An economic approach to the equilibrium of trophic networks

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Upwelling Ecosystems Research Unit

Ecology and economics

- We formulate in mathematical terms the principles of networks economics applied to trophic systems.
- We present a model of a pelagic ecosystem and compute its equilibrium state; we examine with this approach the identification of controls (top-down / bottom-up).

From biology to economics and back

- Quesnay
- Leontieff, Hannon, Povolina
- MacArthur-Pianka, Charnov
- Tschirhart, Finoff

B. Hannon, The use of analogy in biology and economics. From biology to economics and back. Structural change and economic dynamics (1997), 471

Networks economics and ecology

Networks economics

Making explicit:

- Conservation equations
- Complementarity equations

Applications

- Traffic
- Electricity network
- Structural mechanics
- Spatial economics
- Migration studies

What's in ecology ?

A. Nagurney. Network economics. A variational inequality approach. Kluwer Academic Publishers, Dortmund, 1993

Networks economics and ecology

Conservation equations : Mass balance

Notations

- B_i biomass of species i;
- X_{ij} trophic flow form species i (prey) and species j (predator)
- E_i energy inflow of species i; ($E_i = 0$ for heterotroph species)

Equations

$$\begin{aligned} \text{Production} &= \text{Consumption} \\ \text{Assimilated inflow} &= \text{Mortality due to predation} \\ &\quad + \text{Somatic maintenance} + \text{Other mortality} \\ \gamma_i(E_i + \sum_j X_{ji}) &= \sum_j X_{ij} + \mu_i B_i \end{aligned}$$

B. Hannon, The structure of ecosystems, Journal of theoretical biology 41 (1973)

Conservation equations : Mass balance

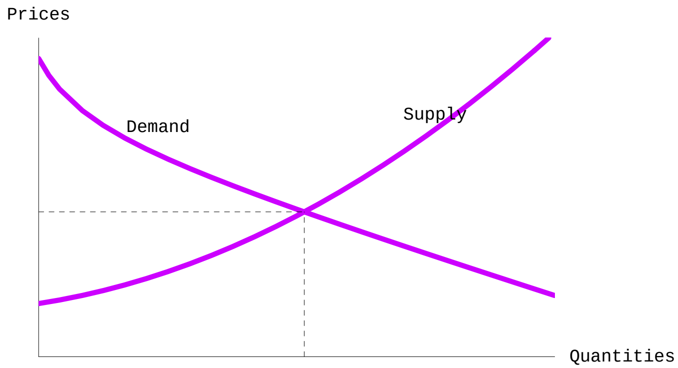
- Flows determine biomass :

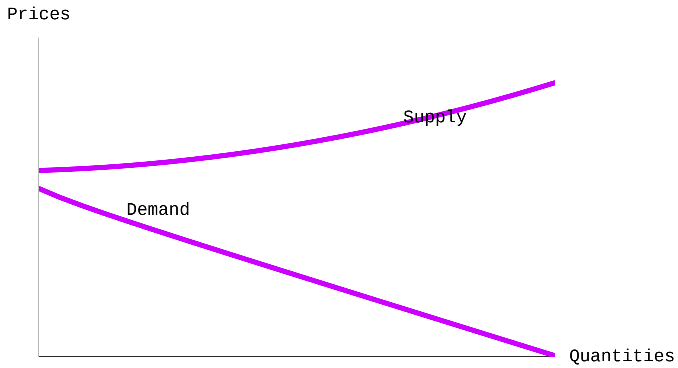
$$B_i = (\gamma_i(E_i + \sum_j X_{ji}) - \sum_j X_{ij})/\mu_i$$

- There are constraints on flows; K is the set of flows X_{ij} such that
  1. $X_{ij} \geq 0$
  2. $B_i \geq 0$

Networks economics and ecology

Complementarity equation :





Walras' law

- demand : $P = F(Q)$
- supply : $P = G(Q)$
- surplus : $E(Q) = G(Q) - F(Q)$
- complementarity : either $\overline{Q} \geq 0$ and $E(\overline{Q}) = 0$, or $\overline{Q} = 0$ and $E(\overline{Q}) \geq 0$

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Complementarity equation

We assume that F_{ij}, the costs for a predator j to feed on a prey i, is the sum of:

- A constant term: ϕ_{ij},
- A negative linear term: $-\kappa_i B_i$, expressing the easiness of predation due to the abundance of prey B_i
- A positive linear term: $\lambda_j B_j$, expressing intra specific competition for predator species

$$\phi_{ij} - \kappa_i B_i + \lambda_j B_j$$

As flows determine biomass through:

$$B_i = (\gamma_i (E_i + \sum_j X_{ji}) - \sum_j X_{ij}) / \mu_i$$

We have :

Theorem 0.1 *Intensities of flows on all paths determine predation costs on all paths. There is a function :* $X \rightarrow F(X)$*, where* $X = \{X_{ij}\}$ *and* $F = \{F_{ij}\}$

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Complementarity equation

Equilibrium is due to the following mechanism:

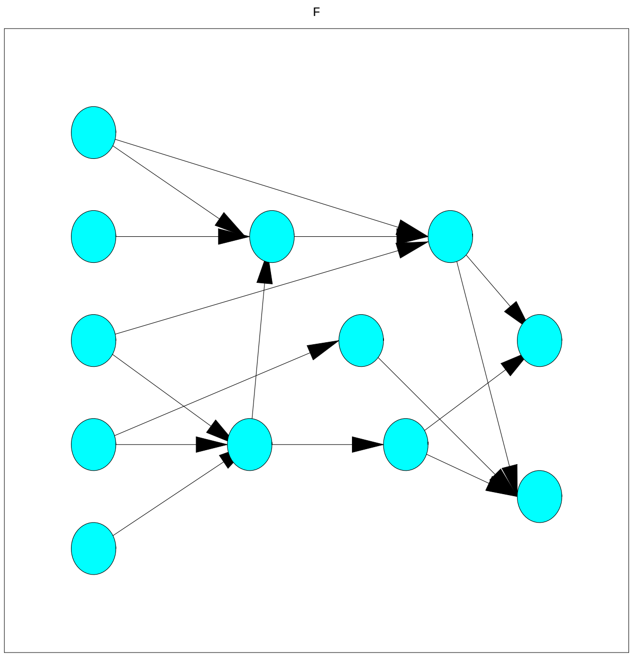
- if $F_{ij} > 0$, prey is not enough accessible; flows decrease; biomass of preys B_i increases; costs decrease.
- if $F_{ij} < 0$, there are many accessible preys; flows increase, B_i decreases, costs increase.

The system is moved towards a situation where

- either $X_{ij} > 0$ and $F_{ij} = 0$,
- or $F_{ij} > 0$ and $X_{ij} = 0$.

Definition 0.2 *Let $X^* = \{X^*_{ij}\} \in K$ (it satisfies the natural constraints, issued from the mass balance equations) and $F^* = \{F^*_{ij}\}$ the associated predation costs. Then it is a solution of the complementarity equations, if for all i and j, one has $X^*_{ij} > 0$ and $F^*_{ij} = 0$, or $F^*_{ij} > 0$ and $X^*_{ij} = 0$.*

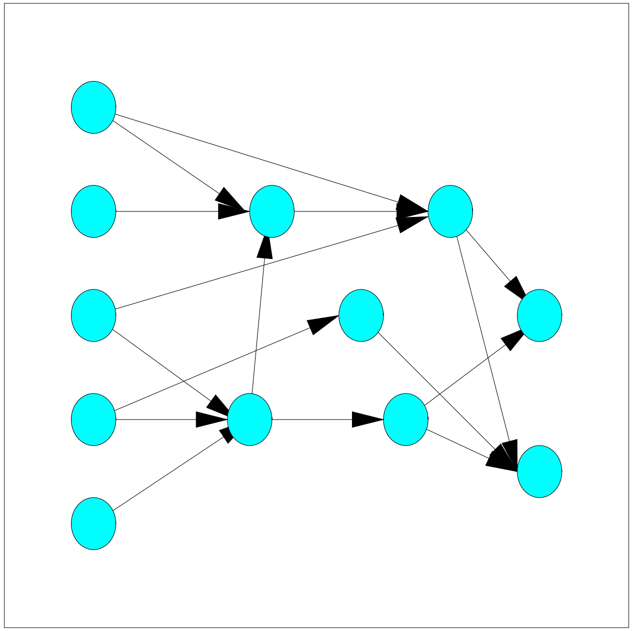
Input/output trophic systems



Assumptions

- We restrict ourselves to "input/output" oriented systems, that is we assume that the network is "oriented" between an input part and an output part. There are no loop, for example no cannibalism.
- Predation costs are based on a ratio-dependance principle. On a path ij, predation cost is defined by : $F_{ij} = \phi_{ij} - \kappa_i B_i + \lambda_j B_j$.
- We consider compartments corresponding to fisheries using exactly the same formalism as for species compartments

Input/output trophic systems



Mass balance equations :

- $\gamma_i(E_i + \sum_j X_{ji}) = \mu_i B_i + \sum_j X_{ij}$
- $B_i = (\gamma_i(E_i + \sum_j X_{ji}) - \sum_j X_{ij})/\mu_i$

Complementarity equation :

- $X_{ij} > 0 \Rightarrow \phi_{ij} - \kappa_i B_i + \lambda_j B_j = 0$
- $X_{ij} = 0 \Rightarrow \phi_{ij} - \kappa_i B_i + \lambda_j B_j \geq 0$

K is the set of flows X_{ij} such that

- $X_{ij} \geq 0$
- $B_i \geq 0$

Input/output trophic systems

Mathematical approach

Theorem 0.3 *K is a polyhedron in the set of flows. Moreover K is compact (closed and bounded).*

Theorem 0.4 *To $X = (X_{ij}) \in K$ we associate $F(X) = (F_{ij})$. Then $X \to F(X)$ is a linear function*

Theorem 0.5 *X^* is an equilibrium state if and only if it satisfies the affine variational inequality $F(X^*).(X - X^*) \geq 0$ for all $X \in K$*

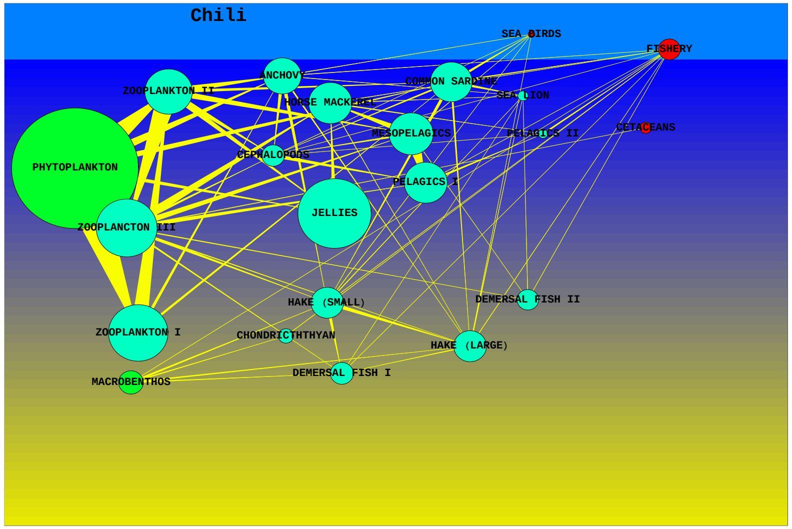
Theorem 0.6 *Solution set of the affine variational inequality is not empty*

Theorem 0.7 *Solution set of the affine variational inequality can be computed using projection algorithms*

Nagurney. Economic networks. A variational inequality approach

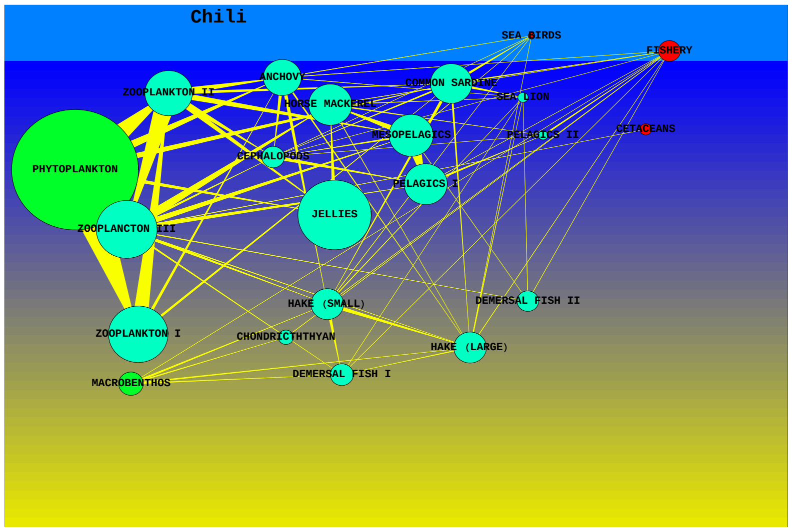
A pelagic system

The coastal pelagic ecosystem of Chile



S. Neira

Control Mid Trophic



	predation costs ϕ_{ij} for small pelagic j X	predation costs ϕ_{jk} for predator k of small pelagic j X
1	0.5	2
2	0.53	0.186
3	0.57	0.174
...	...	...
18	0.174	0.57
19	0.186	0.53
20	2	0.5

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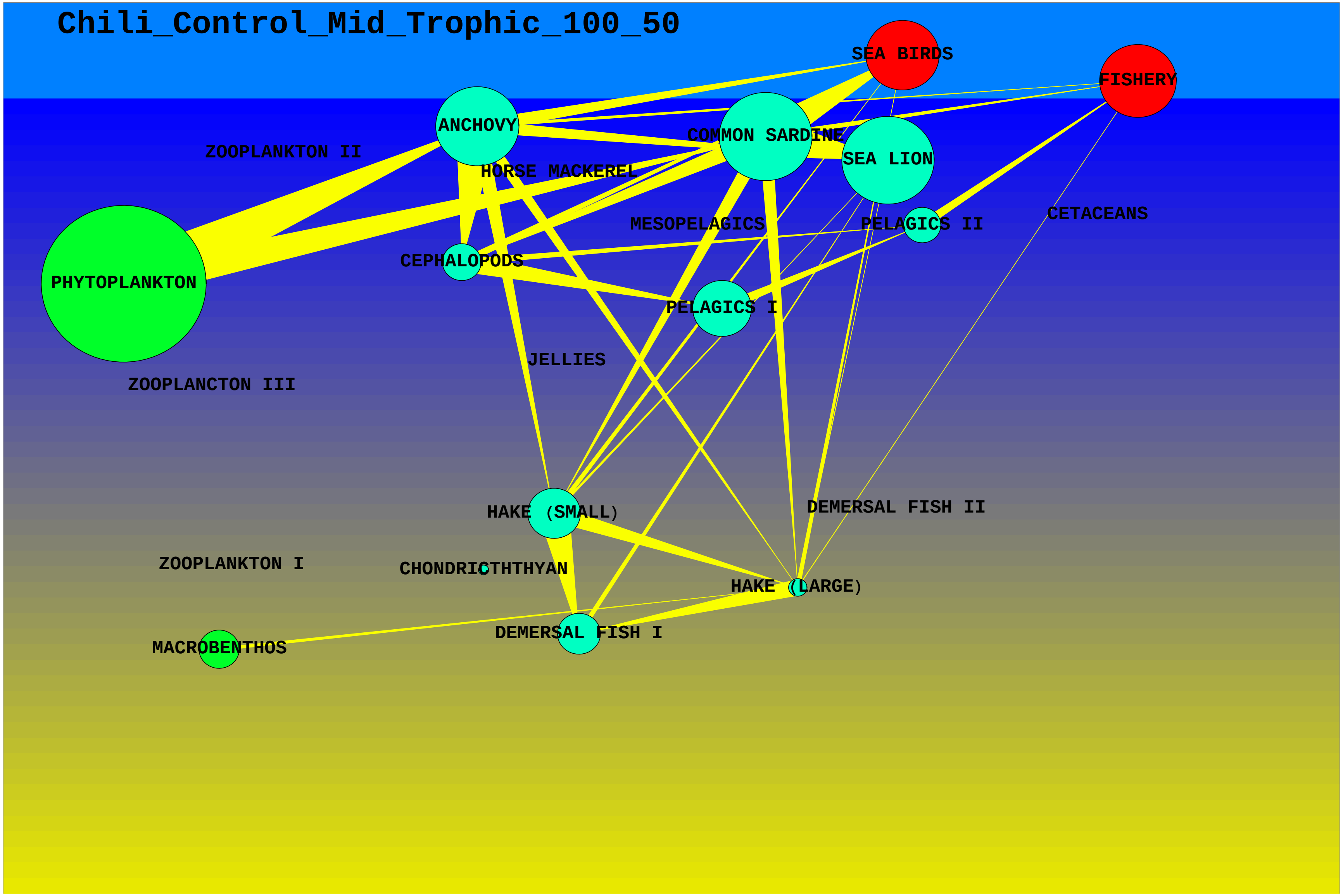

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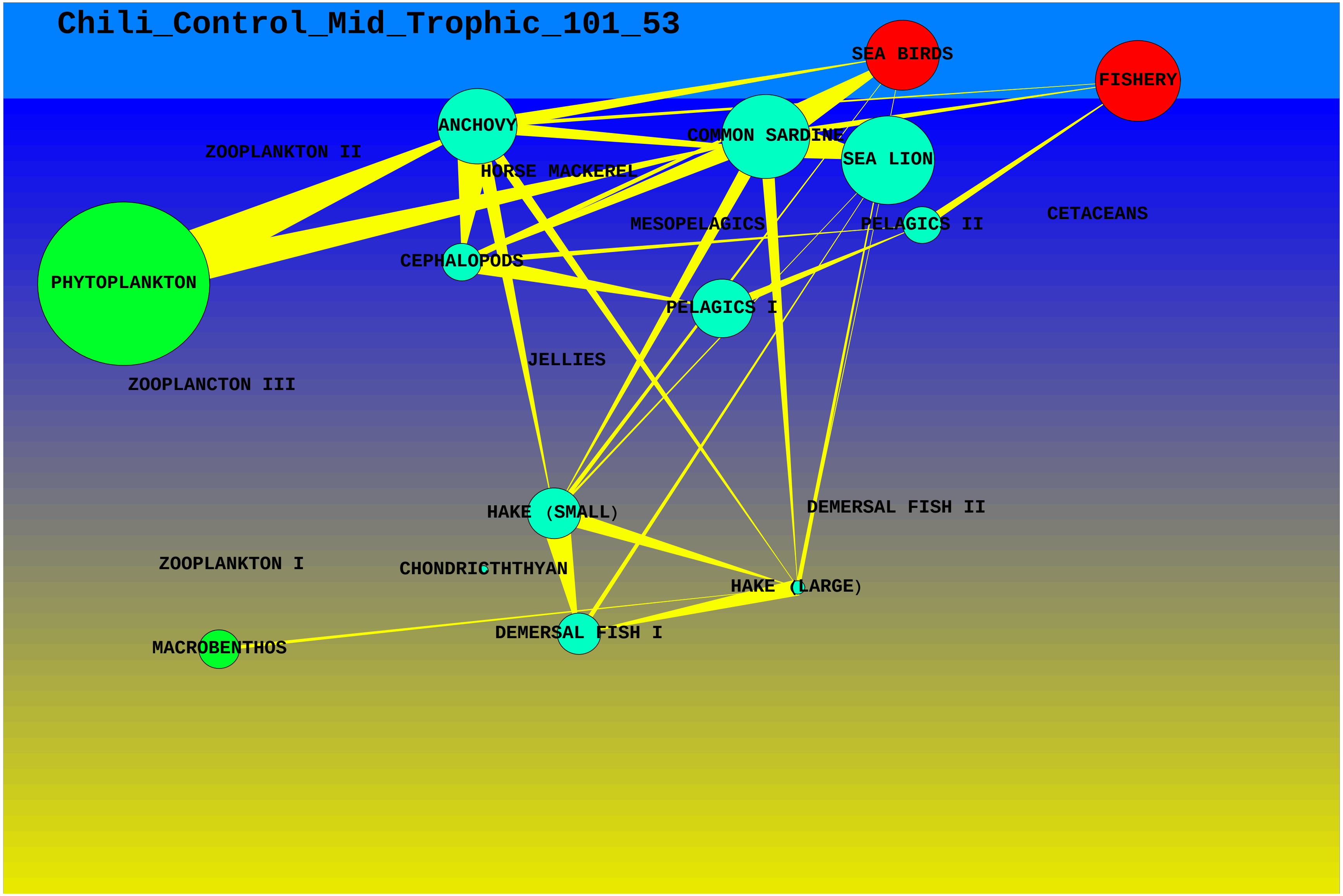

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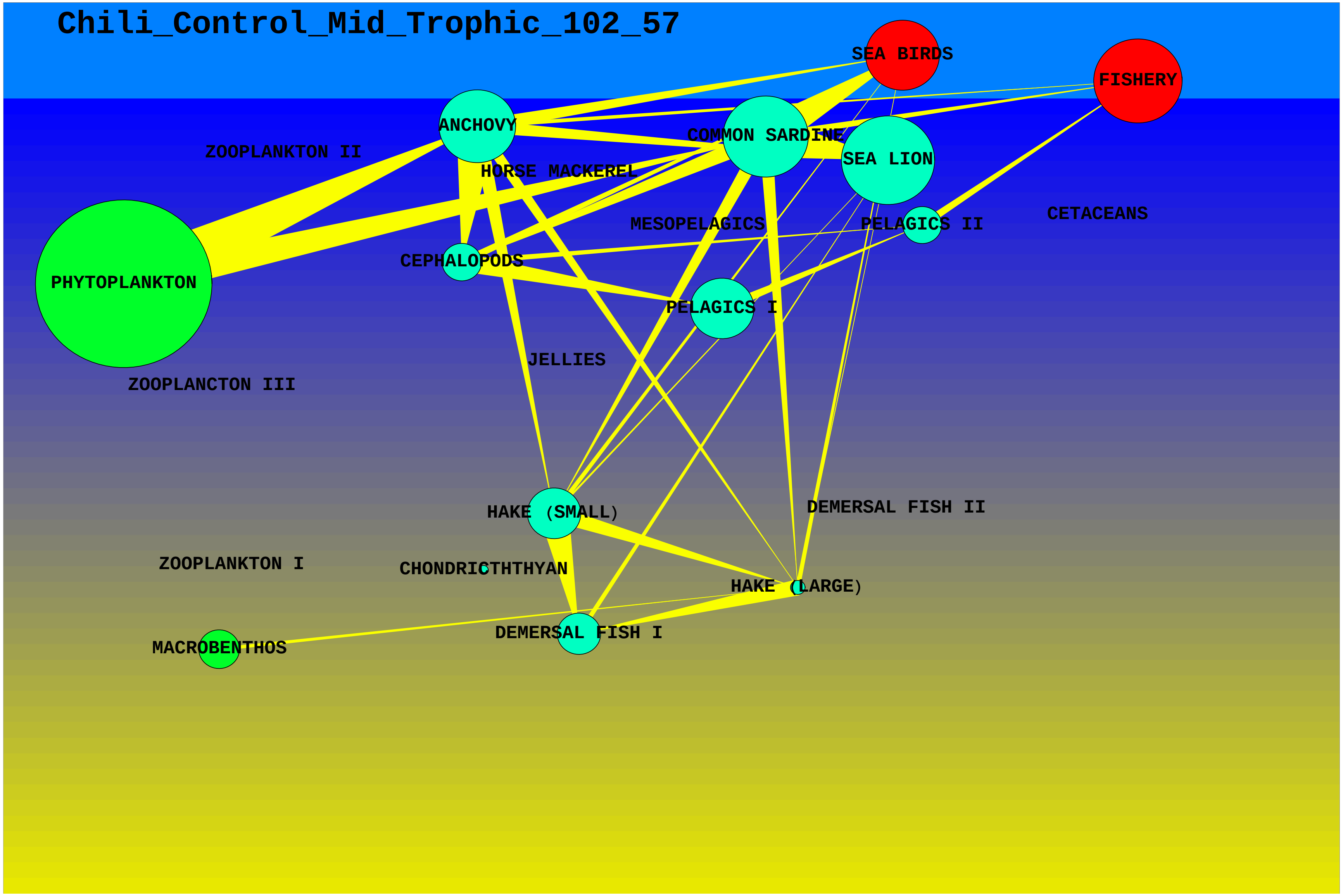

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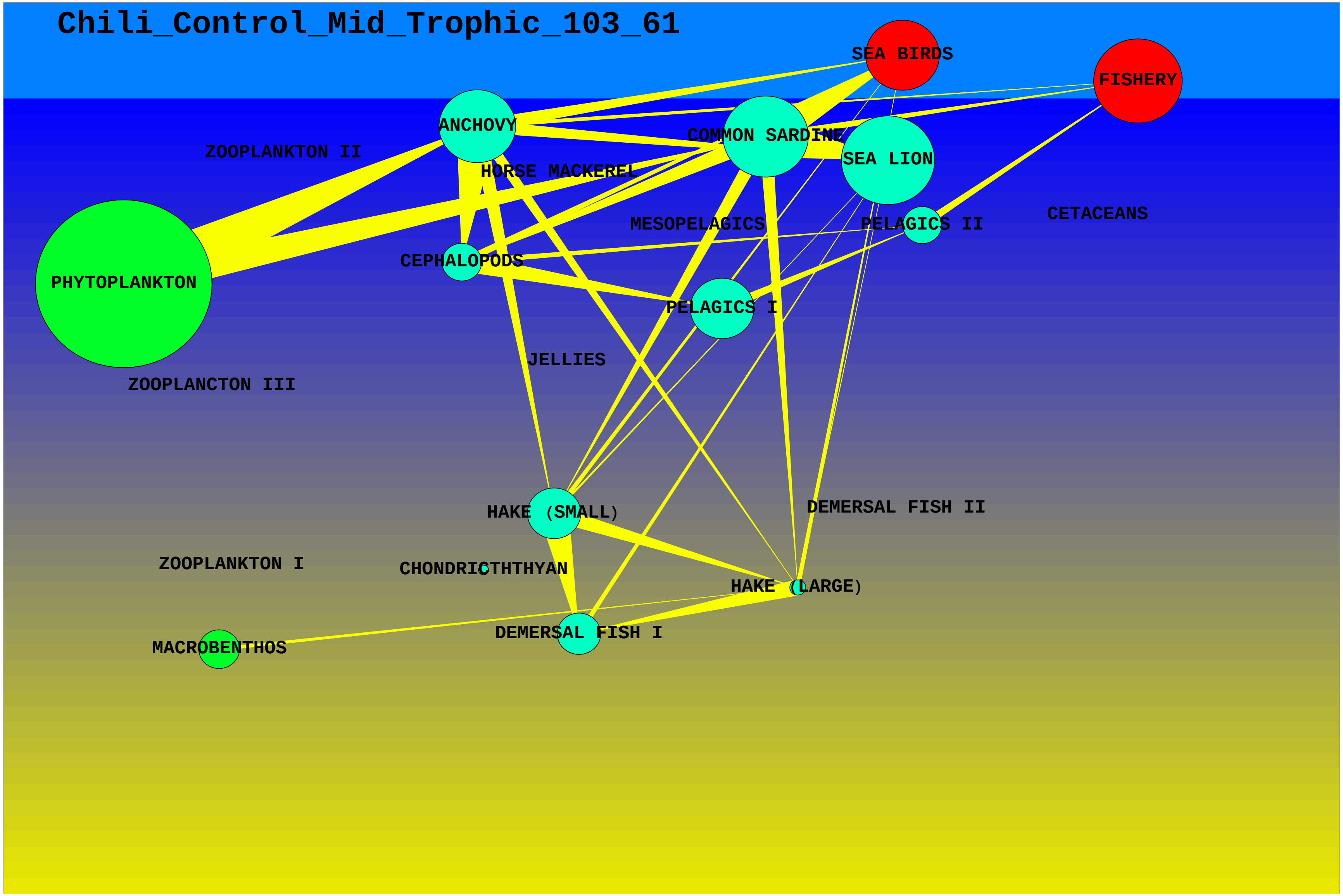

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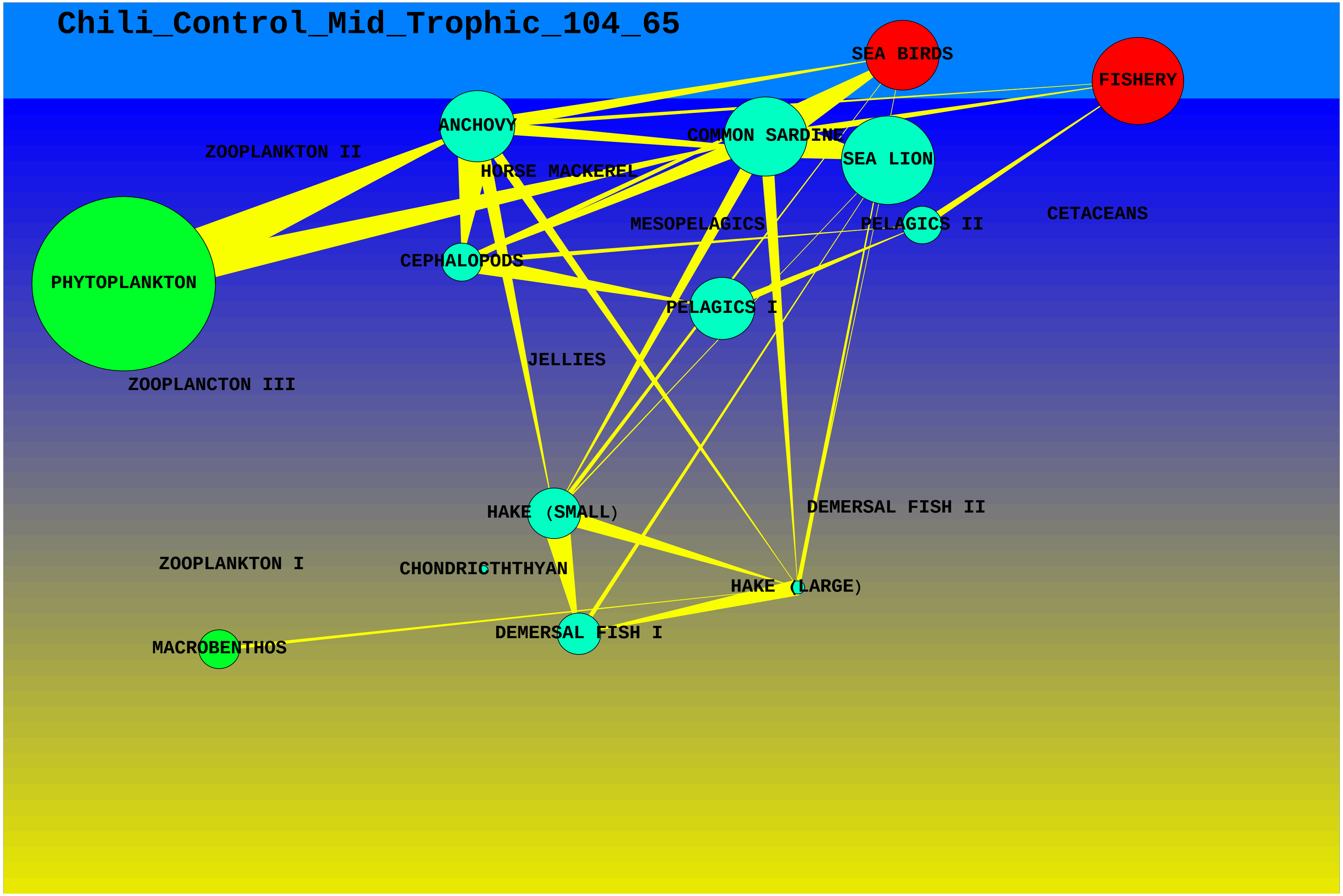

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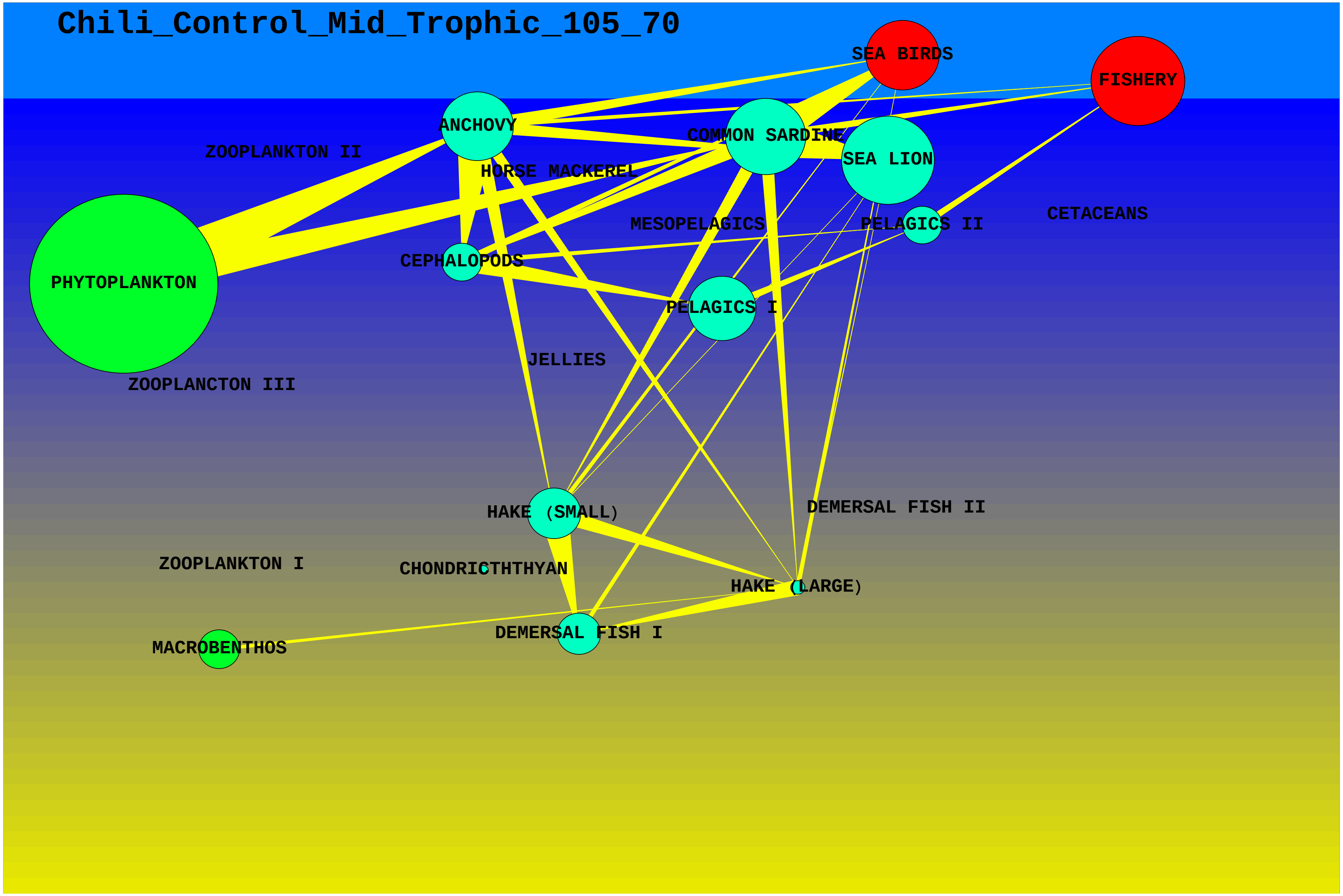

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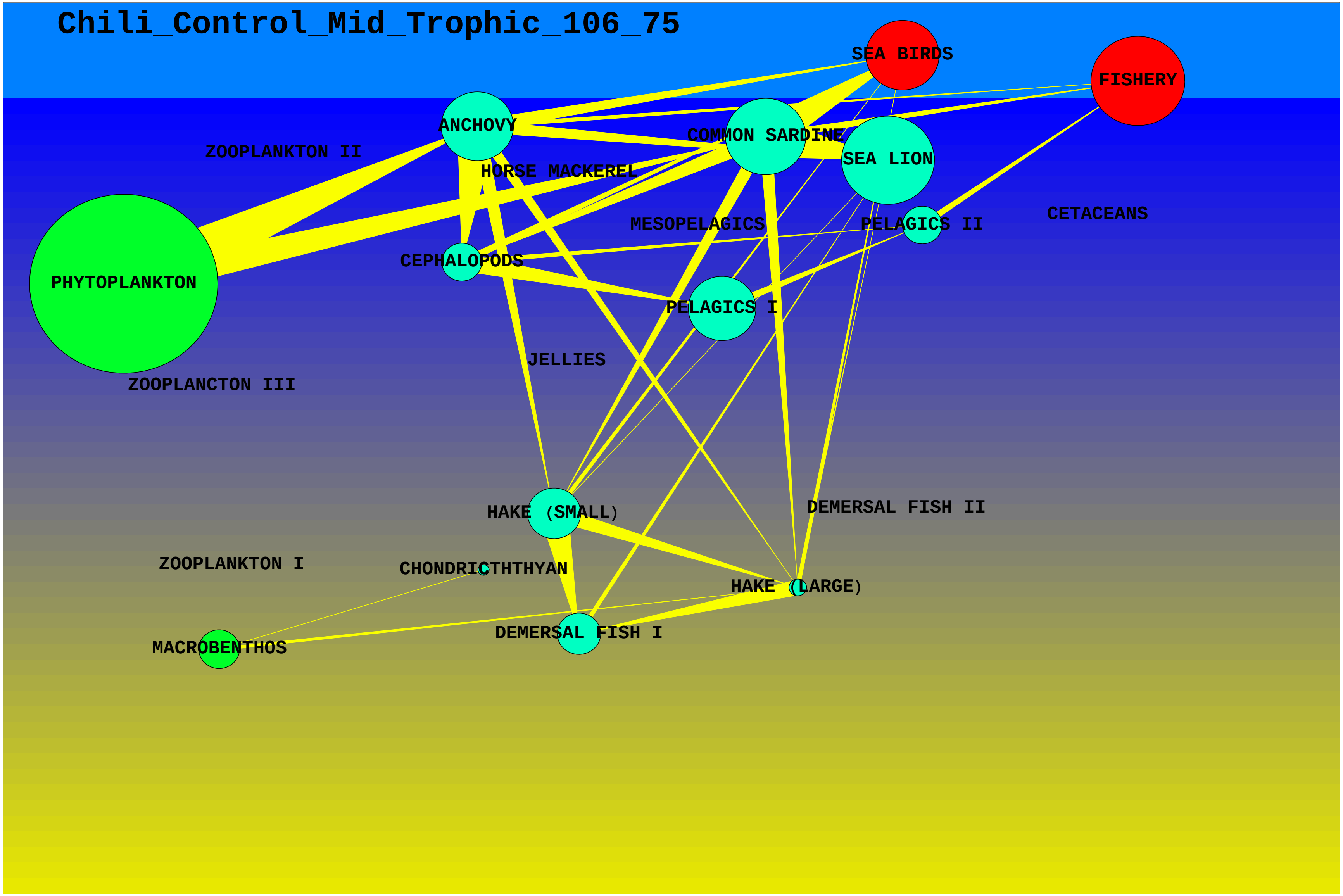

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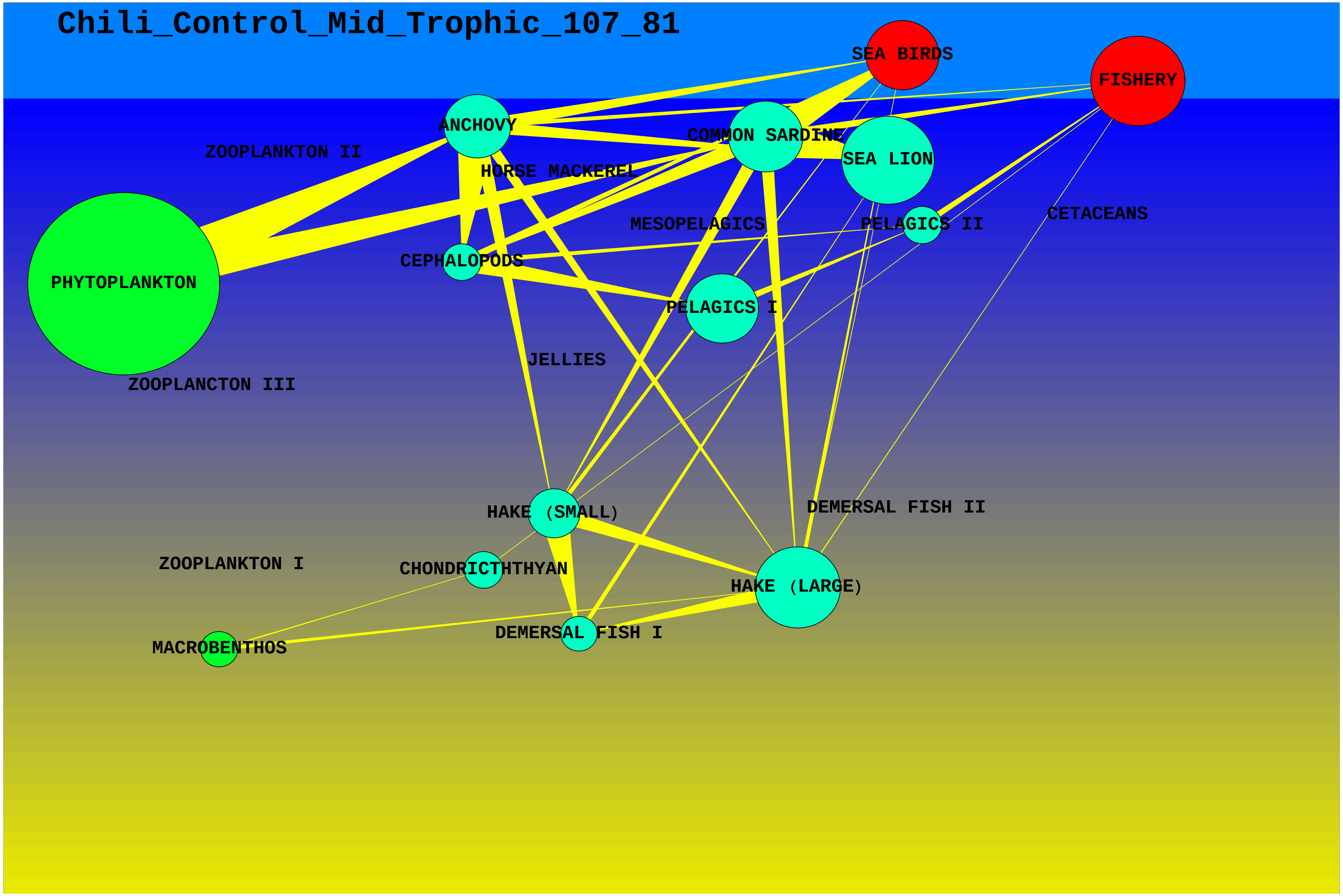

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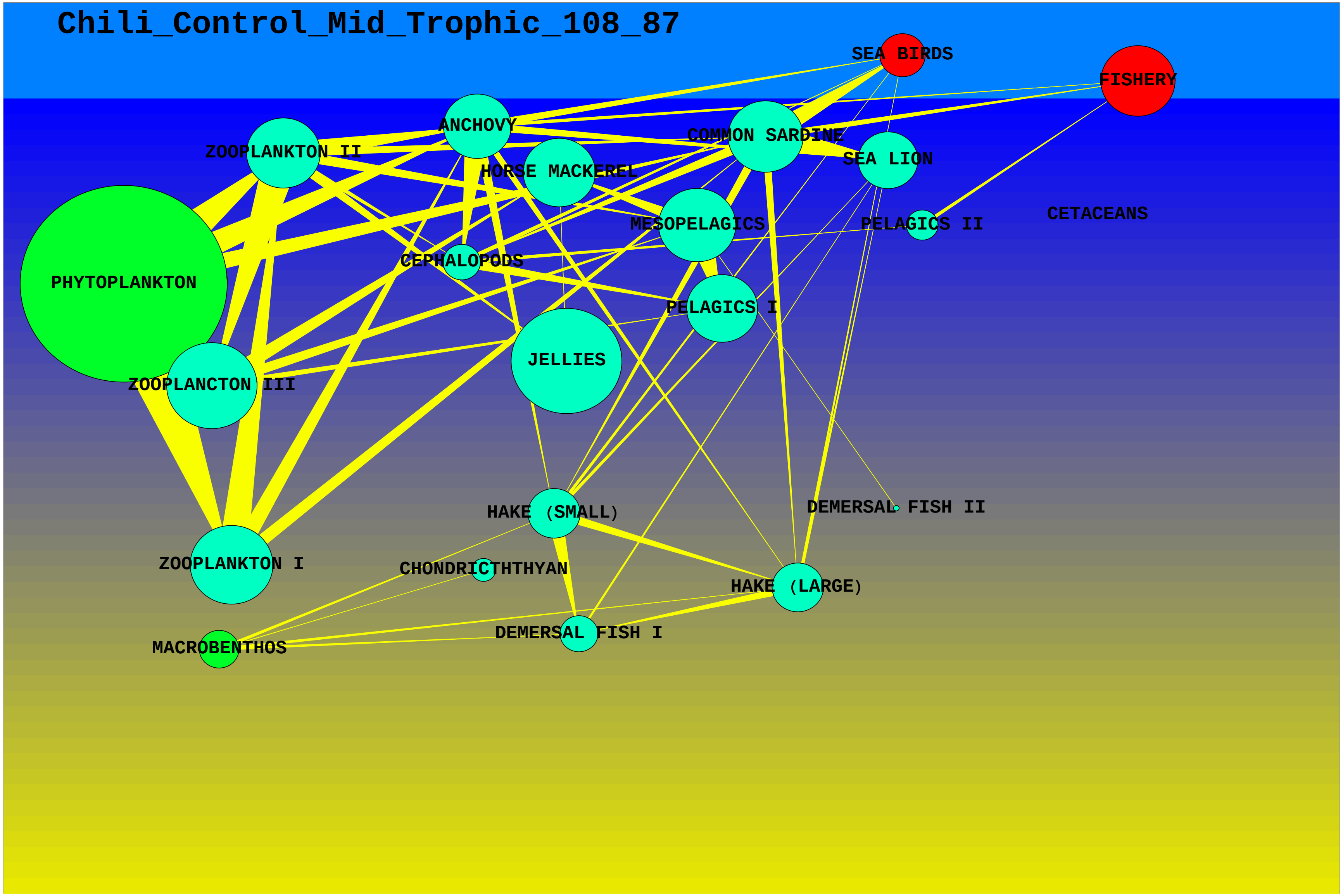

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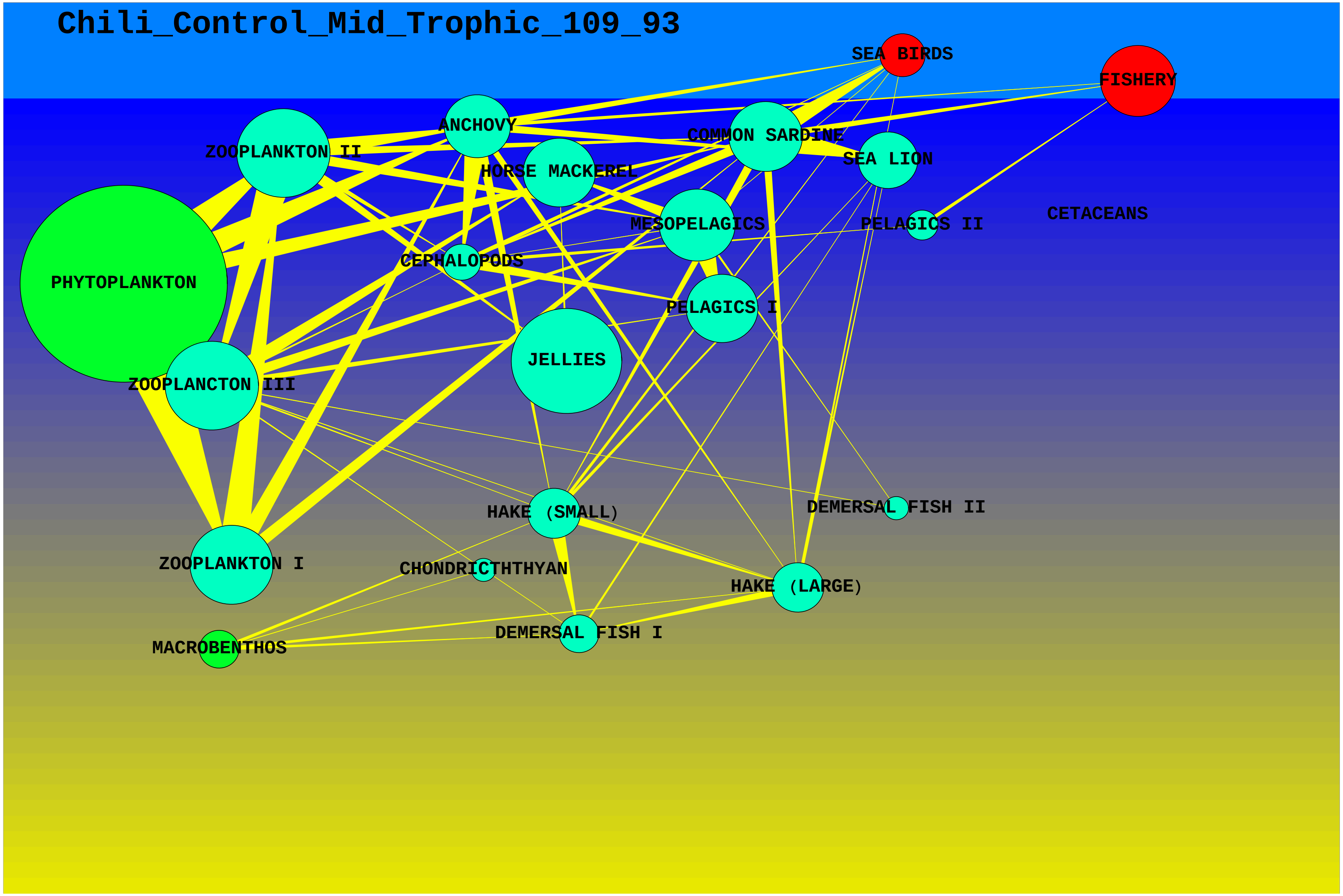

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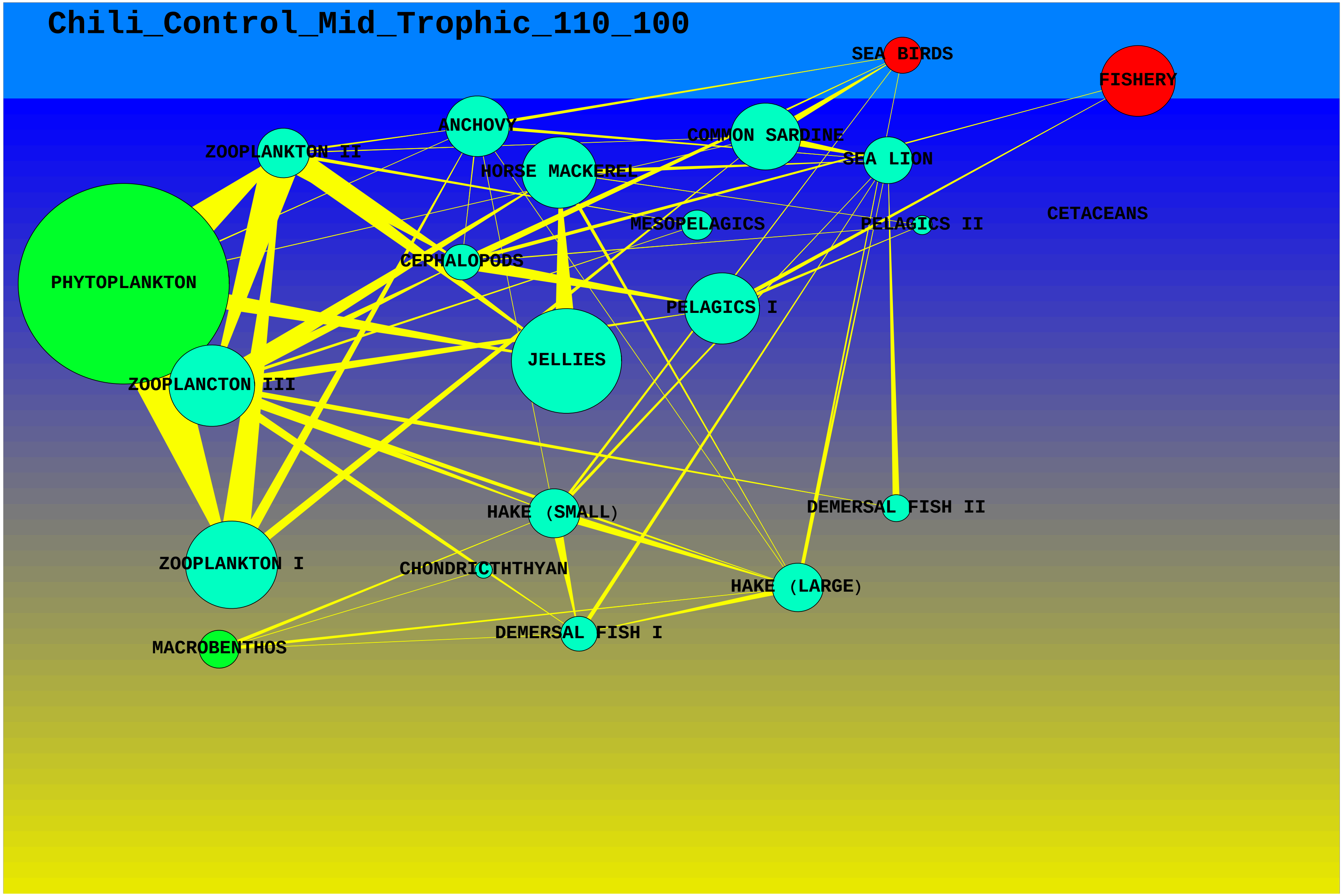

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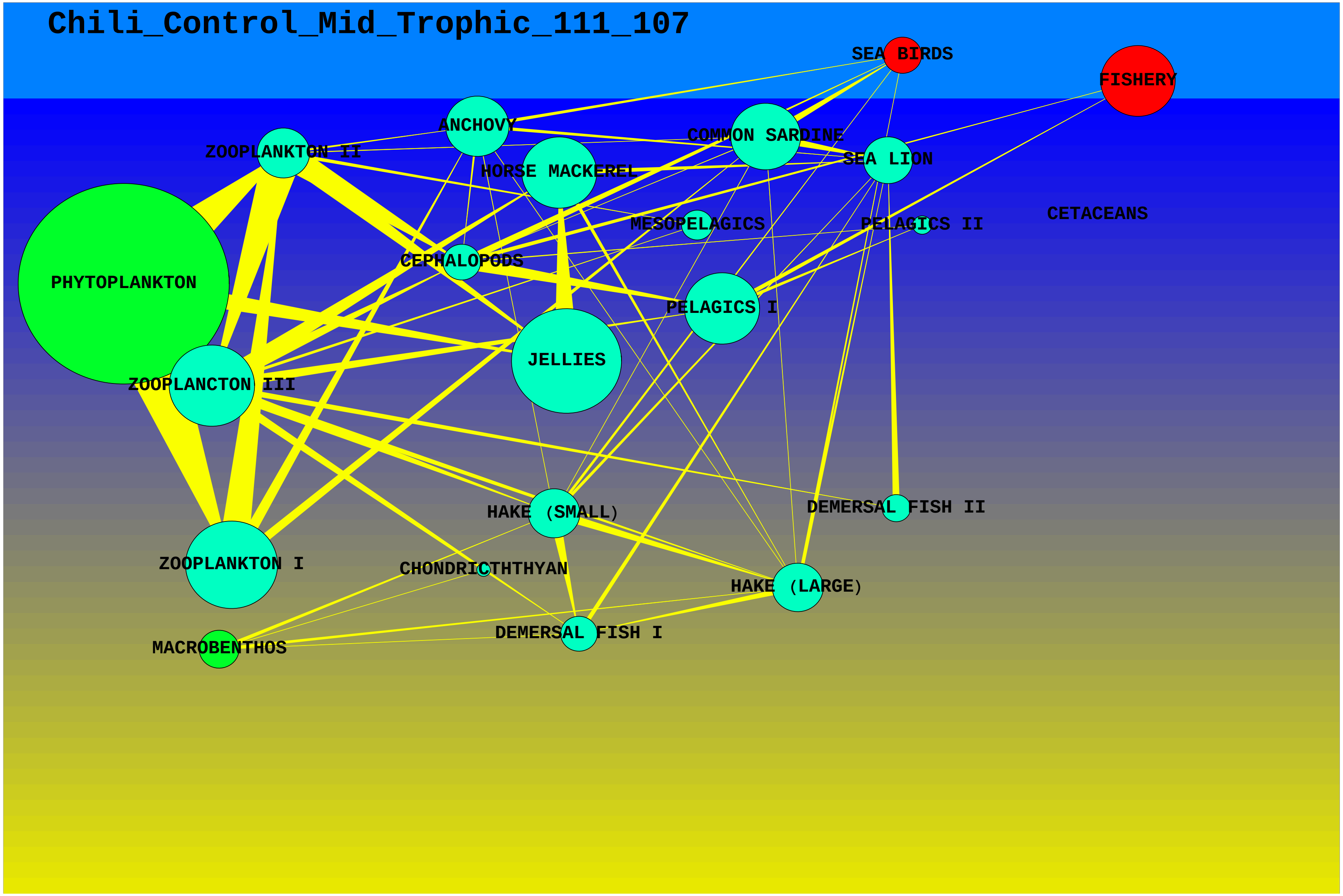

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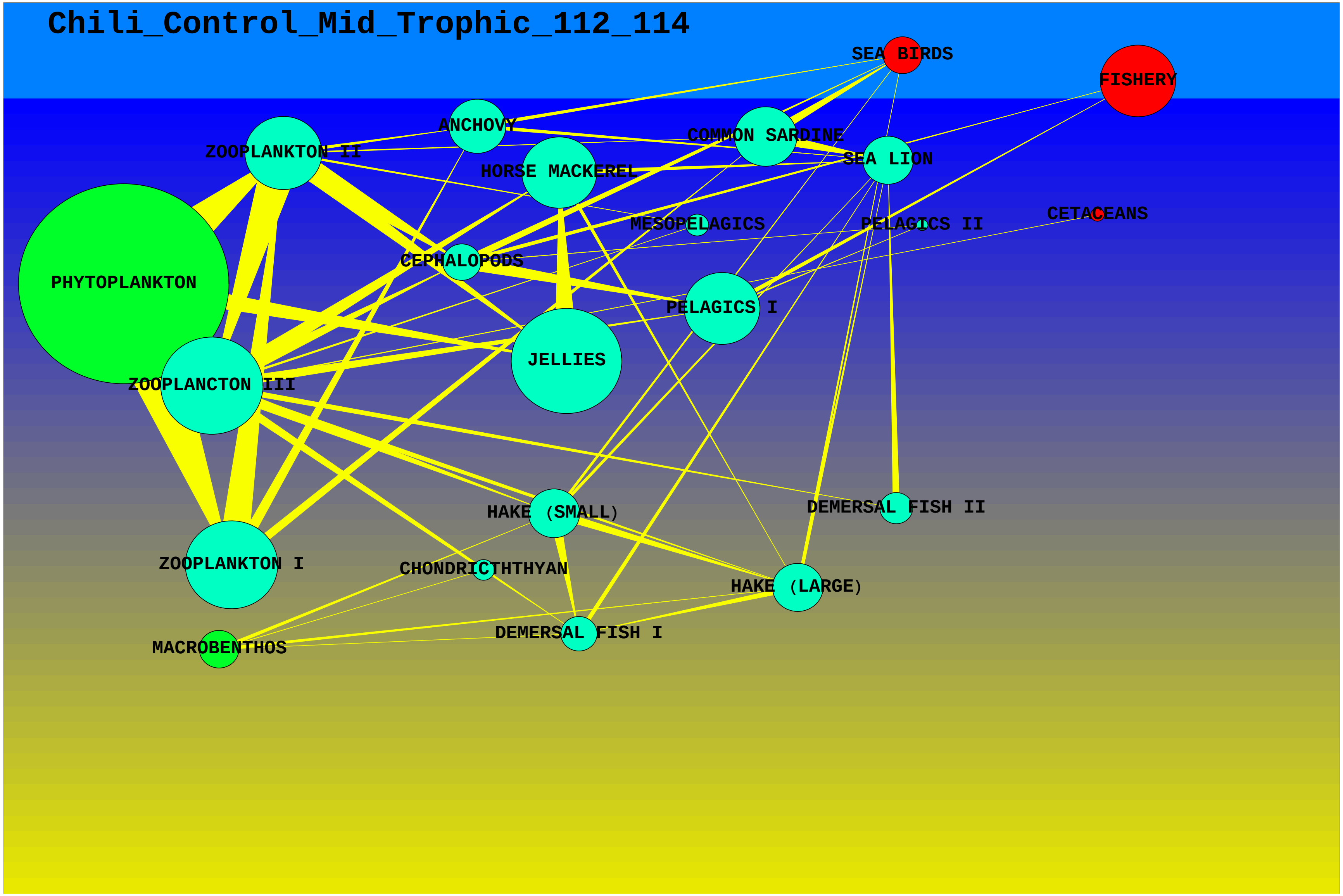

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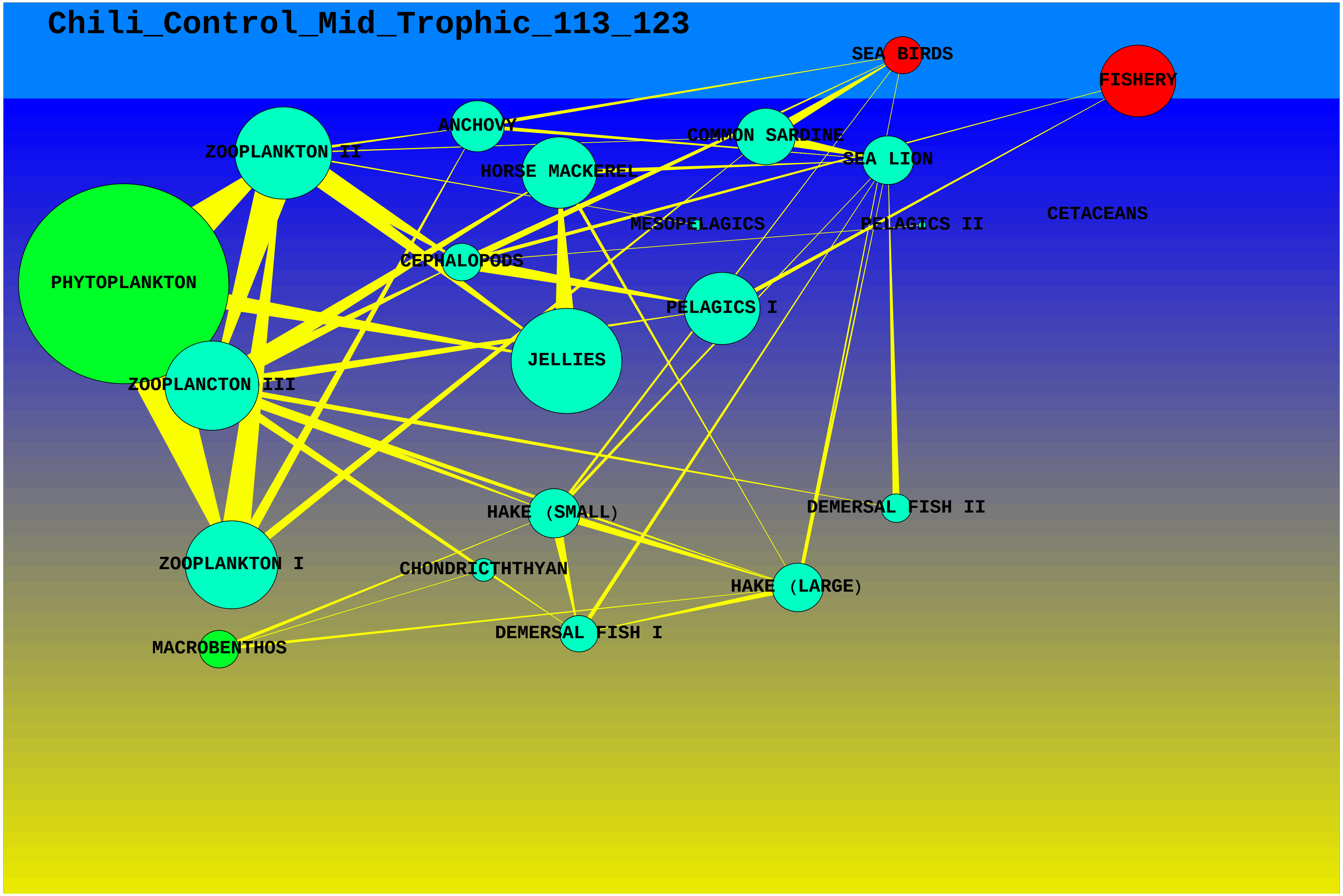

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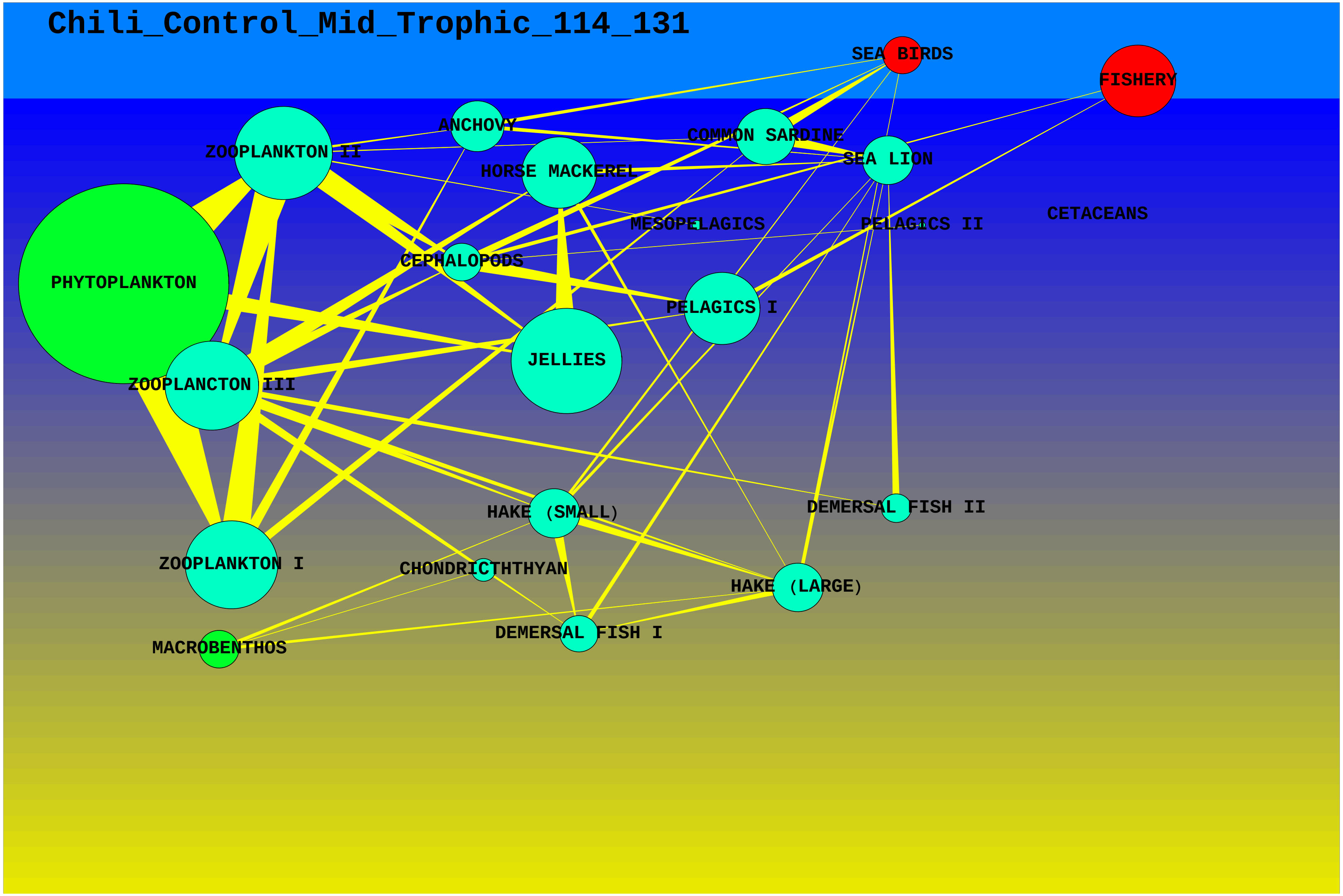

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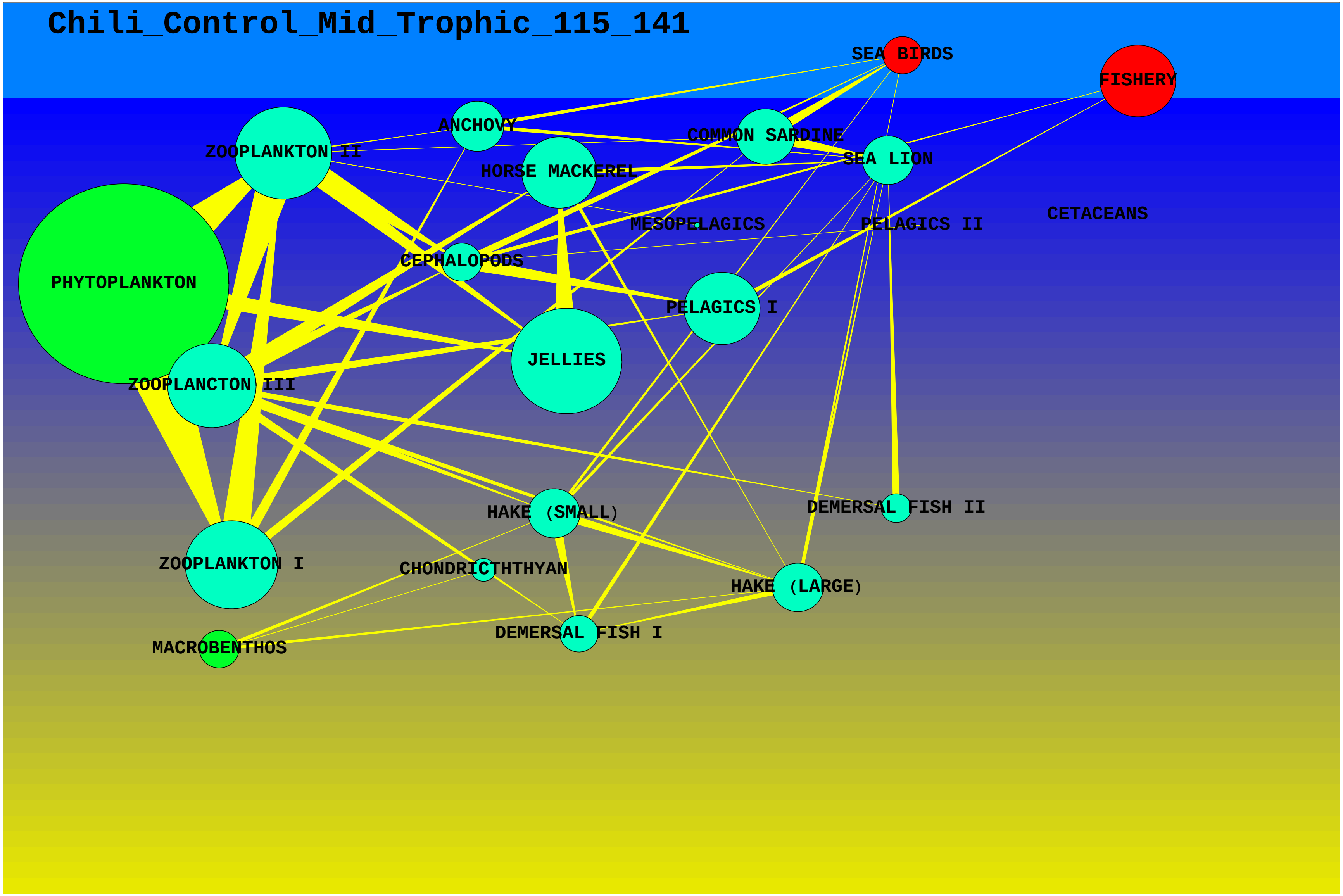

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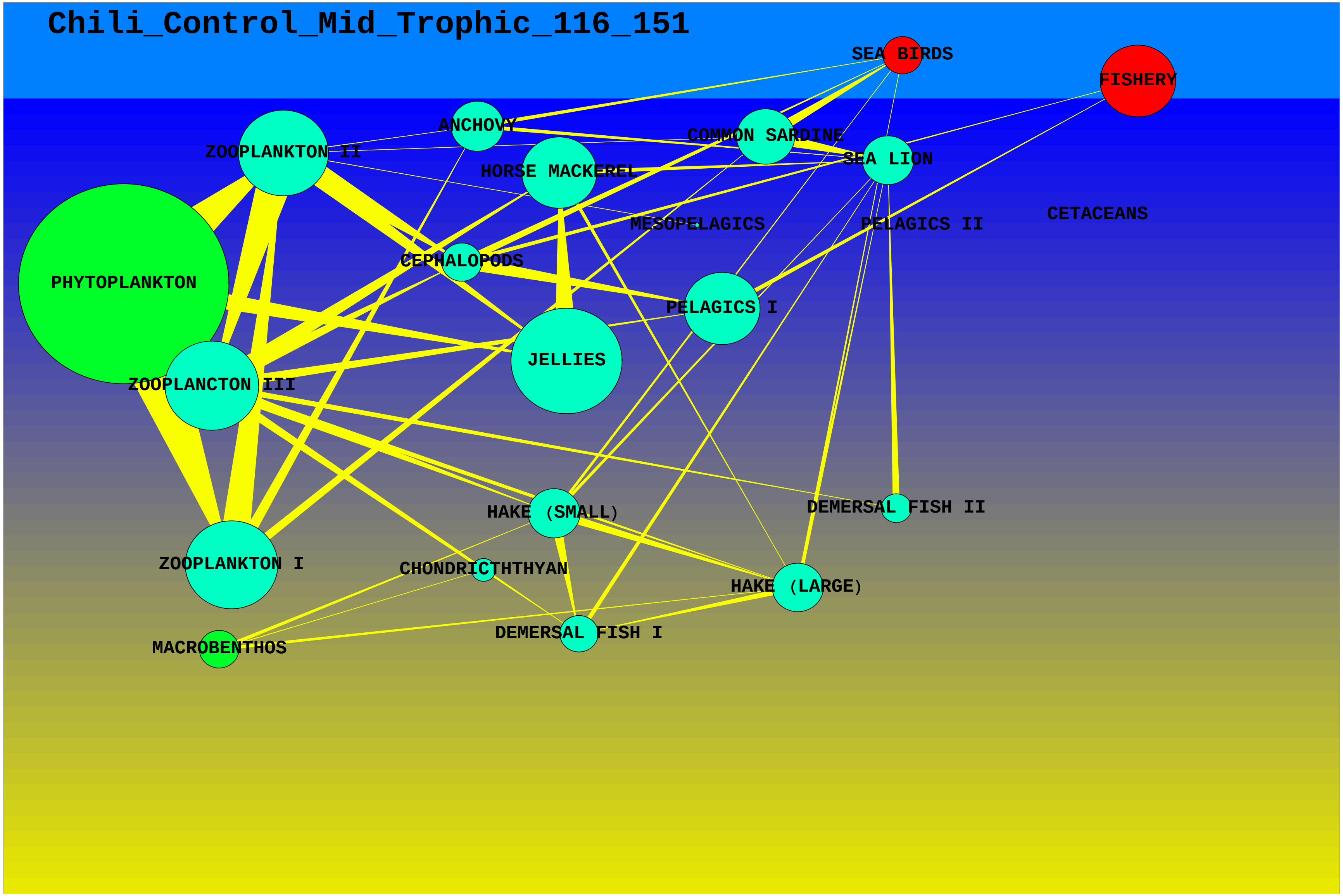

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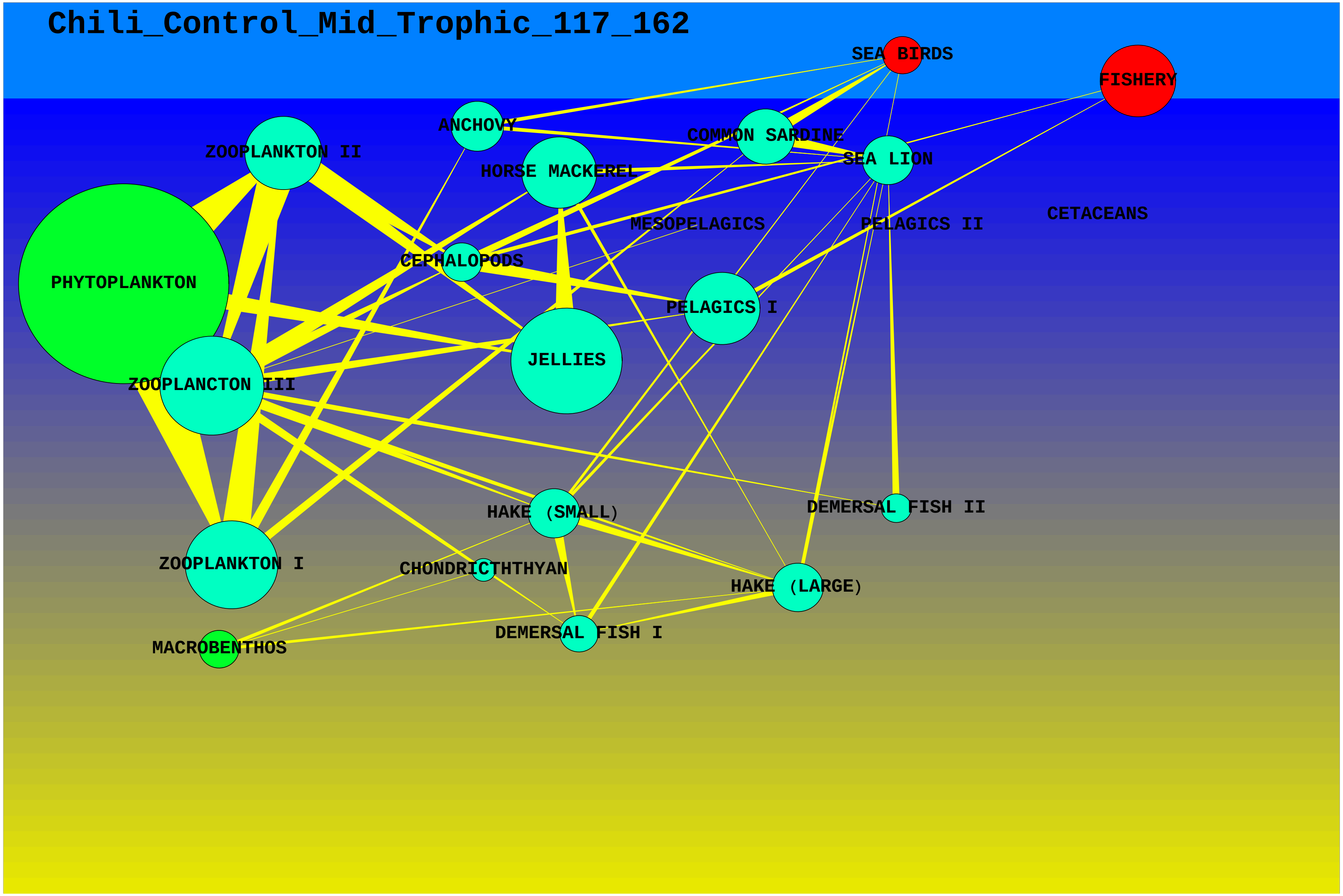

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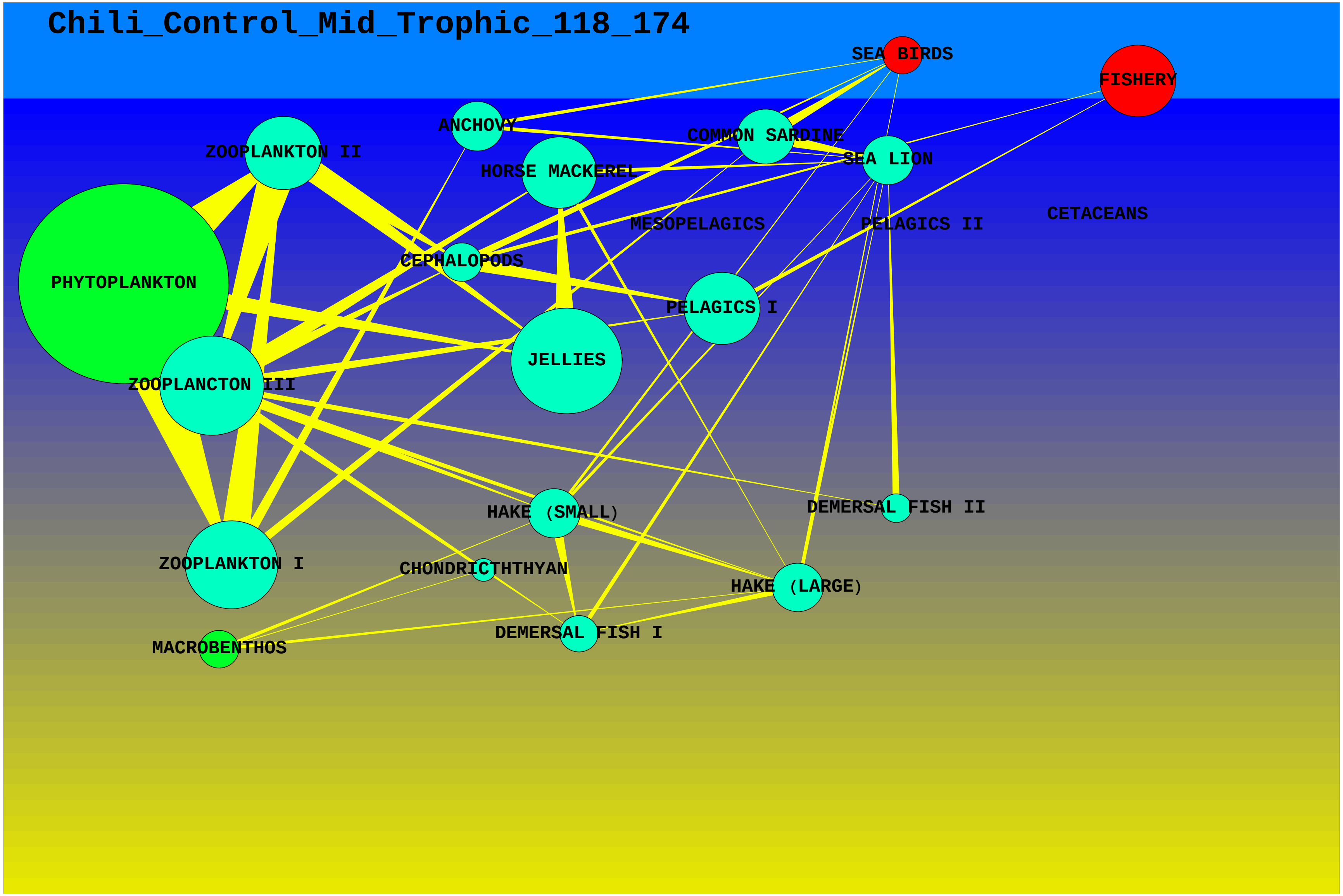

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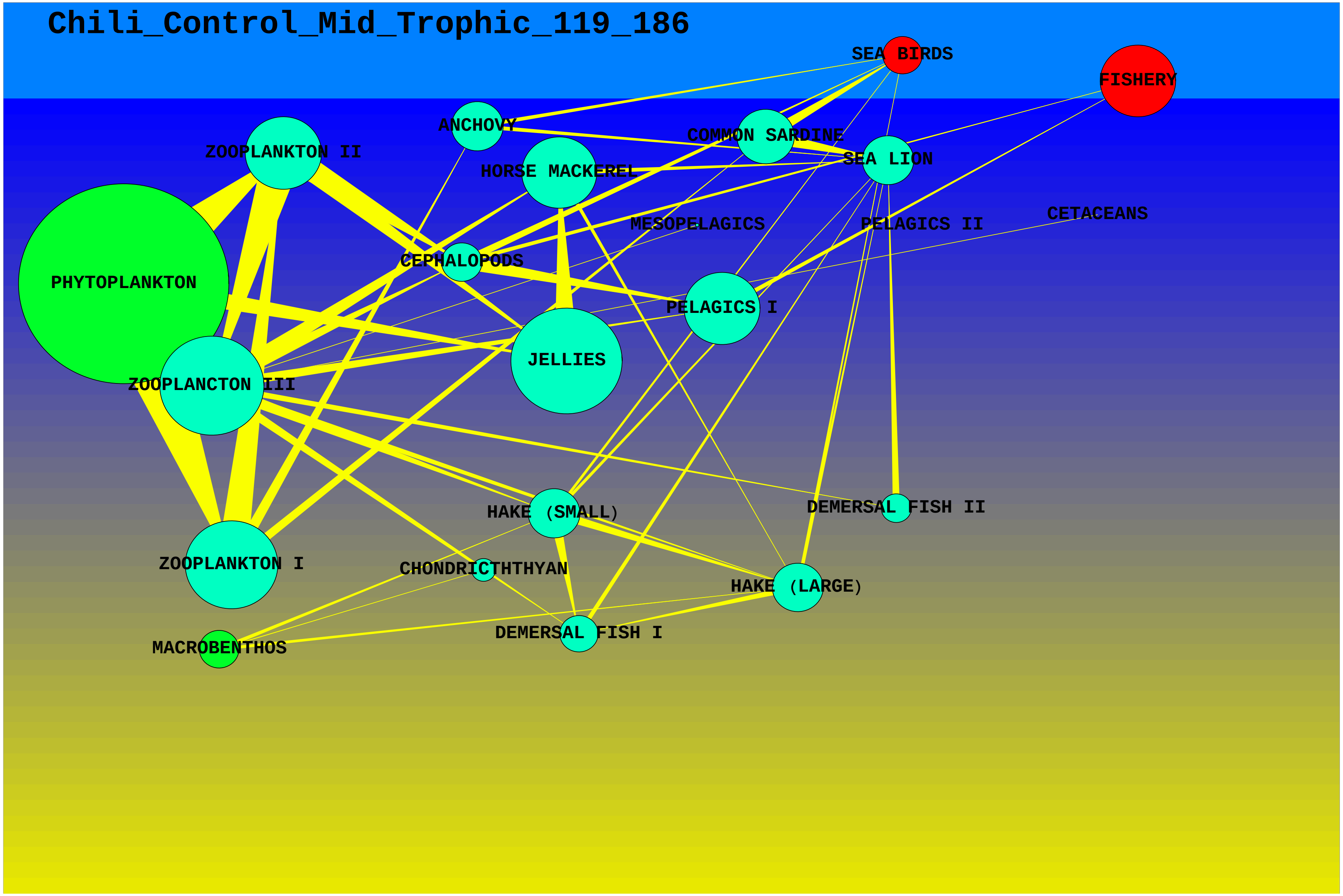

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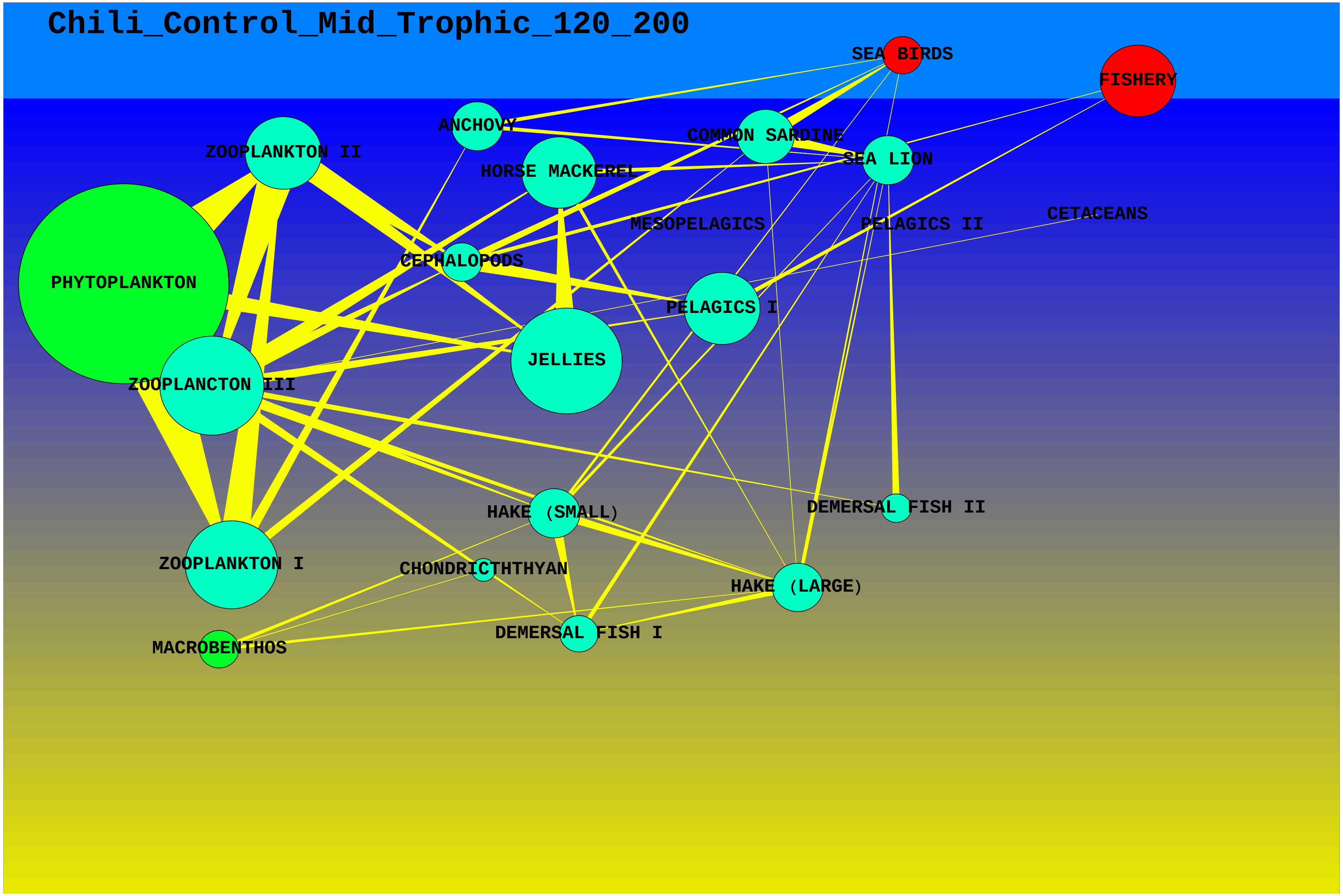
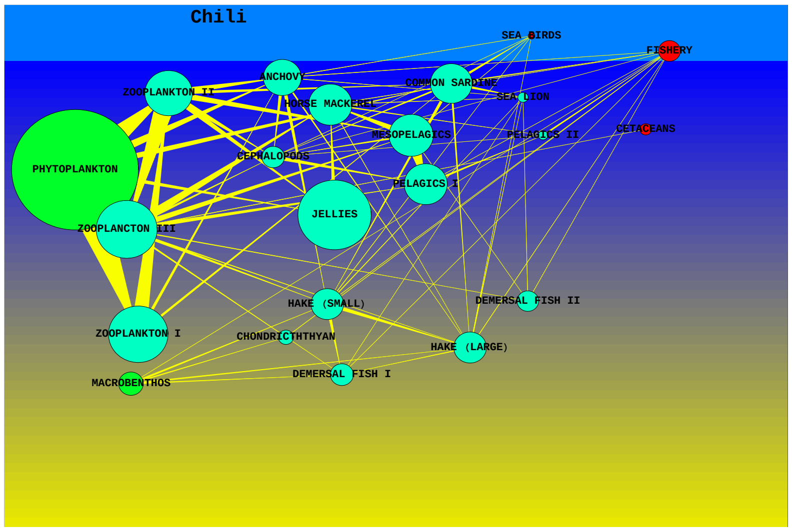


Determining keystone species



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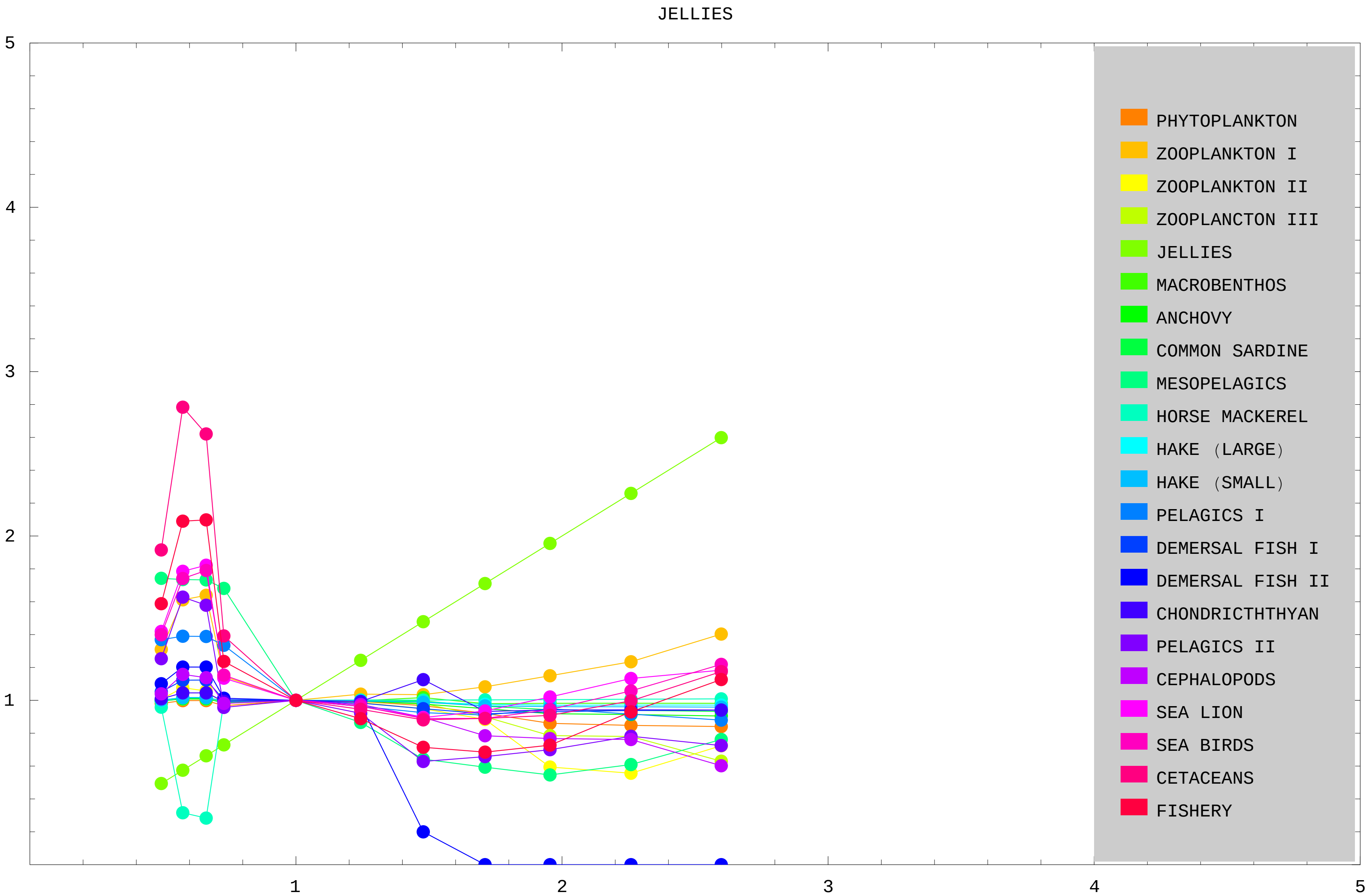
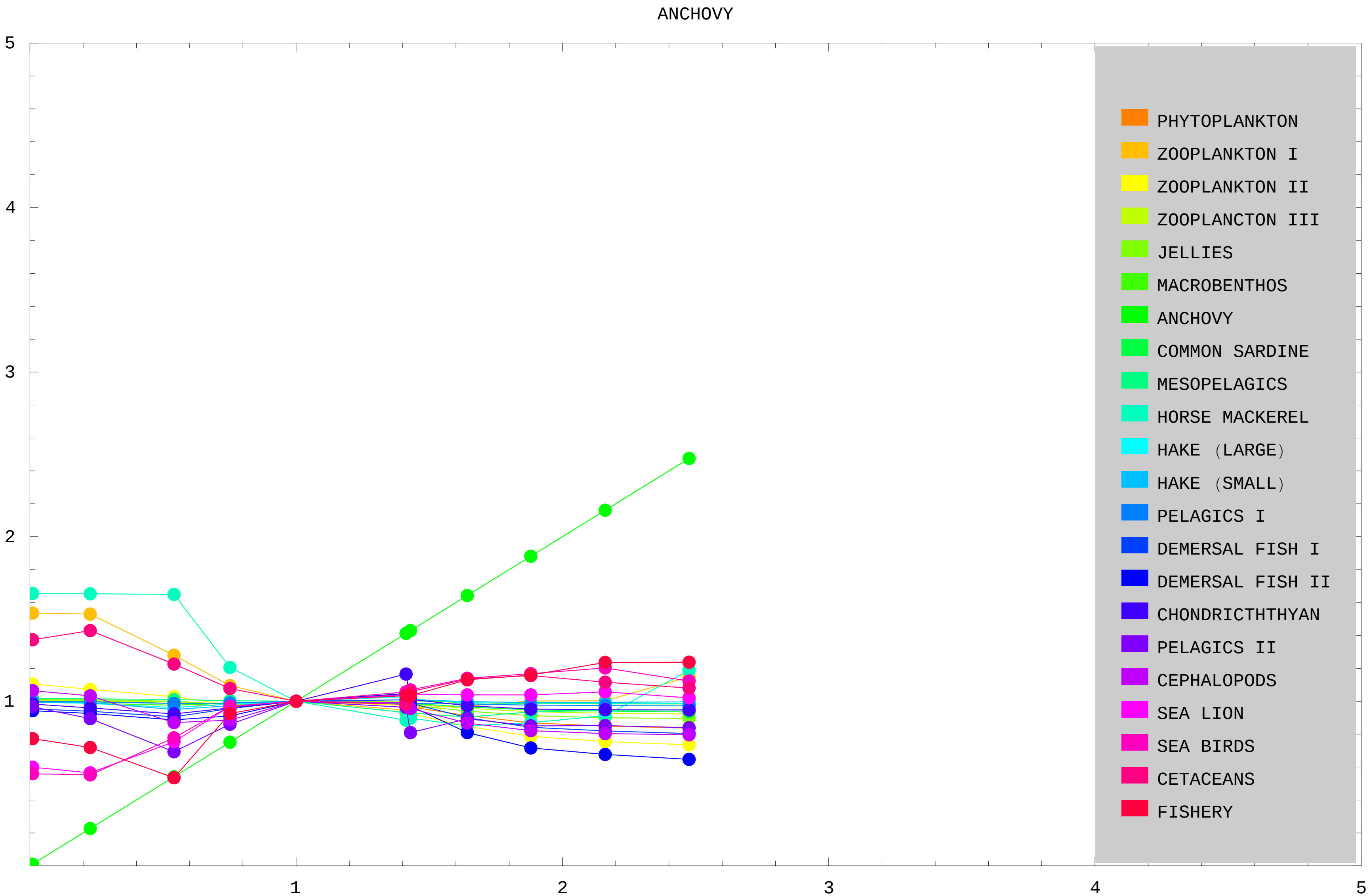
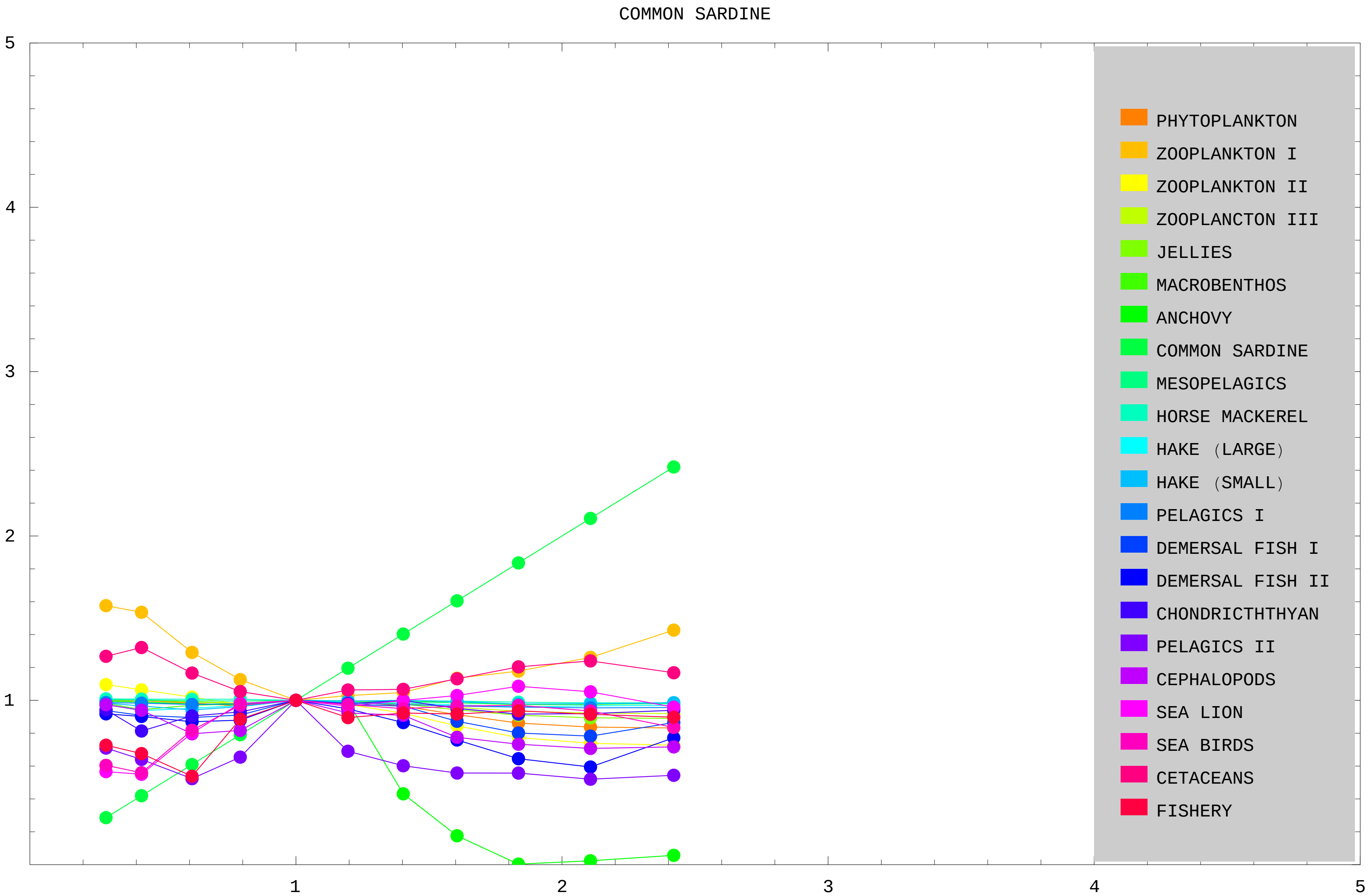
Keystone species



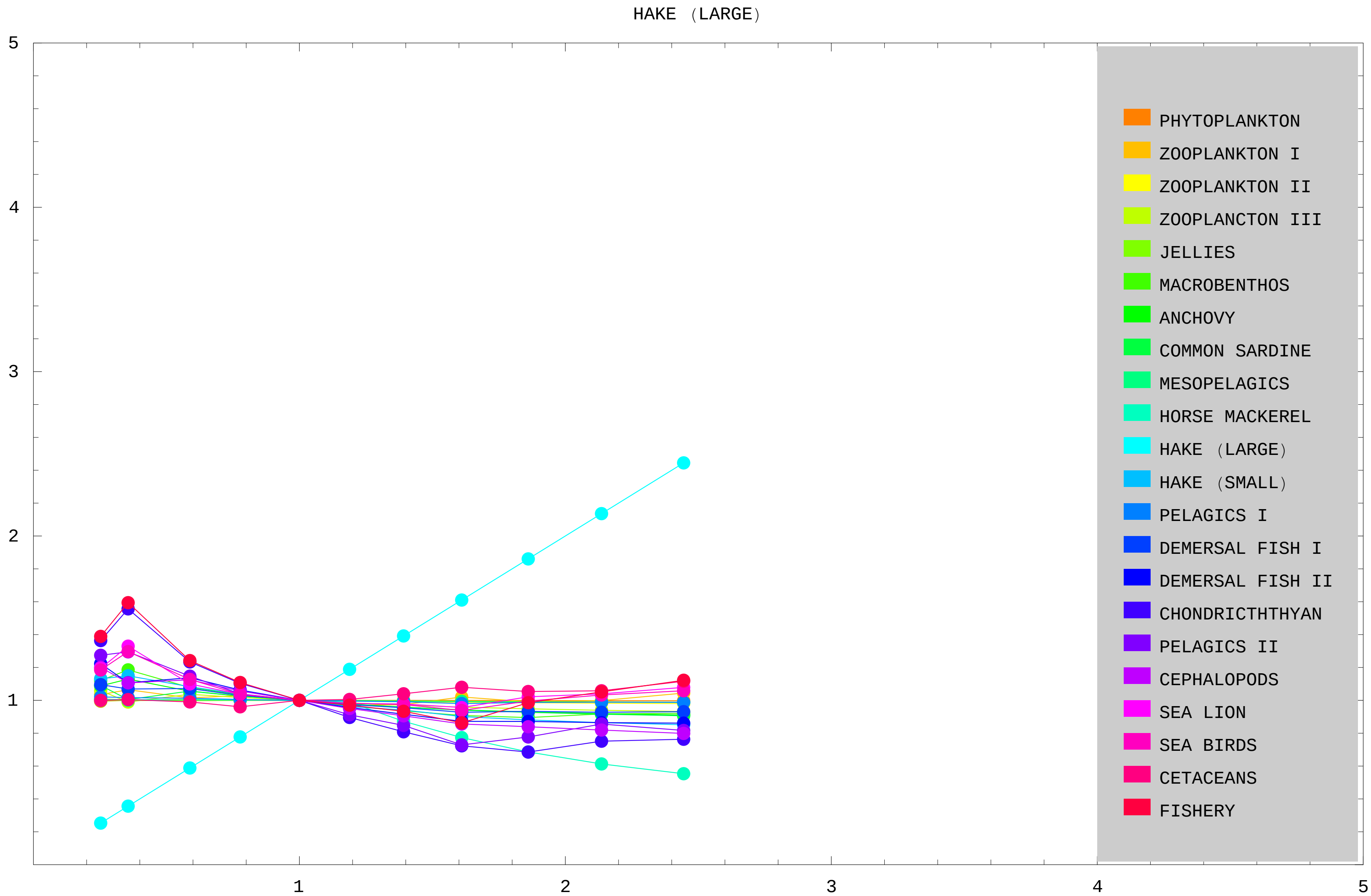
Keystone species



Keystone species

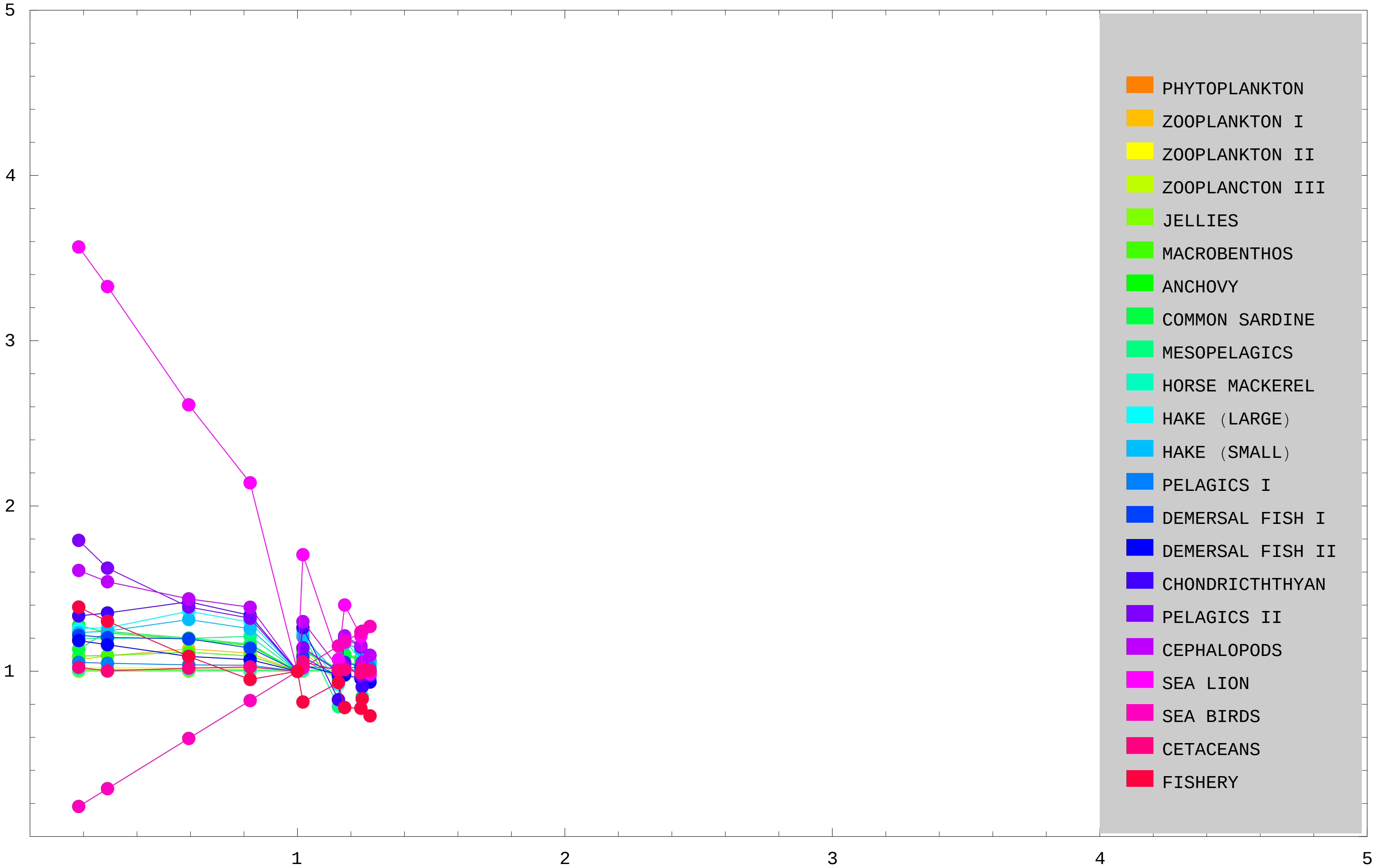


Keystone species



Keystone species

SEA BIRDS



Discussion

- Possibilities : a simple formalism allows representing specific dynamics of trophic systems, cascades, shifts, controls
- Difficulties :
  - Parametrization
  - Computing
- Mixing dynamic systems approach and economic approach
- Emphasis on accessibility, intra specific competition and predation costs.

- Paradigm : Global change $\longrightarrow$ Change in precipitation $\longrightarrow$ Increase of stratification $\longrightarrow$ Decrease in winter mixing $\longrightarrow$ Decrease in nutrient supply $\longrightarrow$ Decrease in phytoplankton $\longrightarrow$ Decrease in zooplankton.
- However what's if : Increase of stratification $\longrightarrow$ Changes in accessibility.

Parametrization

- From mass balance trophic models:
  1. Biomass B_i
  2. Flows X_{ij}
  3. Energetic input of autotroph species E_i
  4. Trophic assimilation efficiency γ_i
  5. Natural mortality rate μ_i
- Equilibrium assumption : $\phi_{ij} = \kappa_i B_i + \lambda_j B_j$
- Strong equilibrium assumption $\kappa_i = \lambda_i \gamma_i$
- Intraspecific competition λ_i related to gregarious (schooling) behavior