











A food web example : Woodlark Basin



Chubacarc cruise: connectivity and regional patterns of biodiversity in back-arc basins of Western Pacific

Hourdez & Jollivet (2019): <u>https://doi.org/10.17600/18001111</u>



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La Scala vent field, Woodlark Basin

communications earth & environment

ARTICLE

https://doi.org/10.1038/s43247-022-00387-9

OPEN

Check for updates

Active hydrothermal vents in the Woodlark Basin may act as dispersing centres for hydrothermal fauna

Cédric Boulart [™], Olivier Rouxel [®]², Carla Scalabrin [®]², Pierre Le Meur³, Ewan Pelleter², Camille Poitrimol^{1,4}, Eric Thiébaut¹, Marjolaine Matabos [®]⁴, Jade Castel¹, Adrien Tran Lu Y^{5,6}, Loic N. Michel⁴, Cécile Cathalot², Sandrine Chéron², Audrey Boissier², Yoan Germain², Vivien Guyader², Sophie Arnaud-Haond⁷, François Bonhomme⁵, Thomas Broquet [®]¹, Valérie Cueff-Gauchard⁸, Victor Le Layec^{1,6}, Stéphane L'Haridon⁸, Jean Mary¹, Anne-Sophie Le Port¹, Aurélie Tasiemski⁹, Darren C. Kuama¹⁰, Stéphane Hourdez⁶ & Didier Jollivet¹

Open access paper: <u>https://doi.org/10.1038/s43247-022-00387-9</u>

La Scala vent field, Woodlark Basin

Discovery of several active smokers, depth \approx 3400 m


Close to active chimneys: communities dominated by symbiont-bearing gastropods that act as foundation species





On inactive chimneys and peripheral zones: dense cirriped bushes Not typical of SW Pacific hydrothermal vents, but described in nearby oceanic trenches (e.g. Tonga)

Document functional ecology of this newly discovered system



Document functional ecology of this newly discovered system

Identify main production pathways supporting animal populations



Document functional ecology of this newly discovered system

Identify main production pathways supporting animal populations

Assess potential energy fluxes between active sites and inactive, peripheral habitats





ROV sampling of biomassdominant benthic fauna

Dissection and extraction of relevant tissues

Use of stable isotope ratios of C, N and S



ROV sampling of biomassdominant benthic fauna

Dissection and extraction of relevant tissues

Use of stable isotope ratios of C, N and S





Taxon

- Alviniconcha boucheti
- Alviniconcha kojimai
- Ifremeria nautilei









Taxon

- Alviniconcha boucheti
- Alviniconcha kojimai
- Ifremeria nautilei
- \triangle *Provanna* sp.
- ✓ Phymorhynchus sp.



Provanna sp.



Phymorhynchus sp.

Provanna sp.: Relatively low trophic position, most likely bacterial grazer

Phymorhynchus sp.: $\delta^{15}N$ higher than grazers but similar to symbiont feeders. Seems to feed at a lower trophic position than often assumed.



△ Provanna sp.





Provanna sp.



Phymorhynchus sp.



B. segonzaci



Taxon

- Alviniconcha boucheti
- Alviniconcha kojimai
- Ifremeria nautilei
- △ *Provanna* sp.
- *∇ Phymorhynchus* sp.
- Ampharetidae
- Branchinotogluma segonzaci
- Austinogrea sp.
- Rimicaris variabilis
- Vulcanolepas sp. nov.



Austinogrea sp.

Vulcanolepas sp. nov.



 δ^{15} N of crabs and shrimps higher, yet similar. Both omnivores? Differences in trophic position masked by baseline differences?

Marked δ^{13} C differences among shrimps: high intraspecific trophic diversity





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- Alviniconcha boucheti
- Alviniconcha kojimai
- Ifremeria nautilei
- △ *Provanna* sp.
- ✓ Phymorhynchus sp.

AmpharetidaeBranchinotogluma segonzaci

- Austinogrea sp.
 Rimicaris variabilis
 Vulcanolepas sp.
- Porifera (bottom)
- Isididae (top)
- Actiniaria (middle)









- Alviniconcha boucheti
- Alviniconcha kojimai
- Ifremeria nautilei
- \triangle *Provanna* sp.
- Phymorhynchus sp.
- Ampharetidae Branchinotogluma segonzaci
- Austinogrea sp.
- Rimicaris variabilis
- *Vulcanolepas* sp. nov.

- Actiniaria
- Brisingidae (top)
- *Chiridota* sp. (bottom)









What do these animals with intermediate $\delta^{13} C$ feed on?

Exported photosynthetic production?

Mix of chemosynthesis-derived OM produced through multiple pathways?















Typical SI analysis output : points in "isospace"



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Position of consumers in the isospace is driven by

1) Differences in consumed resources (different preys can have different isotopic compositions)

Typical SI analysis output : points in "isospace"



Position of consumers in the isospace is driven by

1) Differences in consumed resources (different preys can have different isotopic compositions)

2) Differences in foraging habitat(the same prey can have different isotopic compositions in different habitats)

Geometric approach (Layman *et al.* 2007):



CAN STABLE ISOTOPE RATIOS PROVIDE FOR COMMUNITY-WIDE MEASURES OF TROPHIC STRUCTURE?

Craig A. Layman,^{1,5} D. Albrey Arrington,² Carmen G. Montaña,³ and David M. Post⁴

Ecology, 88(1), 2007, pp. 42–48

Geometric approach (Layman *et al.* 2007):

Fit a convex hull (i.e., the smallest possible surface that encompasses all points) to the data

This convex hull represents the isotopic niche of the group of consumers (proxy for their realized ecological niche)



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Set of complementary metrics including total area of the convex hull: proxy of the total resource diversity used by the organisms

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Some hull-based metrics (including its total area) are highly sensitive to the presence of extreme points

According to your research question, it can be a good or a bad thing...





Journal of Animal Ecology

Journal of Animal Ecology 2011

doi: 10.1111/i.1365-2656.2011.01806.x

Comparing isotopic niche widths among and within communities: SIBER – Stable Isotope Bayesian Ellipses

Standard ellipse vs. convex hull (SD vs. full range)

Represents "core isotopic niche" of the group of consumers



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Comparing isotopic niche widths among and within communities: SIBER – Stable Isotope Bayesian Ellipses

Standard ellipse vs. convex hull (SD vs. full range)

Represents "core isotopic niche" of the group of consumers

Main metric: standard ellipse area (SEA), proxy for the diversity of most commonly used ecological resources

More robust and less sensitive to extreme values and small sample size

Ellipses and hulls can be complementary

Stable isotopes as niche proxies

Comparison of groups :

Hull or ellipse size


Stable isotopes as niche proxies

- Comparison of groups :
- Hull or ellipse size
- Hull or ellipse overlap: the greater the overlap, the more the organism groups are likely to rely on shared resources



Stable isotopes as niche proxies

- Comparison of groups :
- Hull or ellipse size
- Hull or ellipse overlap: the greater the overlap, the more the organism groups are likely to rely on shared resources





Spedicato et al. 2020

Snake Pit hydrothermal field (Mid-Atlantic Ridge)



Pierre Methou (Then Ifremer, now JAMSTEC)

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Research



Cite this article: Methou P, Michel LN, Segonzac M, Cambon-Bonavita M-A, Pradillon F. 2020 Integrative taxonomy revisits the ontogeny and trophic niches of *Rimicaris* vent shrimps. *R. Soc. Open Sci.* **7**: 200837. http://dx.doi.org/10.1098/rsos.200837 Integrative taxonomy revisits the ontogeny and trophic niches of *Rimicaris* vent shrimps

Pierre Methou^{1,2}, Loïc N. Michel², Michel Segonzac³, Marie-Anne Cambon-Bonavita¹ and Florence Pradillon²

Shrimp swarms notably containing two congeneric species in variable densities and proportions



Shrimp swarms notably containing two congeneric species in variable densities and proportions

Rimicaris exoculata: enlarged cephalothoracic cavity hosting abundant episymbiotic communities on which they depend for their nutrition





Shrimp swarms notably containing two congeneric species in variable densities and proportions

Rimicaris exoculata: enlarged cephalothoracic cavity hosting abundant episymbiotic communities on which they depend for their nutrition

Rimicaris chacei: smaller, no obvious morphological adaptations to symbiosis, mixotrophic species (depend both on symbiotic associations and "classical" feeding)







Not only adults, but also juveniles / immature individuals



R. exoculata

Juvenile stade A

Juvenile stade B

Juvenile stade C (Subadult) R. chacei

Juvenile stade A

Juvenile stade B (Subadult)



Not only adults, but also juveniles / immature individuals



R. chacei *R. exoculata* Juvenile stade A Juvenile stade A Juvenile stade B Juvenile stade B (Subadult) Juvenile stade C (Subadult)



What do these species rely on throughout their life cycle stages occuring in vent ecosystems? Are there ontogenetic niche shifts?





 Rimicaris exoculata

 Adult
 Subadult

 Juvenile stage B
 Juvenile stage A

 Rimicaris chacei

 Adult
 Subadult

 Juvenile stage A

Early stages (A):

Mostly photosynthetic nutrition reflecting larval stages in the water column

No overlap between the two species: larval niche segregation (trophic, habitat, or both)? Maternal carry-over effect?





Early stages (A):

Mostly photosynthetic nutrition No overlap between the two species

Intermediate stages (B and/or C)

Transition towards reliance on chemosynthesis Some overlap between the species, but no overlap between successive stages in *R. exoculata*



 Rimicaris exoculata

 Adult
 Subadult
 Juvenile stage B
 Juvenile stage A

 Rimicaris chacei

 Adult
 Subadult
 Juvenile stage A

Early stages (A):

Mostly photosynthetic nutrition No overlap between the two species

Intermediate stages (B and/or C)

Transition towards reliance on chemosynthesis

Adult stages

Chemosynthetic nutrition and marked niche separation *R. exoculata*: narrow niche consistent with sole reliance on their symbionts. Big gap between subadults and adults linked with strong ecological and morphological changes *R. chacei*: much wider niche (greater trophic diversity): mixotrophy and/or reliance on multiple symbiotic partners







R. exoculata

Mostly rely on Campylobacterota (Epsilonproteobacteria) that dominate their symbiotic communities and use the rTCA cycle to oxidize sulfides

 δ^{15} N increase in adults unlikely to be linked with trophic position increase, but rather preferential assimilation of nitrates by those symbionts





R. exoculata

Mostly rely on Campylobacterota (Epsilonproteobacteria) that dominate their symbiotic communities and use the rTCA cycle to oxidize sulfides

 $\delta^{\rm 15}N$ increase in adults unlikely to be linked with trophic position increase, but rather preferential assimilation of nitrates by those symbionts

R. chacei

Rely on multiple pathways of carbon fixation, with large interindividual differences (not opportunistic feeding!)

Stable isotopes alone cannot settle the relative importance of reliance on a diverse symbiont pool (CBB-using Gammaproteobacteria + rTCA-using Campylobacterota) vs. grazing on diverse bacterial mats along the vent gradient

Symbiotrophic Rimicaris exoculata

Mixotrophic *Rimicaris chacei*

Phagotrophic Mirocaris fortunata Alvinocaris markensis











Both phagotrophic species have higher $\delta^{15}N$: omnivory?



Both phagotrophic species have higher $\delta^{15}N$: omnivory?

M. fortunata only relies on endogenous vent production, but *A. markensis*' niche is very wide and this species apparently feeds on a mix of photosynthesis- and chemosynthesis-derived items



Both phagotrophic species have higher $\delta^{15}N$: omnivory?

M. fortunata only relies on endogenous vent production, but *A. markensis*' niche is very wide and this species apparently feeds on a mix of photosynthesis- and chemosynthesis-derived items





Joan Alfaro-Lucas (Then Ifremer, now U Victoria)

High environmental stress and productivity increase functional diversity along a deep-sea hydrothermal vent gradient

J. M. Alfaro-Lucas D,^{1,4} F. Pradillon D,¹ D. Zeppilli D,¹ L. N. Michel D,¹ P. Martinez-Arbizu D,² H. Tanaka D,³ M. Foviaux,¹ and J. Sarrazin¹

Ecology, 101(11), 2020, e03144

Lucky Strike hydrothermal field (Mid-Atlantic Ridge)



Deployment of artificial substrates along a vent proximity gradient for 2 years

Analysis of settled communities in terms of taxonomic, functional and isotopic diversity









Partial reliance on chemosynthesis at the far site (100 m from any active vent): spatial subsidy extends way beyond areas under direct venting influence



Partial reliance on chemosynthesis at the far site (100 m from any active vent): spatial subsidy extends way beyond areas under direct venting influence



Lucky Strike vent field

Eiffel Tower & Capelinhos (~ 1.5 km apart)



Alfaro-Lucas et al., In review







General shift towards more positive $\delta^{13}C$, particularly marked in the foundation species *Bathymodiolus azoricus* (5)

Strong shift of the whole community towards higher $\delta^{34}S$



Higher contribution of photosynthetic OM? Unlikely: overall low $\delta^{15}N$ + similar depth and oceanographic features as other LS vents where export of photosynthetic OM is considered low to negligible



Local differences in geochemistry: different rock/fluid interactions leading to isotopically heavy sulfides and/or coreliance of the vent community on CBB thiotrophy and methanotrophy (seen in other MAR vents like Rainbow)



iew

Baseline variation at large spatial scale



Baseline variation at large spatial scale



Hulls built using isotopic compositions of symbiotrophic foundation species (Alviniconcha spp., Ifremeria nautilei, Bathymodiolus spp.)

Baseline variation at large spatial scale



Hulls built using isotopic compositions of symbiotrophic foundation species (Alviniconcha spp., Ifremeria nautilei, Bathymodiolus spp.)
Woodlark



North Fiji **Futuna** Lau

Strong inter-basin differences in hull shape and size

No clear longitudinal effect...

Hulls built using isotopic compositions of symbiotrophic foundation species (Alviniconcha spp., Ifremeria nautilei, Bathymodiolus spp.)

Baseline variations: δ³⁴S



Alviniconcha boucheti
 Alviniconcha kojimai
 Alviniconcha strummeri

Bathymodiolus brevior

Bathymodiolus manusensis

🖨 Ifremeria nautilei



Presence of global shifts, e.g. lower and more variable $\delta^{34}S$ in Manus

Alviniconcha boucheti
 Alviniconcha kojimai
 Alviniconcha strummeri

Bathymodiolus brevior

Bathymodiolus manusensis

🖨 Ifremeria nautilei



Some conserved relative positions, *e.g. A. boucheti* > *A. kojimai* : species-specific patterns in isotope fractionation during sulfide uptake by symbionts?

Alviniconcha boucheti
 Alviniconcha kojimai
 Alviniconcha strummeri

- Bathymodiolus breviorBathymodiolus manusensis
- *Ifremeria nautilei*



Some conserved relative positions, *e.g. A. boucheti* > *A. kojimai* : species-specific patterns in isotope fractionation during sulfide uptake by symbionts? Alviniconcha boucheti
 Alviniconcha kojimai
 Alviniconcha strummeri

- **申** Bathymodiolus brevior
- **Bathymodiolus manusensis**
- 🖨 Ifremeria nautilei



Alviniconcha boucheti
 Alviniconcha kojimai
 Alviniconcha strummeri



No consistent trends from one basin to another

Strong changes in relative positions (*e.g. A. boucheti, A. kojimai* and *I. nautilei*) Alviniconcha boucheti
 Alviniconcha kojimai
 Alviniconcha strummeri

Bathymodiolus brevior
Bathymodiolus manusensis
Ifremeria nautilei











Woodlark

North Fiji

Futuna



Basin
Manus
Woodlark
North Fiji
Futuna
Lau

To understand the trophic ecology of a species, info about its "isotopic landscape" (isotopic composition of baseline items, of other species, of previous sampling events, of its place in other comparable systems, etc...) highly desirable...



Basin
Manus
Woodlark
North Fiji
Futuna
Lau

To understand the trophic ecology of a species, info about its "isotopic landscape" (isotopic composition of baseline items, of other species, of previous sampling events, of its place in other comparable systems, etc...) highly desirable...

...Yet often hard to obtain due to constraining sampling logistics, analytical limitations, etc.

SEANOE

Deeplso - a global open database of stable isotope ratios and elemental contents for deep-sea ecosystems

- Date 2021-08-17
- Temporal 1985 -2018
- extent
- Author(s) Michel Loïc N.¹[®][™], Bell James B.¹[®]², Dubois Stanislas F.¹[®]³, Le Pans Mathilde¹, Lepoint Gilles[®]⁴, Olu Karine[®]¹, Reid William D. K.¹[®]⁵, Sarrazin Jozee[®]¹, Schaal Gauthier[®]⁶, Hayden Brian[®]⁷
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Example of targeted taxa: tubeworms Escarpia southwardae and mussels Bathymodiolus aff. boomerang from cold seeps. Picture: Ifremer, WACS cruise, 2011 (depth: 3160 m).



Freely available at <u>https://doi.org/10.17882/76595</u> under CC-BY licence

SEANOE

Deeplso - a global open database of stable isotope ratios and elemental contents for deep-sea ecosystems

Date	2021-08-17
Temporal extent	1985 -2018
Author(s)	Michel Loïc N. ^{©1⊠} , Bell James B. ^{©2} , Dubois Stanislas F. ^{©3} , Le Pans Mathilde ¹ , Lepoint Gilles ^{©4} , Olu Karine ^{©1} , Reid William D. K. ^{©5} , Sarrazin Jozee ^{©1} , Schaal Gauthier ^{©6} , Hayden Brian ^{©7}





Example of targeted taxa:

Goals:

Produce a global, easily discoverable, available and reusable compilation of stable isotope ratios and elemental contents in organisms from deep-sea ecosystems

Provide the deep-sea community with an open data analysis tool that can be used in the context of future ecological research, and to help deep-sea researchers to use stable isotope markers at their full efficiency.

Freely available at https://doi.org/10.17882/76595 under CC-BY licence

Deeplso: core working group



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Deeplso: data contributors





38335 measurements of 7 parameters



7248 distinct samples from multiple ecosystems, including 3164 (44%) from chemosynthesis-based ecosystems



881 distinct taxa (+ sediment, detritus, suspended particulate organic matter, bulk plancton, etc.)



Worldwide spatial coverage





Integrate Deeplso with larger scale initiatives such as IsoBank



Integrate DeepIso with larger scale initiatives such as IsoBank



 Keep building up the database and maximising its scope by integrating more data

- Integrate DeepIso with larger scale initiatives such as IsoBank
- Keep building up the database and maximising its scope by integrating more data
- We are looking for people willing to share data, either underlying published articles, grey literature or even unpublished
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- Integrate DeepIso with larger scale initiatives such as IsoBank
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Feeling like contributing? Questions? Feedback? Get in touch!



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- Consider archiving your data openly you'll likely benefit from it and so will the rest of the scientific community

Acknowledgements



Many friends and colleagues that helped me, directly or indirectly, to perform this research



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ISblue

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Thanks for your attention



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