Network-based food availability affects the keystoneness of predators and functional diversity of the marine food web

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ABSTRACT: Marine predators play an important role in food webs, and their food availability affects the structure and function of marine ecosystems. In this research, we calculated 6 network-level topological indices and the keystone index for predator nodes. We also quantified the functional homogenization degree of the food web by using a measure of functional diversity. We simulated food availability variation by adding or deleting a link to each predator node and recalculating the above indicators in turn when generating a new network. We found that increased food availability can increase the topological complexity in food webs, yet top predators show less plasticity in network structure than lower predators. The resulting variability in average path length may be related to the threshold at which omnivory affects food web stability. When food availability ranges from 0.3 to 0.6, predators at higher trophic levels may have a positive impact on the stability of the food web, as an interplay between bottom-up and top-down mechanisms. In addition, high food availability may lead to functional homogenization, particularly in predators with lower trophic levels. For top predators, reduced food availability is more conducive to the resilience of network functional diversity. Finally, increasing food availability increases the relative positional importance of predator nodes in the network. Especially for top predators, this amplifies their top-down effects on lower levels in the food web. This research reveals the mechanistic basis of the homogenization of marine food webs and contributes a theoretical basis for the effective management of marine ecosystems.

KEY WORDS: Food availability · Keystoneness · Topological properties · Functional homogenization · Trophic level · Network-based · Marine food web

1. INTRODUCTION

Predators in ecosystems usually have the capability to control the population size of organisms at lower trophic levels (Belgrad et al. 2023), which plays an important role in maintaining the balance of material and energy transfer in the food chain (Ritchie et al. 2012, Atkinson et al. 2017). In marine ecosystems, since primary productivity is mainly achieved through the photosynthesis pathway of phytoplankton (Cloern et al. 2014, Vallina et al. 2014), it often presents the character-

istics of resource homogeneity (Olden et al. 2004), which satisfy the resource-dependence population dynamics for most high-trophic marine species (Anderson et al. 2012, Aldasoro-Said & Ortiz-Lorano 2021). Yet, this population growth pattern is susceptible to food availability (McLean et al. 2016). Food availability is the mechanism of bottom-up community control, related to the richness of energy pathways (MacArthur 1955) and network topology (Jordán & Molnár 1999).

In subtropical coral reef areas, higher biodiversity brings multiple food sources, increasing food avail-

ability for predators (Skinner et al. 2021). Meanwhile, in areas of northern Europe close to the Baltic Sea, large numbers of herring aggregations will attract predators such as Atlantic cod from the North Atlantic seeking to obtain plenty of food (Ducrotoy & Elliott 2008, Dziaduch 2011). In addition, for individual organisms, the complex effects of long-term genetic evolution and the environment jointly created differentiation in food habits (Price et al. 2003). For example, if marine fish possess the carnitine palmitoyltransferase I metabolic enzyme in their mitochondria, this may affect their ability to metabolize fatty acids, thereby indirectly impacting their preference for high-fat foods (Leaver et al. 2008, Jin et al. 2020). The formation of *chiA*, *chit*1, and other related genes involved in the production of chitinases, can enhance the ability of fish to digest crustaceans more effectively (Chen et al. 2021, Holen et al. 2023). This is especially true for fish that specifically feed on crustaceans, which may exhibit higher chitinase enzyme activity in their digestive fluids (i.e. in the gut lumen), facilitating more efficient digestion of chitin-rich prey (Fines & Holt 2010, Abro et al. 2014). Therefore, food availability involves 3 levels: (1) the number of species that can be used as food resources (Heithaus & Dill 2002); (2) the biomass of the species (e.g. weight, protein content) (Bluhm & Gradinger 2008), which reflects the maximum population size that the predator can maintain; and, finally, (3) an understanding of the feeding habits.

Many population dynamics models consider food availability as an input parameter (Charles et al. 2004), such as the EcoPath model (Haputhantri et al. 2008, Adebola & de Mutsert 2019), which mainly mentions just the first 2 aspects of food availability. According to previous research, species with a wide range of feeding habits can expand their population size even in environments where food resources are scarce (Sánchez-Hernández et al. 2011). We usually call them an omnivorous species (Šimek et al. 2019), and the presence of omnivorous species has a deep impact on ecosystem stability (Wootton 2017). Related research reported that omnivorous species increased food web stability within a certain interval range, while when this interval range was exceeded, there was a negative impact on stability (Neutel et al. 2007, Kratina et al. 2012). The omnivory—stability debate is one of the most important research hotspots in ecology (Gellner & McCann 2012). Based on predictions about marine life, there is a high probability that more generalist species will appear in the ocean in the future (Wilson et al. 2008), driving the homogenization of marine food webs (Clavel et al. 2011). Although nobody can simply assess whether the homogenization process

will be positive or negative, one can assume that the structural and systemic variations in the food web will pose unprecedented challenges to fishery resource utilization and ecosystem management for human beings in the future (Thompson et al. 2012, Mueter et al. 2021).

High-trophic organisms not only provide food resources for humans but also play a role as a top-down control in the food web. The fishery resources utilized by humans mostly derive from the predators in the marine food web (Maxwell et al. 2013), such as the Japanese hairtail *Trichiurus lepturus* and large yellow croaker *Larimichthys crocea* commonly distributed in the eastern China Sea (Hu et al. 2022, Zhu et al. 2023). Based on carbon and nitrogen stable isotopes measurement, it is clear that these species possess trophic levels exceeding 3 (the top predator is usually around 4) (Wang et al. 2023). In addition, bluefin tuna *Thunnus maccoyii* (an expensive food item), which lives in the North Atlantic, is a natural opportunistic predator with its hemoglobin-rich muscle system (Golet et al. 2015). Additional predators such as sharks and whales are also present. Food availability for these predators requires more attention from researchers. Although the feeding habits of a species have evolved through long-term natural selection and genetics, they can remain relatively stable within a certain time range, and the latest research reveals that there is a correlation between feeding habit variability and climate change (Nagelkerken et al. 2020). It is an adaptive strategy for metapopulations or functional groups within the food web to respond to disturbances. At present, with the significant trend of ecosystem homogenization, there is still a lack of relevant research on the coping strategies of marine food webs. In a homogenized food web, structural simplification, resource centralization, and functional non-redundancy are 3 important aspects (Xu et al. 2023). Actually, these 3 aspects interact with one another directly or indirectly, but structural homogenization mainly focuses on the species node topological composition, while resource homogenization concentrates mainly on the problem of resource nodes. Considering the food availability of predators, more evidence is needed to reveal its influence on the functional homogenization processes. Furthermore, the status and keystoneness changes in predator nodes in food webs may in turn exert a driving forces effect on these functional homogenization processes (Bezerra et al. 2019). Therefore, it is important to explore the impact of food availability on the network properties and functional diversity of marine predators. However, related research is still in its initial stages.

In this research, we aim to discuss how network-based food availability affects the keystoneness of predators and functional diversity of marine food webs. We selected one food web which we considered as the research object. From a network perspective, all predator nodes in the food web were identified and divided into 2 types. We have quantified the functional homogenization degree of the food web through functional diversity (interaction profiled diversity, IPD). In addition, we calculated 6 topological attribute indicators of the network and the keystone index of predator nodes. As the next step, we established certain rules for adding or deleting a link to each predator node (as a change in food availability) and recalculated the above indicators in turn when generating a new network. By analogy, we analyzed the relationship between the indicator values generated by all networks and food availability. Correlation analysis and other methods were used to further analyze the interaction between food availability and network topological properties, the keystoneness of predator nodes, and network functional homogeneity. This research will provide methodological guidance for revealing the intrinsic mechanism of the homogenization of marine food webs and will contribute a theoretical basis for the effective management of marine ecosystems.

2. MATERIALS AND METHODS

2.1. Case selection

We collected the food web using a literature review (www.isiknowledge.com) and an Ecopath database (http://ecobase.ecopath.org/). We needed to filter out food webs from many data sets containing complete background data (i.e. a weighted predator matrix, species trophic levels, climate and environment data of the sampling sites, and a list of species information). Therefore, in order to assure that the simulation effect was statistically significant and the computer load reduced, we implemented a quantitative regulation of the number of nodes and links in the food web. We also filtered out marine food webs with the number of nodes in the range of 30 to 60 and the number of links in the range of 150 to 250. A detailed description of this process is shown in the PRISMA 2020 flow diagram in Fig. 1 (see https://libguides.derby.ac.uk/literature-reviews/prisma-lr). Finally, we picked a Norwegian sea food web as our case study (Bentley et al. 2017). The case study food web contains 34 nodes and 207 links. Most of the data comes from the International Council for the Explora-tion of the Sea which records collective catches and assessments dating back to 1950 (http://ices.dk/marine-data). For the relevant information, please see Tables S1 & S2 and Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m747p001_supp.pdf.

2.2. Identifying predator nodes

Based on the network perspective, to identify the predator nodes in a food web, we introduced the predator coefficient (Pre), reflecting the proportion of indegree and outdegree. The equation is as follows:

$$Pre = \frac{k_i^{\text{out}}}{k_i^{\text{in}}} \quad k_i^{\text{in}} \neq 0, \ \ 0 \leq Pre < 1 \qquad (1)$$

where k_i^{in} represents the indegree of node i and characterizes the number of prey nodes that node i needs to prey. k_i^{out} represents the outdegree of node i and characterizes the number of predator nodes that node i is preyed upon by predators. As a predator node, there must be at least one link entering into node i, so the k_i^{in} is above 0. When $Pre \in (0,1)$, the node i is considered to be a predator node (P). In addition, when $Pre = 0$, the node i is considered as a top predator (T). Different from using trophic levels (TL) for predator identification, the Pre approach places emphasis on the structural relationship of nodes in the network. Thus, it is possible that Pre can identify some nodes that are lower in the TL but lack the predatory behavior of high TL species for some reason (such as toxicity, concealment, or poor living environment) and are identified as predators or even top predators, as shown in Fig. 2.

2.3. Food availability in the food web

Based on the network perspective, the definition of food availability can rely on the concept of node degree in network science. A food web usually can be regarded as a directed network. When a predator node i shows a predator—prey relationship with a prey j, it is believed that there is a link directed from node j to node i. Then, the in-degree k_i^{in} of predator node i is equal to 1. Therefore, we can define the food availability (Ava) of node i as the probability of the prey node being available for predator node i. When the food web is a weighted network, the node weight can be assigned as a standardized coefficient of the total number or biomass of prey species. When the food web is a weightless network, food availability reflects the feeding habits of predator nodes. It depends on
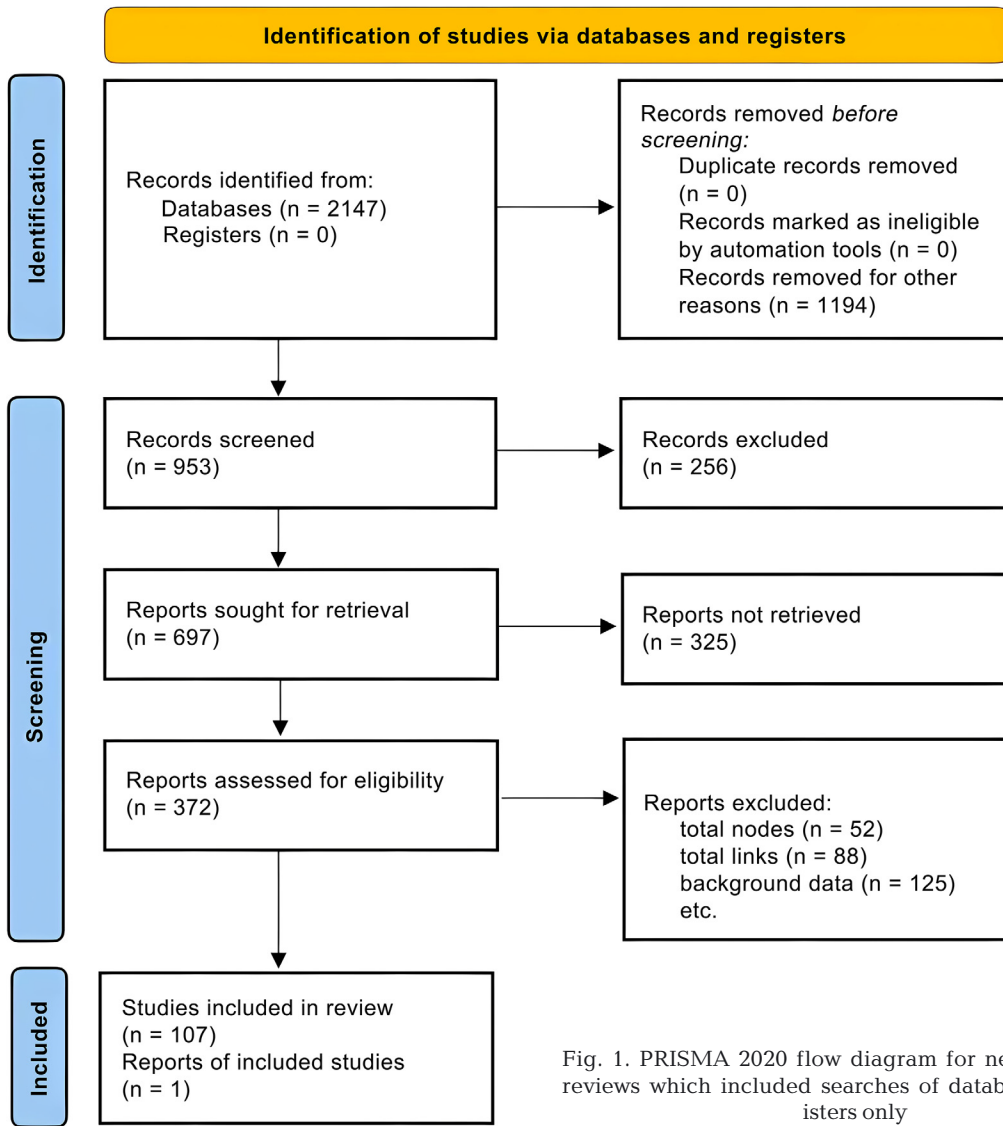
Fig. 1. PRISMA 2020 flow diagram for new systematic reviews which included searches of databases and registers only

the actual state of the food web data we are using. Since the situation with weights will be more complicated, including edge weights and node weights, we only discuss the food availability in an unweighted network here. We will cover the calculation of food availability in the weighted network in subsequent research. The *Ava* equation is as follows:

$$Ava_i = \begin{cases} \dfrac{k_i^{\text{in}}}{F(k_i^{\text{in}})} & \text{node } i = T \\[2mm] \dfrac{k_i^{\text{in}}}{F(k_{i,i \neq T}^{\text{in}})} & \text{node } i = P \end{cases} \qquad Ava_i \in (0, 1] \quad (2)$$

where Ava_i represents the food availability of node i. When node i is identified as T, $F(k_i^{\text{in}})$ refers to the fully connected in-degrees of node i itself. The total number of prey (N) satisfies $N = S - 1$,

where S represents the total number of nodes in the food web. When node i is identified as P, $F(k_{i,i \neq T}^{\text{in}})$ refers to the fully connected in-degrees of node i excluding node i itself and all top predator (T) nodes. The total number of prey (N) satisfies $N = S - 1 - N(T)$, where $N(T)$ represents the total number of top predator nodes. This approach makes it easy to understand the structural relationship of predator nodes, which facilitates data analysis and the management of complex networks.

2.4. Network attributes

We calculated several indices of network structure, characterizing the network-level and node-level topo-
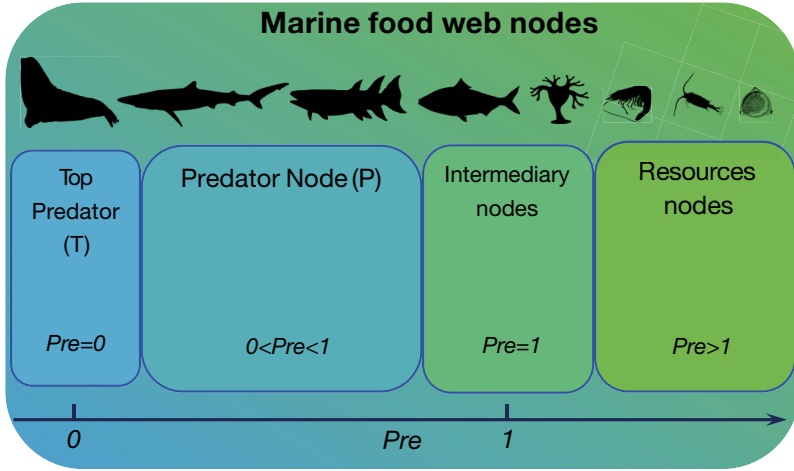
Fig. 2. Schematic diagram of marine food web nodes identified by predator coefficient (*Pre*), reflecting the proportion of indegree and outdegree

logical properties of the network, functional diversity in the food web, and the keystoneness of predator nodes.

2.4.1. Topological properties

We selected 6 topological indices, as follows:

(1) Clustering coefficient (*cc*). The *cc* is a commonly used topological indicator in network analysis, which is used to evaluate the degree of aggregation of nodes in the network, that is, the density of connections between a node's neighbor nodes (Saramäki et al. 2007). In this paper, we use the global *cc* to characterize the overall clustering trend of the network.

$$cc = \frac{1}{S} \sum_{i=1}^{S} \frac{2E_i}{k_i(k_i-1)} \qquad (3)$$

where k_i represents the degree of node i in an undirected graph, which represents relationships between different species in an ecosystem without indicating the direction of the interaction; E_i represents the total number of edges that exist between all neighbors of node i.

(2) Network diameter (*d*). Assume that d_{ij} represents the distance between any 2 nodes i and j in a network *g*. There are usually multiple edges between the 2 nodes, and the length of each path is usually different. The d_{ij} refers to the distance of the shortest path between i and j. *d* is defined as the maximum value of d_{ij} in the entire network.

$$d = \max_{i,j \in g} (d_{ij}) \qquad (4)$$

A network with a small *d* indicates that the species interaction is close to each other and information or

energy can spread through the network faster. At the same time, it will be more sensitive to environmental variation (Digel et al. 2014).

(3) Network edge density (*den*). *Den* can evaluate the proportion of the number of edges in the network relative to the maximum number of possible edges, which is the one of measures of network complexity. For a directed network, *den* can be calculated by the following equation:

$$den = \frac{L}{S(S-1)} \qquad (5)$$

where *L* represents the total number of links in a food web.

(4) Average path length (*len*). *Len* is an important concept that measures the average length of paths between nodes in a network. It is calculated by using the average of the shortest path lengths between all pairs of nodes in the graph. Theoretical ecologists believe that the *len* is intrinsically linked to the total system throughflow, which indirectly affects ecosystem stability (Finn 1976).

$$len = \frac{2}{S(S-1)} \sum_{i=1}^{S} \sum_{j=i+1}^{S} d(i,j) \qquad (6)$$

(5) Connectivity (*C*). *C* is an important index in food web analysis, which reflects the intensity of interactions between species in the food web. In some cases, *C* can serve as an indirect indicator of biodiversity in the ecosystem (Christianen et al. 2017).

$$C = \frac{L}{S^2} \qquad (7)$$

(6) Connection complexity index (SC), describing food web stability. The SC is a metric used to measure the complexity of connections within a network. In landscape ecology, SC can be used to quantify the interactions complexity between different species or habitats (Ings et al. 2009).

$$SC = S\frac{2L}{S^2 - S} \qquad (8)$$

2.4.2. Functional diversity

We have developed the IPD, which serves as a measure of functional diversity or redundancy in ecosystems, capturing the variability in ecosystem traits. Essentially, IPD is an indicator grounded in network theory, focusing on the functional diversity derived

from both positive and negative impacts of species interactions up to n steps (i.e. $E_{ij,n}^+$, $E_{ij,n}^-$). To assess the distinctness of these species interactions, we utilize the complementary Marczewski-Steinhaus index (Lin et al. 2022). This method involves averaging the dissimilarity across 2 interaction profiles, with a higher IPD value indicating greater functional diversity within the food web. The specific formulas used in this approach are as follows:

$$E_{ij,n}^+ = \frac{1}{n}(a_{ij,1}^+ + a_{ij,2}^+ + \ldots + a_{ij,n}^+) \quad (9)$$

$$E_{ij,n}^- = \frac{1}{n}(a_{ij,1}^- + a_{ij,2}^- + \ldots + a_{ij,n}^-) \quad (10)$$

$$diss_{ij} = \frac{\sum_{k=1}^{N}|E_{iu}^+ - E_{ju}^+| + \sum_{k=1}^{N}|E_{iu}^- - E_{ju}^-|}{\sum_{k=1}^{N}\max\{E_{iu}^+, E_{ju}^+\} + \sum_{k=1}^{N}\max\{E_{iu}^-, E_{ju}^-\}} \quad diss_{ij} \in (0,1) \quad (11)$$

$$IPD = \frac{\sum_{i=1}^{N}\sum_{j>i}^{N} diss_{ij}}{(S^2 - S)/2} \quad (12)$$

where $a_{ij,n}$ represents the n-step effect of species i on species j (in this research, $n = 3$). $diss_{ij}$ is utilized to quantify the dissimilarity of interaction profiles for species i and j (where a third node, u, is connected to nodes i and j); a large $diss_{ij}$ reflects high dissimilarity. According to previous research, when IPD ⩽ 0.6, one can assume that the food web has developed a slight trend of functional homogenization. When IPD ⩽ 0.4, there is an intermediate trend of functional homogeneity. When IPD ⩽ 0.2, it can be assumed that serious functional homogenization has occurred in the food web (Xu et al. 2023).

2.4.3. Keystoneness

In the approach described by Jordán et al. (2006), the keystone index for a species within an ecological network is computed by separately evaluating the bottom-up and top-down effects. This method acknowledges the distinct influences that a species can exert through its trophic interactions, either as a consumer (top-down effect) or as a resource (bottom-up effect) (Jordán et al. 1999). By distinguishing these 2 types of effects, the keystone index provides a more nuanced understanding of a species' ecological role and its significance within the ecosystem.

$$K_{bu}(i) = \sum_{P=1}^{n}\frac{1 + K_{bu}(P)}{Prey(P)} \quad (13)$$

$$K_{td}(i) = \sum_{Com=1}^{m}\frac{1 + K_{td}(Com)}{Predator(Com)} \quad (14)$$

$$K_i = K_{bu}(i) + K_{td}(i) \quad (15)$$

where n represents the number of predators consuming species i; Prey(P) is the number of prey of the predator P; $K_{bu}(P)$ is the bottom-up keystone index of node i on its predator P; m represents the number of prey eaten by species i; Predator(Com) is the number of predators of the prey Com; $K_{td}(Com)$ is the top-down keystone index of the prey Com, $K_{bu}(i)$ and $K_{td}(i)$ is the top-down keystone index of species i, respectively.

In addition, the keystone index also includes a description of direct and indirect effects (Giacomuzzo & Jordán 2021). Here, we also calculated the direct keystone index (K_{dir}) and indirect keystone index (K_{indir}):

$$K_{dir}(i) = K_{bu,dir}(i) + K_{td,dir}(i) \quad (16)$$

$$K_{indir}(i) = K_{bu,indir}(i) + K_{td,indir}(i) \quad (17)$$

$$K_{bu,dir}(i) = \sum_{P=1}^{n}\frac{1}{Prey(P)} \quad (18)$$

$$K_{bu,indir}(i) = \sum_{P=1}^{n}\frac{K_{bu}(P)}{Prey(P)} \quad (19)$$

where $K_{bu,dir}(i)$ represents the bottom-up direct keystone index of species i; $K_{td,dir}(i)$ represents the top-down direct keystone index of species i; $K_{bu,indir}(i)$ represents the bottom-up indirect keystone index of species i; $K_{td,dir}(i)$ represents the top-down indirect keystone index of species i; $K_{td,indir}(i)$ represents the top-down indirect keystone index of species i. The calculation approach for $K_{td,dir}(i)$ and $K_{td,indir}(i)$ are similar to $K_{bu,dir}(i)$ and $K_{bu,indir}(i)$.

2.5. Food web simulation

To proceed, we need to formulate guidelines and establish different scenarios to assess the effects of food accessibility alterations in real marine ecosystems on the network topological properties, the functional diversity, and the keystoneness of nodes. A detailed simulation approach is shown in the following steps:

(1) In compliance with Eq. (1), search and identify all predator nodes in a food web g and mark the predator nodes as 'T' or 'P' types based on the Pre value.

(2) In compliance with Section 2.4, calculate the 6 topological mathematics, the IPD, and keystone index of the initial network g (Eqs. 3—12).

(3) Randomly designate a predator node i (including T and P node), add or delete one predator link (indegree) of node i each time, and recalculate the 6 topological attributes, the IPD, and keystone index for the newly formed network g_1.

(4) Add or delete a predator link of node i continuously, and calculate 6 topological attributes, the IPD, and keystone index of network g_2, g_3, ..., g_m. Loop in sequence until the link to node i cannot be increased or decreased and the loop will be stopped.

(5) Calculate the food availability (Ava) of each predator node in the m networks generated after looping m times (Eq. 2).

We need to state that, in the original data, links have weights. Due to the existence of link weights, the impact on food availability is direct and significant. Although we have also tried many methods, such as the arithmetic mean of weights, mode, median, or interpolation, none of them produced the appropriate results. It should be noted that since we cannot effectively assign an appropriate weight to the added link, we consider the link to be unweighted. This is also the reason why we used unweighted indicators in Section 2.4. Additionally, the rules are established for loop termination. When deleting a link, we need to ensure that the predator node has at least one predator relationship. When adding a link, the T node can establish a link with any other node except itself. Furthermore, the P node can establish a link with any other node except itself and T nodes.

3. RESULTS

As shown in Fig. 3, we can identify network-based predator nodes. Among 34 species nodes in the Norwegian Sea food web (Fig. 3a, see also Fig. S1), we have identified 14 species of predators, 5 of which are top predators (T) and 9 of which are common predators (P). The details of these predator nodes are shown in Table 1. Most of the trophic levels of predator nodes identified by Pre are higher than 3, accounting for 85.71% of the total. However, about 14.29% nodes have trophic levels lower than 3 and are still identified as predator nodes. This is similar to the situation discussed previously. As can be seen from Fig. 3b, the T node must be a node with a higher TL (>4). The P nodes are included in more TLs, but most of them are nodes with higher TLs (median TL = 4)

As shown in Fig. 4, the variations in 6 network topological properties are illustrated concerning the food availability of predator nodes. Notably, the trends in C and the SC are consistent with network edge den-

sity (den). Actually, these are redundant metrics that express the same information. Therefore, Fig. 4 only shows 4 network topology indicators. Further details of SC and C can be found in Fig. S2 in the Supplement. In Fig. 4a, the clustering coefficient (cc) showed a significant positive correlation with food availability (Ava). As the Ava of predator nodes increases, the clustering coefficient of the network increases significantly. Similar trends exist for both T nodes and P nodes. Through regression analysis, it is clarified that the slope of the fitted line for T node and Ava is approximately 0.0582, and the intercept is about 0.433 (p = 0.025, R^2 = 0.798). The slope of the fitted line for P node and Ava is approximately 0.0576, and the intercept is about 0.426 (p = 0.012, R^2 = 0.729). Compared to P node, changes in food availability at T node are more sensitive to cc. As shown in Fig. 4b, the diameter (d) remains stable with variations in Ava. Yet, occasional fluctuations occur primarily due to the random addition or removal of links that will generate special structure (such as the creation or loss of linkages with hub nodes). These events lead to variability in the network path. It is worth noting that nodes with lower TLs typically exhibit narrower variations in network diameter. However, this pattern does not satisfy the nodes with higher TLs. The average path length (len), does not follow a simple linear relationship either (Fig. 4c). For nodes with lower TLs, an increase in Ava leads to a slow decrease in len. Conversely, among most predator nodes, alterations in Ava induce a mutation-like shift in len. Once this threshold is surpassed, network length experiences a sudden increase, followed by a gradual decline as Ava continues to rise. For the T node, the variability range occurs roughly between 0.3 and 0.6. As for the P node, the variability range spans approximately from 0.2 to 0.6. In Fig. 4d, the den showed a significant linear growth relationship with Ava. The results of linear regression show that the slope of the fitted line for T node and Ava is approximately 0.0294, and the intercept is about 0.165 (p < 0.001, R^2 = 0.983). The slope of the fitted line for P node and Ava is approximately 0.0296, and the intercept is about 0.167 (p = 0.002, R^2 = 0.881). Interestingly, compared to high TL nodes, changes in Ava for low TL nodes will lead to a higher den. Similar phenomena also occur in C and SC (see Fig. S2).

As shown in Fig. 5a, the IPD showed a significant negative correlation with Ava. It is indicated that as the food availability of predator nodes increases, the functional diversity of the network decreases significantly. Similar trends exist for both T and P nodes. By regression analysis, the slope of the fitted line for
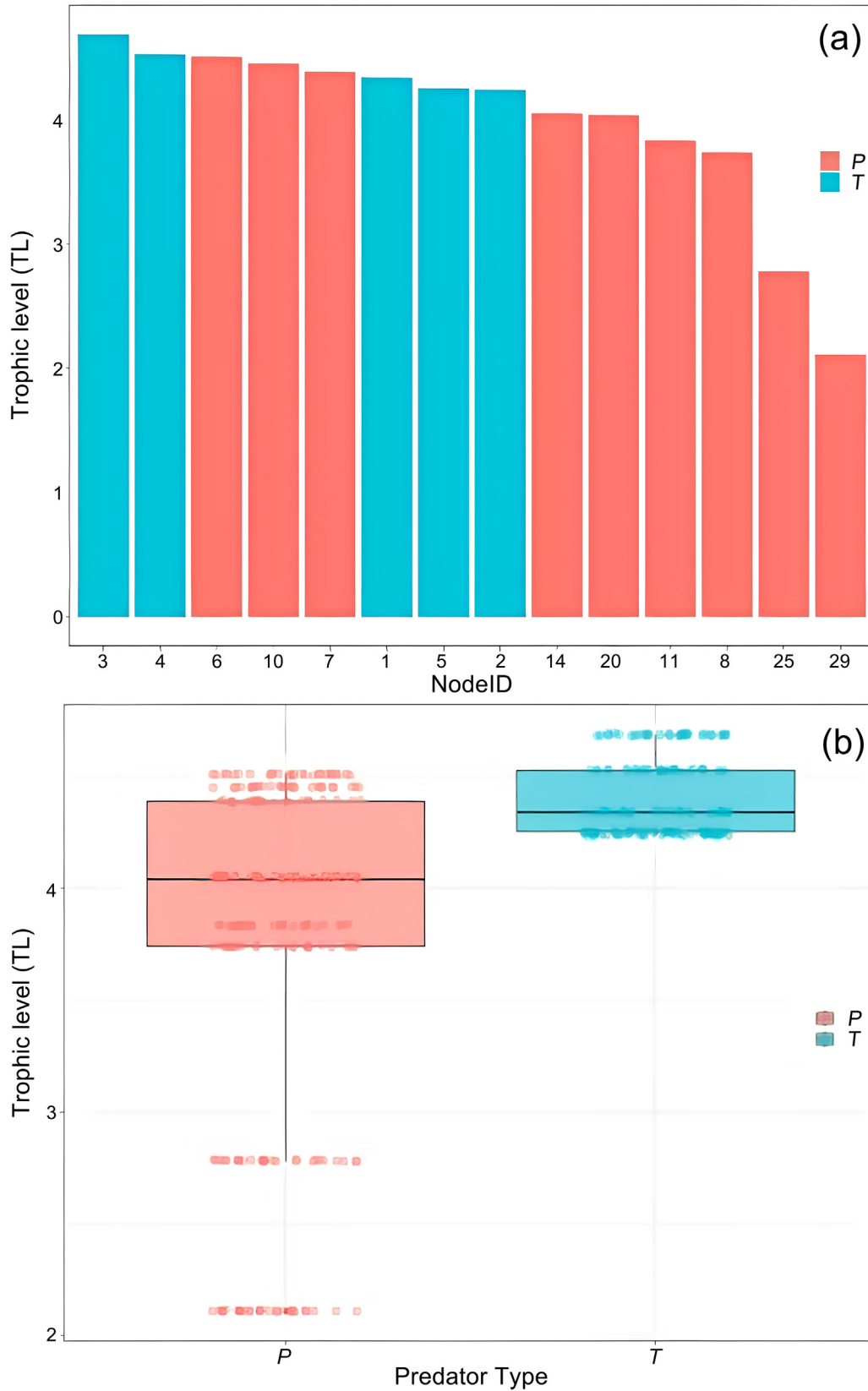
Fig. 3. Statistical plot of identified predator types versus trophic levels (TLs) in the Norwegian Sea food web. (a) TLs of different predator nodes; (b) relationship between node type and TL. *P*: predator nodes apart from top predator; *T*: top predator nodes. Horizontal line: median; upper and lower edges of the box: first quartile and third quartile, respectively. Whiskers: extended range of data; dots: jitter points of the data

T node and *Ava* is approximately −0.0492, and the intercept is about 0.669 (p < 0.001, R^2 = 0.939). The slope of the fitted line for P node and *Ava* is approximately −0.0463, and the intercept is about 0.659 (p = 0.011, R^2 = 0.792). Furthermore, compared to high TL nodes, changes in *Ava* for low TL nodes will lead to lower IPD. In Fig. 5b, there are no differences in the impact of the 2 predator nodes on IPD. Specifically, the P node exhibits lower IPD values (median = 0.6406) with a relatively narrow range of variation (min. = 0.607, max. = 0.663). In contrast, the T node demonstrates relatively higher IPD values (median = 0.6434) with a broader range of variation (min. = 0.615, max. = 0.68). In summary, for top predators, reduced *Ava* could be more conducive to the restoration of network functional diversity. For lower predators, especially for lower predators with lower TLs, the increase in *Ava* will accelerate the reduction of network functional diversity, which may lead to the problem of functional homogenization in the marine food web.

In addition, we also calculated the keystone values of the predator nodes in the m food webs obtained by adding or deleting links each time and counted the changes in different keystone indicators at the predator nodes (K, K_{bu}, K_{td}, K_{dir}, and K_{indir}). We proceeded by normalizing these values to a normalized value between 0 and 1 and drew them into a heat map (Fig. 6). As shown in Fig. 6, variations in K, K_{bu}, and K_{indir} exhibit no significant impact on the node's keystoneness, except when the food availability for the top predator is high. For K_{td}, the food availability changes at the T nodes can have a significant impact. When *Ava* is greater than about 0.4, it has a greater impact on the top-down keystone index for the T node, and the normalized values of K_{td} are higher than 0.8. In contrast, the impact on the P node is small. When *Ava* is between 0.26 and 0.38, K_{td} increases to a maximum of approximately 0.6. This reflects that when food availability improves, top predators will have a higher top-down control effect on prey, and this control effect of the P node is not significant. In addition, as food availability increases, the K_{dir} of both predator nodes gradually rises. This indicates that each additional link to a node exerts an influence on the prey nodes directly connected to it. In essence, an augmentation in food availability will heighten the keystoneness of predator nodes within the network. Especially for top predators, this amplifies their top-down control effects on the food web.

Finally, we used the Spearman correlation coefficient to calculate the correlation between the 14 parameters appearing in this research and visualized them

Table. 1. The predator nodes in the selected food web case study (Norwegian Sea). T: top predator node; P: predator node; numbers in parentheses show cod age classes

Node ID	Species	Trophic level	Predator types
1	Minke whales	4.341	T
2	Other baleen whales	4.242	T
3	Toothed whales	4.688	T
4	Seals	4.528	T
5	Seabirds	4.255	T
6	Cod (4+)	4.510	P
7	Cod (1−3)	4.389	P
8	Haddock1	3.741	P
10	Saithe	4.455	P
11	Other benthic fish	3.835	P
14	Mackerel	4.054	P
20	Large pelagic fish	4.040	P
25	Prawns and shrimps	2.783	P
29	Benthic micro-organisms	2.111	P

in the correlation matrix by using cluster analysis, as shown in Fig. 7. The cluster analysis divides these parameters into 5 categories. Among them, the parameters of C (corr = 0.951), SC (corr = 0.951), *den* (corr = 0.951), K_{dir} (corr = 0.952) and *cc* (cor = 0.866) exhibit a statistically significant positive correlation with *Ava* (p < 0.001). The parameters *len* (corr = 0.576), d (corr = 0.431), and K_{td} (corr = 0.559) show a moderate positive correlation with *Ava* (p = 0.015). Conversely, K (corr = 0.277), K_{bu} (corr = 0.272), and K_{indir} (corr = 0.316) display a weaker positive correlation with *Ava* (p = 0.025). No statistically significant correlation was observed for TL (p = 0.08). Finally, the parameters of IPD (corr = −0.885) exhibit a statistically significant negative correlation with *Ava* (p = 0.039). On the other hand, the parameters of C (corr = −0.198), SC (corr = −0.198), and *den* (corr = −0.198) exhibit a statistically weak negative correlation with TL (p = 0.012). The parameters of d (corr = 0.397), *len* (corr = 0.433), and K_{td} (corr = 0.503) exhibit a statistically moderate positive correlation with TL (p = 0.031). Interestingly, the parameters of IPD (corr = 0.237) exhibit a weak positive correlation with TL (p = 0.011). This seems to reveal a critical role of low trophic level predators in affecting the functional homogenization process of the marine food web.

4. DISCUSSION

In this paper, we used the Norwegian Sea food web as a case study to study the intrinsic relationship between food availability (*Ava*) and 6 network topo-
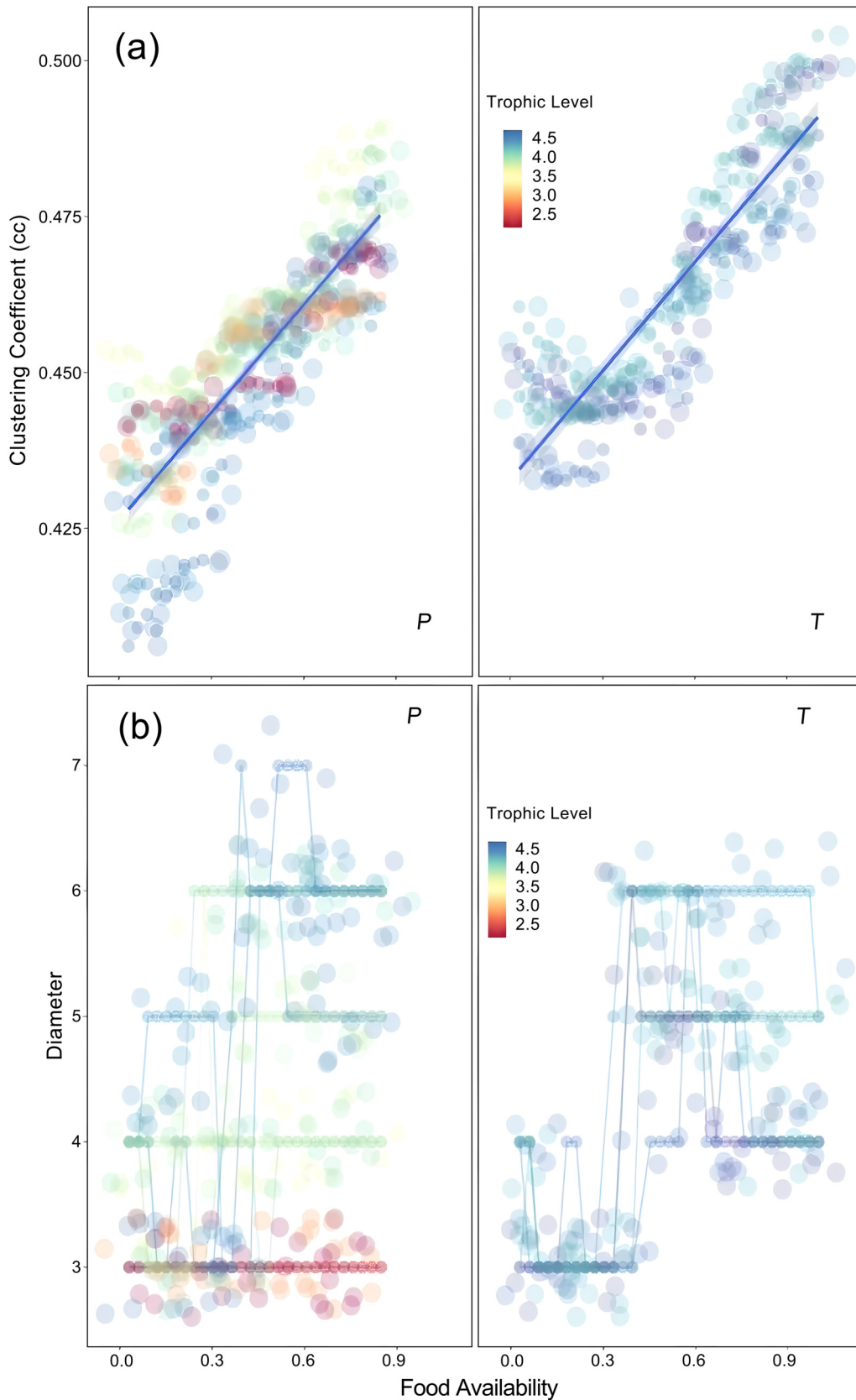
Fig. 4. Variation in different network topology indices with food availability. Figure facets represent different types of predators; scatter colors represent the trophic levels. (a) Clustering coefficient (*cc*); (b) diameter; (c) average path length; (d) network edge density. *P*: predator nodes apart from top predator; *T*: top predator nodes

Fig. 4 (continued)

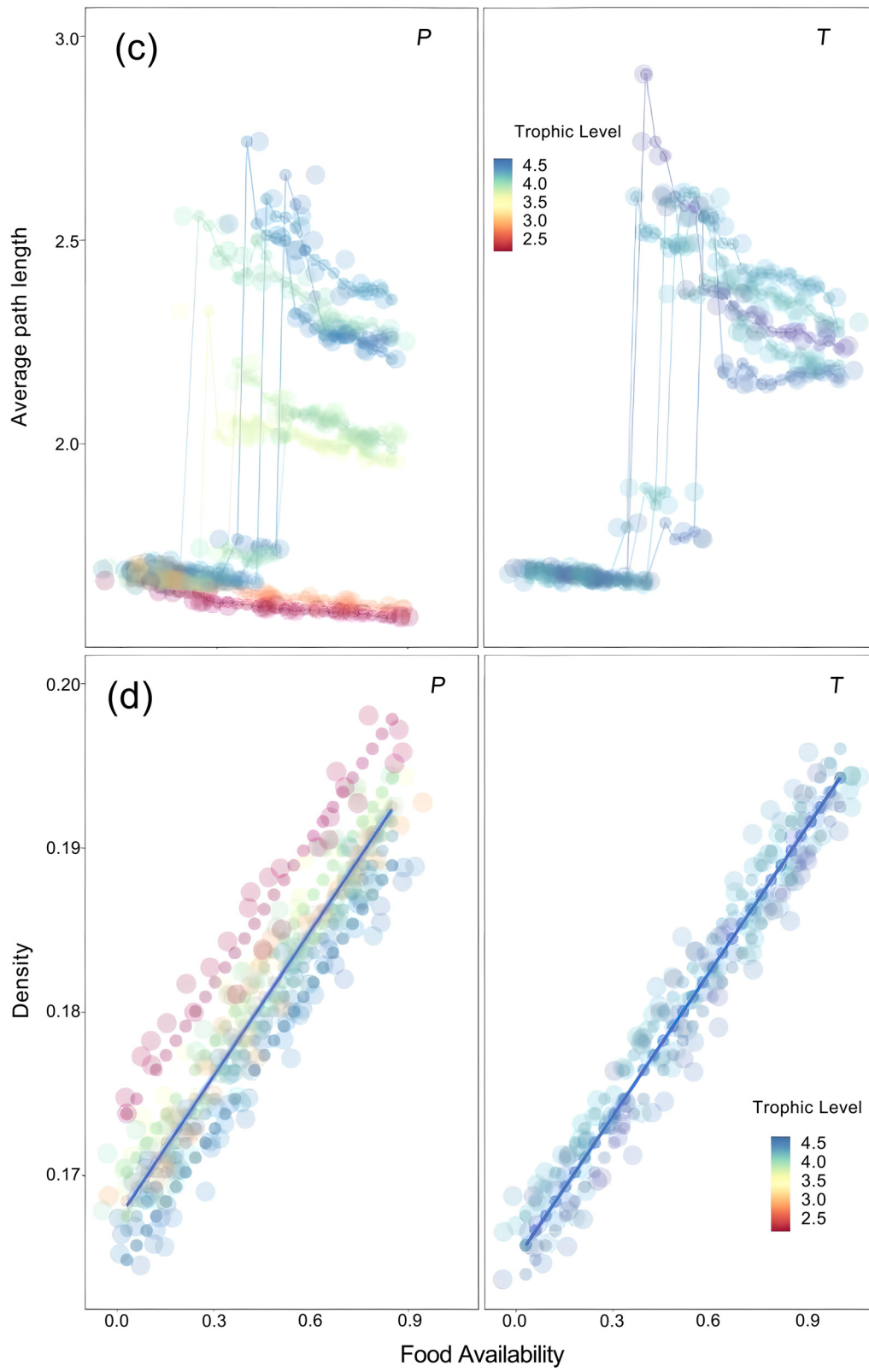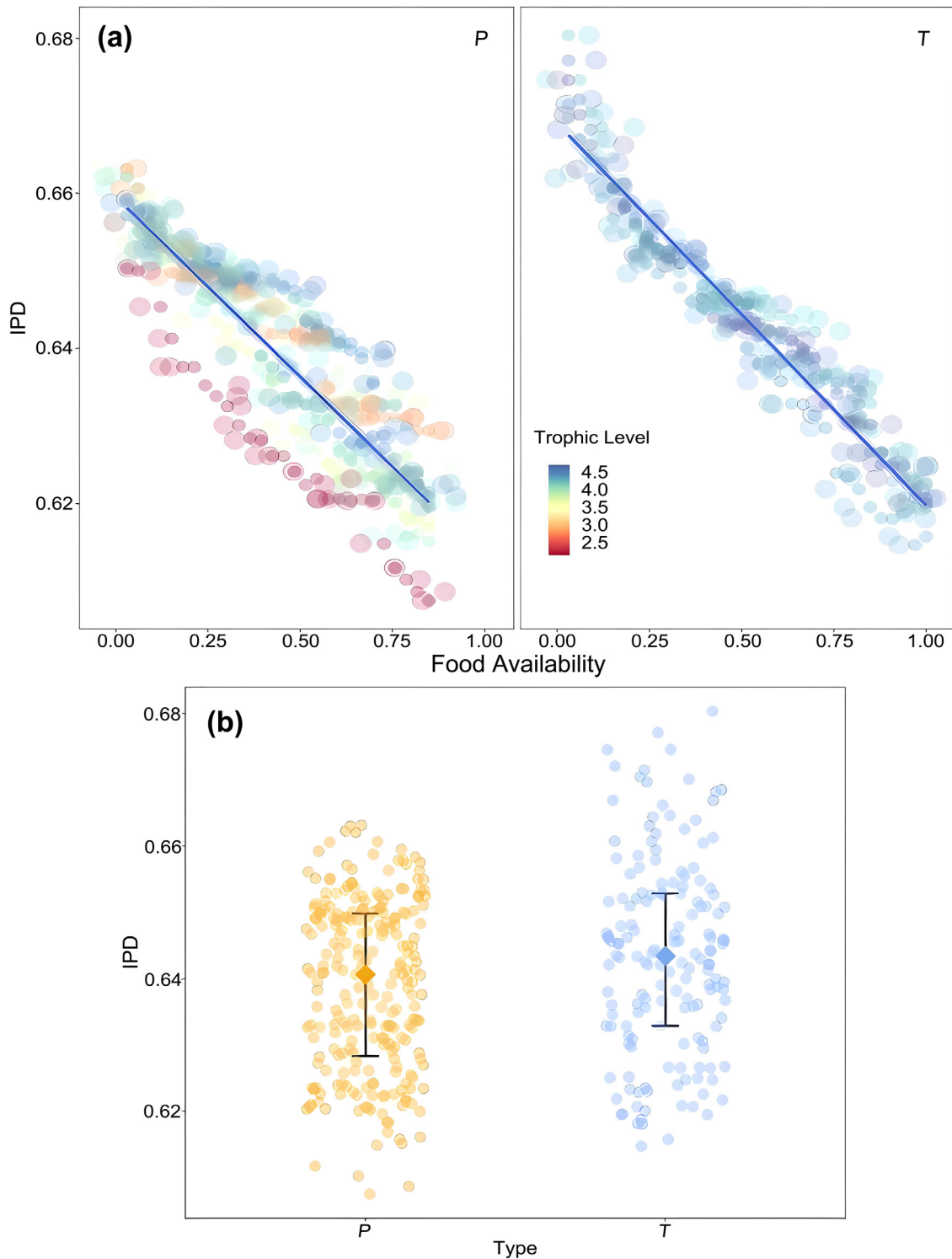Fig. 5. (a) Variation in the interaction profiled diversity (IPD) index with food availability. Figure facets represent different types of predators; scatter colors represent the trophic levels. (b) IPD distribution under different predator node types. *P*: predator nodes apart from top predator; *T*: top predator nodes. Error bar indicates the extended range of data

logical properties, the keystoneness of predator node, and IPD. We established certain rules by adding or removing links to each predator node to simulate

changes in food availability and to sequentially calculate relevant indices to generate new networks. The results revealed interesting patterns in response to
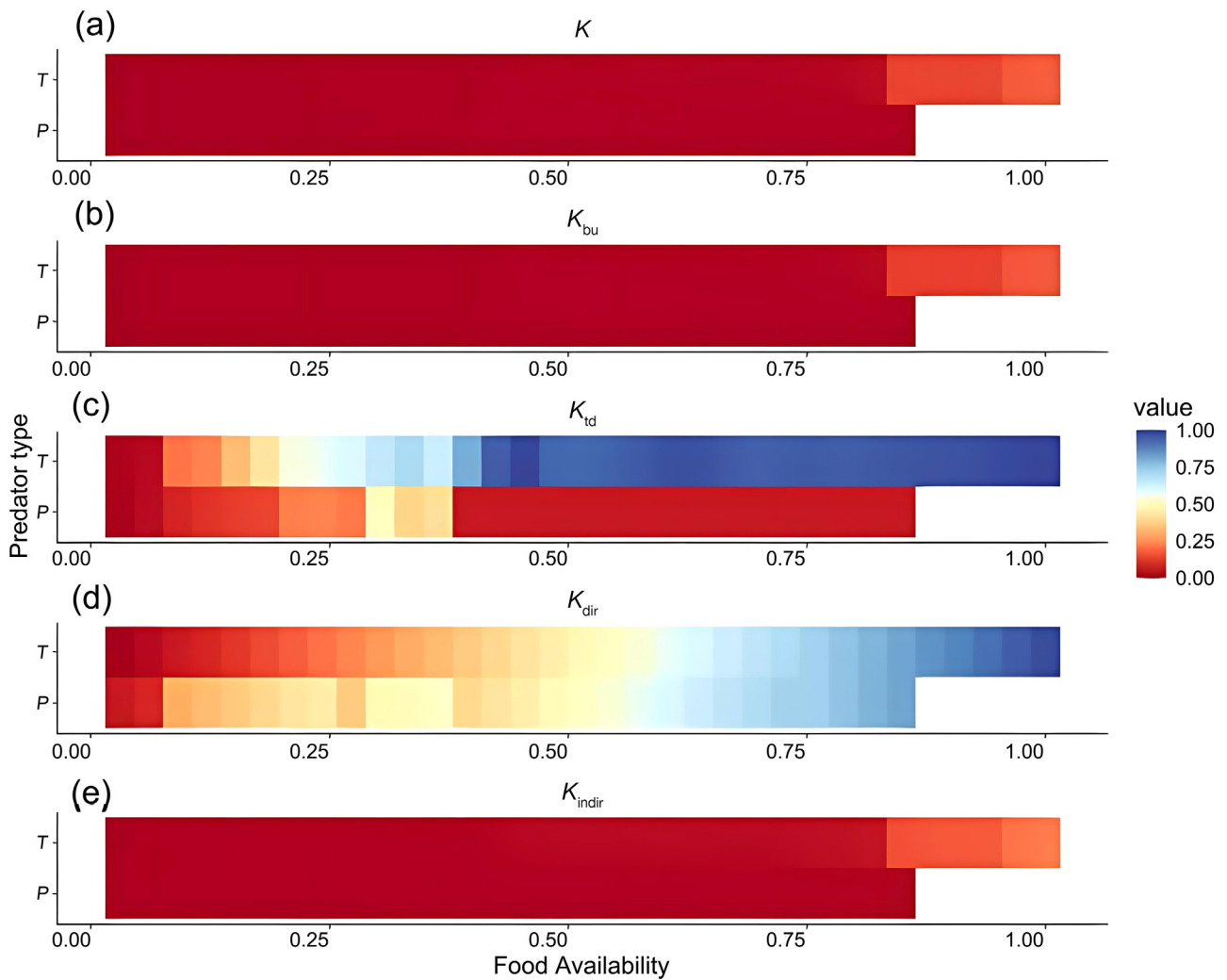
Fig. 6. Heat map showing the variation of the keystone index and its components as a function of food availability. (a) K: total keystone index; (b) K_{bu}: bottom-up keystone index; (c) K_{td}: top-down keystone index; (d) K_{dir}: direct keystone index; (e) K_{indir}: indirect keystone index

changes in food availability as shown by an analysis of network topological properties. The clustering coefficient (cc) has a positive correlation with Ava, suggesting that as the availability of food increases, the network tends to have more interconnected clusters. This indicates that predators become more connected to each prey when there is higher abundance of food.

Moreover, the average path length (len) suggested that the existence of variability values, as shown in Fig. 4c, may be related to the threshold at which omnivory affects food web stability. According to previous research, the omnivory—stability theory suggests that when a species has strong omnivory, it will destroy the food web stability (Kratina et al. 2012, Wootton 2017). In freshwater ecosystems, species which we labeled as invasive species or alien species that can colonize new environments in large

numbers mostly have a wide range of feeding habits (Mooney & Cleland 2001, Gkenas et al. 2012). Relevant studies indicate that an omnivory sub-web could reconstruct the network structure. In marine ecosystems, species with higher omnivory and stronger migration abilities (i.e. the generalist species) can occupy relatively high ecological niches and contribute to the food web rewiring (Bartley et al. 2019). Coupled with the pressure from climate change, ecosystems will also undergo adaptive variability (Berec et al. 2010). However, weak omnivores can enhance network stability to a certain extent. Strong omnivores are often able to exploit many different food resources, which gives them a broader range of nutritional strategies in the food web. However, when the degree of omnivory exceeds a certain threshold, it will lead to network instability. This may be due to their en-

Fig. 7. Correlation matrix between various indices with single-linkage clustering. IPD: interaction profile diversity; K_{indir}: indirect keystone index; K: total keystone index; K_{bu}: bottom-up keystone index; TL: trophic levels; K_{td}: top-down keystone index; cc: clustering coefficient; SC: connection complexity index; den: network edge density; C: connectivity; K_{dir}: direct keystone index; Ava: food availability; d: network diameter; len: average path length

hanced ability to control multiple species (reflected in the positive correlation of cc, C, SC and den). Once these predator nodes with strong control effects are affected by specific disturbances, it will affect the whole network. In contrast, weakly omnivorous species may positively impact the stability of the food web (McLeod & Leroux 2021). The definition interval of weak omnivory varies for different nodes, but it is generally between 0.3 and 0.6. Additionally, the weak positive correlation between the link length (len) and the TL of the predator node implies that predators at higher trophic levels or top predators are crucial for maintaining the stability of the food web. On the other hand, indices such as den, C, and SC exhibit a significant linear growth relationship with average

vulnerability (Ava). This indicates that these metrics are influenced by a broad range of food resources. However, the weak positive correlation between these metrics and TL suggests that predators at lower TLs also play a vital role in shaping the complexity of the network's topological structure.

Additionally, the analysis of functional diversity, measured by IPD, revealed a negative correlation with food availability. When new nodes (representing new food resources) are added to the network, the interaction profiles of species preying on these nodes will become more similar if multiple species exploit the same new resources. This can decrease the dissimilarity measure, thus reducing the overall IPD. Conversely, if only one species preys on a new re-

source, the interaction profile dissimilarity might increase. Still, this scenario is less common in highly interconnected networks where new resources are typically utilized by multiple species (Williams et al. 2002). Our findings suggest that high food availability may lead to functional homogenization, particularly in lower predators with lower TLs. Because more species share the same food resources, the diversity of unique interactions is reduced. This homogenization is particularly evident in lower TLs where resource overlap is more frequent. We expect more food availability will increase functional diversity by providing more diverse resources. However, in the context of our study, the observed trend toward functional homogenization with increased food availability can be attributed to the specific structure and dynamics of the trophic network. This may be related to the specificity of the Norwegian Sea food web. Still, it can in part reflect the real structural relationship in marine empirical food webs.

As food resources increase, species at lower TLs exploit similar resources due to overlapping niches. This overlap reduces the differentiation in their interaction profiles, leading to a lower IPD. While functional redundancy (multiple species performing similar roles) enhances network resilience to perturbations, it also contributes to functional homogenization as species interactions become more uniform (Schleuning et al. 2015). This has implications for ecosystem stability, as a decrease in functional diversity may impact the ability of the food web to respond to disturbances (de Bello et al. 2021). In fact, previous research results have hinted at this problem (Rooney & McCann 2012). Many generalist species in the ocean are not the top predators (usually carnivores feeding only on a few large species) in a food web, but they are highly adaptable to environmental changes. The wide range of feeding habits creates high food availability and may rewire the food web (Bartley et al. 2019). According to the analysis of our modelling results, increased food availability for top predators can only result in limited enhancements in network complexity, with less plasticity in network structure and function than for lower TL predators.

Finally, the findings about the keystone index revealed that food availability had an impact on the top-down keystone index (referred to as K_{td}) of predators (T nodes), suggesting that more food available for top predators had a stronger top-down effect on the food web. This interplay of bottom-up and top-down effects (Hunter & Price 1992) can be especially interesting in the case of wasp-waist ecosystems, where organisms at intermediate TLs exert control in both directions (Cury et al. 2000). This highlights the role that top predators play in shaping and influencing the structure and dynamics of marine food webs. Furthermore, the directed keystone index (K_{dir}) demonstrated that increased food availability amplified the importance of predator nodes. This indicates that the alterations in *Ava* can affect how predator nodes control their prey, which could potentially influence the stability and dynamics of the entire food web.

To validate our findings, we conducted a simulation and analysis of 5 marine food webs from various regions. While there were variations in the results due to food web structures, marine ecosystem types, climate characteristics and other factors, we still observed patterns. For example, the biodiversity of the Norwegian Sea food web is quite limited compared with warmer regions, which might lead to differences in homogenization mechanisms. More diverse food webs tend to have weaker interactions and greater modularity than simpler communities and are more stable (D'Alelio et al. 2019). In addition, some food webs showed nonsignificant trends. But this does not mean that the key trends are irrelevant; they certainly have limitations that should be addressed and explored.

In this research, we used just one specific case, but we can explore possible differences with other food webs in order to enrich future studies. We expect similar results in more diverse natural systems. For instance, similar food webs exist in warm-temperate and tropical regions, which are more biodiverse. In shallower coastal areas with higher food availability and trophic groups (Angel & Ojeda 2001) or in hard-bottom reefs (Harborne 2013) (which are known to be nursery areas, where juveniles are usually omnivores), it is important to examine whether they fit the omnivory—stability hypothesis. Furthermore, future studies should consider incorporating weight-related factors such as biomass data from monitoring to broaden our understanding. There is a need for the development of modeling methods that account for food availability in interconnected networks. The factors influencing the homogeneity of marine food webs are complex and encompass climate conditions, oceanic physical characteristics, chemical processes within the oceans, biological interactions, and more. Thus, while taking a network-based approach is valuable in exploring homogeneity within food webs, it is only one aspect. Future research should encompass additional fields to gain further insights. While it may not be possible to draw conclusions about the changes occurring in real-world marine food webs from this study alone, it does stimulate discussions regarding the underlying mechanisms driving func-

tional homogenization within these ecosystems. We anticipate that this study will serve as a guide for unraveling the mechanisms behind homogenization in marine food webs and provide a theoretical foundation for effective ecosystem management.

5. CONCLUSIONS

In this research, we discussed that network-based food availability affects the keystoneness of predators and the functional diversity of marine food webs. There were some conclusions drawn as follows: (1) The parameters of C, SC, *den*, and *cc* exhibit a significant positive correlation with *Ava*, and a weak negative correlation with TL. It was shown that increased food availability can strengthen the topological complexity in the food web. Yet, top predators have less plasticity in network structure than lower TL predators. (2) The existence of variability values in the average path length (*len*), may be related to the threshold at which omnivory affects food web stability. Weakly omnivorous species may have a positive impact on the stability of the food web. The definition interval of weak omnivory differs for different nodes, but usually it is between 0.3 and 0.6. In addition, the weak positive correlation between *len* and the TL of the predator node seemed to imply that high TLs or top predators are important for maintaining the stability of the food web. (3) IPD exhibited a significant negative correlation with *Ava* (corr = −0.885) and a weak positive correlation with TL (corr = 0.237). This suggests that high *Ava* may lead to functional homogenization, particularly in lower predators with lower TLs. For top predators, reduced *Ava* is more conducive to the restoration of network functional diversity. (4) Both K_{dir} and K_{td} exhibited a positive correlation with *Ava*, and a weak positive correlation with TL (corr = 0.237). This indicates that increasing *Ava* will heighten the keystoneness of predator nodes within the network, especially for top predators, amplifying their top-down control effects on the food web. It highlights the role of top predators in shaping and influencing the structure and dynamics of marine food webs. This research will provide methodological guidance for revealing the intrinsic mechanism of the homogenization of marine food webs and contribute a theoretical basis for the effective management of marine ecosystems.

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