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Impacts of El Niño–Southern Oscillation (ENSO) Events on Trophodynamic Structure and Function in Taiwan Bank Marine Ecosystem

Po-Yuan Hsiao [1], Kuo-Wei Lan [1,2,*], Wen-Hao Lee [1], Ting-Yu Liang [1], Cheng-Hsin Liao [1] and Nan-Jay Su [1]

[1] Department of Environmental Biology and Fisheries Science, National Taiwan Ocean University, Keelung 202301, Taiwan; 20931002@mail.ntou.edu.tw (P.-Y.H.); 11031011@mail.ntou.edu.tw (W.-H.L.); 21231002@mail.com.ntou.edu.tw (T.-Y.L.); chliao@mail.ntou.edu.tw (C.-H.L.); nanjay@mail.ntou.edu.tw (N.-J.S.)
[2] Center of Excellence for the Ocean, National Taiwan Ocean University, Keelung 20224, Taiwan
* Correspondence: kwlan@mail.ntou.edu.tw

Abstract: Taiwan Bank (TB) is located in the southern Taiwan Strait (TS). The uplifted continental slope and bottom currents in this area result in the formation of upwelling areas, which serve as crucial fishing grounds. Climate-induced fluctuations in fish populations occur in the TS. However, how predation and competition affect the interspecies relationships in the TB ecosystem warrants clarification. In this study, we collected high-grid-resolution data on fishery activity (2013–2019) and constructed ecosystem models using Ecopath with Ecosim (EwE). Three mass-balanced models for determining the influence of El Niño–Southern Oscillation (ENSO) events on the TB ecosystem were constructed using EwE. A range of groups, including representative pelagic, benthic, and reef species, were collected for analyzing the relationship between migratory and sedentary species in terms of ecosystem structure variation due to climate change. The results demonstrated that the total system throughput (TST) was 10,556–11,122 t km^{-2} year^{-1}, with an average transfer efficiency of 12.26%. According to the keystoneness index, calculated through mixed trophic impact analysis, *Polydactylus sextarius* and *Scomber japonicus* were the key species with top–down control and relatively high impact on the ecosystem in normal years. The keystone species also shifted to the predator fish *Thunnus albacares* and *Katsuwonus pelamis* during El Niño and La Niña events, respectively. Moreover, total biomass, TST, consumption, and respiration were noted to increase during ENSO events. However, during La Niña events, the diversity and connectance indexes were relatively low but pelagic species' biomass was relatively high, whereas the biomass of most benthic and reef species was relatively high during El Niño events.

Keywords: Taiwan bank; Taiwan strait; Ecopath; ENSO; ecosystem function; upwelling; South China Sea

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1. Introduction

El Niño–Southern Oscillation (ENSO), the most dynamic interannual climate phenomenon globally, significantly influences marine ecosystems by altering habitat conditions (such as oxygen levels, temperature, and light penetration), ocean currents, and food availability [1,2]. During El Niño events in the equatorial Pacific, particularly the eastern Pacific, reduced upwelling and nutrient supply lead to a decrease in phytoplankton biomass. Zooplankton and micronekton communities respond to these changes, albeit with a time lag of about 1–2 months. This bottom–up (BU) control mechanism subsequently influences the growth, reproduction, and predation of higher-trophic-level predators at the surface [1]. In the northern South China Sea, the warmer temperatures associated with El Niño events have been found to benefit small pelagic fish populations in this ecosystem [3].

ENSO events majorly affect the intensity of upwelling regions in the Taiwan Bank (TB) and change the composition of pelagic and benthic species [4–6]. During La Niña events,

increased upwelling size in the TB region leads to decreased sea temperature and increased primary production [6–8]. ENSO events alter marine environments and affect organism populations through bottom–up [9–12] or top–down (TD) effects [13,14].

The Taiwan Bank is an essential high-productivity fishing ground located in the southern Taiwan Strait. Northward water flows upward along the edge of the continental shelf year-round, forming an upwelling region in the TB [15,16]. The hydrological cycling and upwelling systems in the TB not only provide a substantial nutrient supply, but also increase benthic and pelagic species richness. Regional studies on the TB have focused on the differences in the physical, chemical, and habitat characteristics of different species within the ecosystem (e.g., 4–6,16). Fishing activities influence ecosystem biodiversity, ecological relationships, and ecological processes [17]. Fishing has greatly reduced Atlantic salmon populations in the North Sea and Atlantic Ocean, impacting ecosystem processes like nutrient cycling and predator–prey dynamics through direct exploitation, bycatch, and habitat disruption [18]. Adebola and Mutsert [19] used two Ecopath models for 1985 and 2000 data from Nigerian coastal waters and observed that, as fishing intensity increased, the ecosystem became less structurally complex, as well as less productive. Studying the impact of fishing activities on ecosystems and developing ecosystem-based fisheries management strategies is crucial for achieving sustainable practices and ecosystem conservation. Ju et al. [20] used Ecopath to model the structure of the entire southern Taiwan Strait and revealed the top–down effect as the primary ecosystem control mechanism. However, no study has reported the effects of climatic events on TB's ecosystem structure and trophic relationships.

Ecosystem food webs facilitate the transfer of nutrients and energy through predation, symbiosis, and parasitism among species, enabling continuous growth and operation [21]. Changes in primary productivity directly or indirectly affect the population of all consumers and decomposers within an ecosystem [22]. These trophic cascades, including top–down and bottom–up controls, describe interactions among biological communities and collectively influence the structure and stability of an ecosystem [23]. They also contribute to ecological balance and the maintenance of species diversity, and impact the productivity and energy flow within an ecosystem [24]. This holistic analysis of mass, energy, and nutrient cycling shows how ecosystems respond to and recover from internal and external disturbances [25,26]. Marine ecosystems face multiple pressures, such as extreme environment variation, overfishing, human pollution, and climate change [2,27]. Modeling marine food webs has shown great potential for investigating changes due to environmental variability and climate change [28,29].

The highly intricate nature of ecosystems makes them challenging to comprehensively analyze. Jørgensen (1992) [30] emphasizes the need for a holistic research approach to effectively describe ecosystem characteristics. Ecological models, such as Ecopath with Ecosim (EwE), are crucial for developing multispecies ecosystem structures and identifying ecological indicators for marine conservation and sustainable management [31–34]. These models consider the dynamics of commercial and noncommercial species, including their interactions and the main drivers of exploited marine ecosystems [33,34].

Constructing a comprehensive food web is often the initial step in ecosystem studies. Food web modeling, a mathematical approach, imposes minimal constraints on time and spatial scales and is cost-effective compared to other research methods [1,35]. EwE software (version 6.6.8) facilitates the construction, parameterization, and analysis of mass-balanced trophic models of aquatic and terrestrial ecosystems [36]. Ecopath provides a mass-balanced snapshot of an ecosystem, and is widely used to assess marine ecosystem structures and fisheries' impacts [20,34,36,37].

Models quantify the biomass of living and non-living components within an ecosystem and their energy flows, simplifying the complexities to provide a summarized description of an ecosystem's nature. They also predict ecosystem changes following disturbances [1,38]. Network analysis further enhances our understanding of energy flow direction and magnitude within ecosystems and the efficiency of energy transfer among different groups

of organisms. In mass-balanced models, fisheries data can be integrated to comprehensively understand interspecific interactions, habitat dynamics, and impacts on the physical environment [39,40].

In the present study, we collected high-resolution data on fisheries activity in the TB region and constructed mass-balanced models using EwE to analyze the influence of ENSO events on the TB ecosystem. We think ENSO will cause changes in the ecosystem structure, with each species having a different level of impact on other species within the ecosystem. Developing a holistic ecosystem management system is essential to mitigate the impact of environmental changes on marine ecosystems in TB. Such management systems should consider not only the dynamics of target species, but also nontarget organisms, trophic relationships and energy flows, and environmental factors [34,41]. The current results may be valuable for evaluating the impacts of stressors on the structure and function of various marine ecosystems.

2. Materials and Methods

2.1. The Study Area

Sea-surface temperature (SST) is relatively high in the southern TB region, but in the northern region, cold northern China coastal currents and continental upwelling reduce the SST and bring nutrients, increasing net primary productivity (NPP; Figure 1).

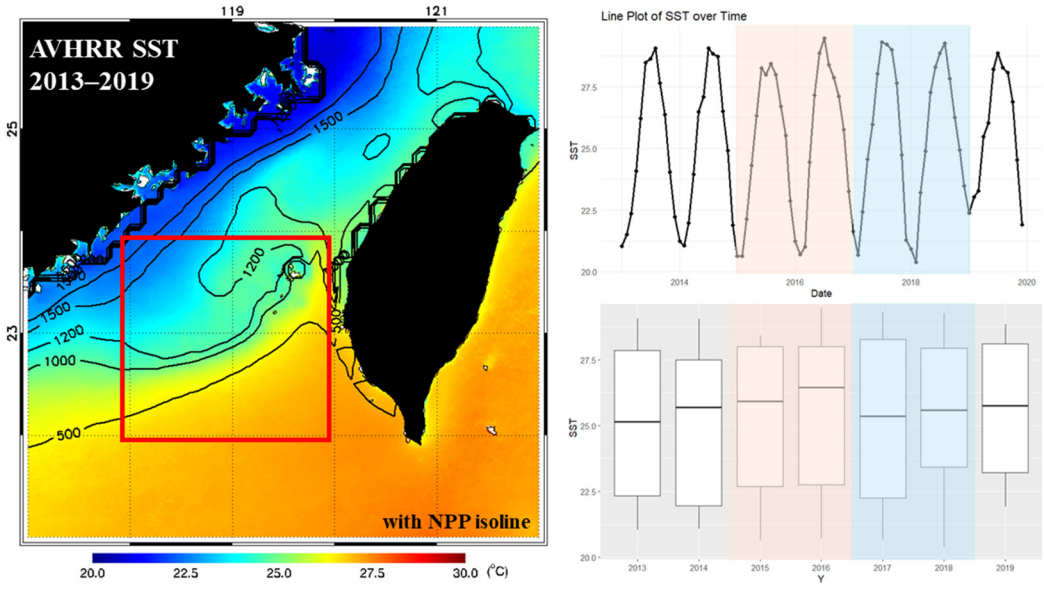


Figure 1. SST (contour) and NPP (isoline) distribution in the TB ecosystem (red frame) from 2013 to 2019: El Niño/La Niña period shows in orange/blue color.

Oceanographic studies have indicated that upwelling and thermal fronts have a considerable impact on biogeochemical processes and ecosystem structure [4,6]. Moreover, fishing methods and fishery resource structures are complex and vary considerably in TB. Also, TB is characterized by a large diversity of coral and reef species, and the currents and water depth create a suitable habitat for migratory species [4,6]. Ecosystem structure and function in the Taiwan Strait have been altered due to changes in multiple climate-related and anthropogenic drivers [6,42,43].

2.2. Data Collection and EwE Modeling

In the study area, the most prominent (>75%) fishing methods involve the use of Taiwanese seines and trawls. Considering the top 30 species in the area, based on daily high-grid-resolution observer-recorded fisheries data and commercially crucial species from previous research, we included 28 groups in our TB ecosystem model. Moreover,

phytoplankton were included as major producers, whereas zooplankton were considered the major consumers. According to life history strategies and the behavioral features of reproductive biology based on the FishBase database (http://www.fishbase.org) [44], the groups were classified further into pelagic and benthic (including reef, demersal, and benthopelagic species).

Our trophic model was constructed using EwE (version 6.6.8) [45], and the energy production and consumption for each species was estimated. Equations (1) and (2) present the mass-balanced Ecopath model:

$$(P/B)_i \times B_i = Y_i + \sum_j B_j \times (Q/B)_j \times DC_{ji} + E_i + BA_j + (P/B)_i \times B_i(1 - EE_i), \quad (1)$$

where i is a group species, j is the predator, (P/B) is the production-to-biomass ratio, B is the biomass (i.e., wet weight in t km^{-2}), Y is the total catch, (Q/B) is the consumption-to-biomass ratio, DC_{ji} is the proportion of i in the diet of j, E is the net migration rate (emigration − immigration), BA is the biomass accumulation rate, EE_i is the ecotrophic efficiency [i.e., the proportion of production or total mortality (where $P/B = Z$) that is actually explained in the model], and $(1 - EE_i)$ is the proportion of unexplained production (i.e., mortality due to reasons other than predation and fishing). These relationships are fundamentally derived from the concept that production equals consumption [46].

$$Q_i = P_i + R_i + GS_i \times Q_i, \quad (2)$$

where Q_i, P_i, R_i, and $GS_i \times Q_i$ are the consumption, production, respiration, and unassimilated food of the group species i, respectively. This equation reflects the fundamental ecological principle that total energy intake (consumption) is partitioned into production, respiration, and the energy lost as unassimilated food.

To analyze the effects of ENSO events on the TB ecosystem, three Ecopath models for normal years (2013, 2014, 2019), El Niño events (2015–2016), and La Niña events (2017–2018) were developed at 118° E–120° E, 22° N–24° N (Figure 1, red frame), and we assumed the net migration rate was 0.

2.3. Ecosystem Attributes

The input data sources and citations for P/B, Q/B, and DC are listed in Tables 1 and 2, and Tables A1–A3. The biomass density estimates for fish, cephalopods, and crustaceans were obtained from daily high-grid-resolution observer-recorded fisheries data and by using the following transform formula:

$$B = \frac{C_i}{G_i \times D_i \times (1 - e^{-F})}, \quad (3)$$

where C_i is the fishery catch in group i, G_i is the occurrence area in group i, D_i is the number of fishing trips in group i, F is fishing mortality, and B is wet weight (in t km^{-2}). The biomass estimate is derived from the equation $B = Y/F$ [47], as proposed by Ullah et al. [48], where Y is the annual average yield of each group and F is the fishing mortality coefficient.

The diet of each fish compartment was used as a weighted average of the diet composition of different species within each compartment (Tables A1–A3). For TB fish without available diet information, data were obtained from FishBase [44]. Fishing data constitute a fraction of the ecosystem, and are calculated in tones per kilometer^2 per year. Zooplankton biomass was estimated via trawl survey data with an ORI plankton net from a government research unit (Fisheries Research Institute, Ministry of Agriculture) and converted from m^{-3} to m^{-2} by multiplying by mean depth (100 m).

Phytoplankton biomass was estimated using chlorophyll-a volume concentrations (mg m^{-3}) determined by a Moderate-Resolution Imaging Spectroradiometer aboard the Aqua Satellite (MODIS Aqua). First, these were converted to surface concentrations (mg m^{-2}) based on the methods of [49]. The surface chlorophyll-a concentrations were

multiplied by a conversation factor of 400 to convert these values to wet weight (mg m^{-2}), as described in Link et al. [50] and Watari et al. [37].

Table 1. Groups and input resources. Biomass of detritus from Ye et al. [51]; grey highlight represents the Benthic groups.

	Groups	Common Name	*P/B*	*Q/B*	*DC*
Predator fish	*Thunnus albacares*	Yellow fin tuna	Fishbase	Fishbase	Fishbase, SeaLife Base, The Fish Database of Taiwan
	Katsuwonus pelamis	Skipjack tuna	Fishbase	Fishbase	
	Coryphaena hippurus	Dolphinfish	Fishbase	Fishbase	
	Scomberomorus commerson	Spanish mackerel	Fishbase	Fishbase	
Pelagic fish	*Scomber australasicus*	Spotted mackerel	Duan [52]	Fishbase	
	Scomber japonicus	Chub mackerel	Duan [52]	Fishbase	
	Trachurus japonicus	Japanese jack mackerel	Duan [52]	Fishbase	
	other mackerels	other mackerels	Duan [52]	Fishbase	
	Auxis rochei rochei	Bullet tuna	Duan [52]	Fishbase	
Small pelagic fish	*Etrumeus micropus*	Pacific round herring	Duan [52]	Fishbase	
	Sardinella spp.	*Sardinella* spp.	Duan [52]	Fishbase	
	Decapterus maruadsi	Round scad	Lin [53]	Fishbase	
Benthic and Reef fish	*Seriola dumerili*	Amberjack	Lin [53]	SeaLife Base	
	Mene maculata	Moonfish	Lin [53]	Fishbase	
	Decapterus kurroides	Mackerel scad	SeaLife Base	Fishbase	
	Polydactylus sextarius	Polynemid fish	Duan [52]	SeaLife Base	
Cephalopod	*Uroteuthis chinensis*	Mitre squid	Lin [53]	Lin [53]	
	Loliginidae	Squids	Lin [53]	Lin [53]	
Crustaceans	*Portunus sanguinolentus*	*Portunus sanguinolentus*	Lin [53]	Lin [53]	
	Penaeus japonicus	*Penaeus japonicus*	Wang [54]	Wang [55]	
	Penaeus penicillatus	*Penaeus penicillatus*	Wang [54]	Wang [55]	
	Metapenaeopsis barbata	*Metapenaeopsis barbata*	Wang [54]	Wang [55]	
	Metanephrops thomsoni	*Metanephrops thomsoni*	Wang [54]	Wang [55]	
Zooplankton	Zooplankton_P	Zooplankton_Pelagic	Lin [53]	Lin [53]	
	Zooplankton_B	Zooplankton_Benthic	Lin [53]	Lin [53]	
Phytoplankton	Phytoplankton_P	Phytoplankton_Pelagic	Lin [53]		
	Phytoplankton_B	Phytoplankton_Benthic	Lin [53]		
Detritus	Detritus	Detritus			

Table 2. Basic parameters of three Ecopath models (normal; El Niño; and La Niña).

	No.	Group Name	Group Name	El Niño Biomass (t/km^2)	La Niña Biomass (t/km^2)	Normal Biomass (t/km^2)	El Niño Landing (t/Year)	La Niña Landing (t/Year)	Normal Landing (t/Year)	*P*/*B* (/Year)	*Q*/*B* (/Year)	*P*/*Q* (/Year)
Predator fish	1	*Thunnus albacares*	Yellow fin tuna	0.822	**1.019**	0.704	0.287	**0.494**	0.449	2.65	11.64	0.228
	2	*Katsuwonus pelamis*	Skipjack tuna	0.455	**0.518**	0.380	0.158	0.280	**0.294**	2.62	12.53	0.209
	3	*Coryphaena hippurus*	Dolphinfish	**1.366**	0.046	0.248	0.114	0.001	**0.211**	3.71	8.48	0.438
	4	*Scomberomorus commerson*	Spanish mackerel	0.212	**0.615**	0.598	0.796	0.005	**0.861**	4.5	11.4	0.395
Pelagic fish	5	*Scomber australasicus*	Spotted mackerel	3.519	**4.187**	2.136	1.470	**1.613**	1.358	4.3	8.8	0.489
	6	*Scomber japonicus*	Chub mackerel	2.275	0.980	**2.423**	**0.167**	0.156	0.066	4.8	11.7	0.410
	7	*Trachurus japonicus*	Japanese jack mackerel	**1.240**	0.684	0.607	**1.494**	1.037	1.247	4.11	10	0.411
	8	other mackerels	other mackerels TD	4.724	**18.574**	0.052	0.062	**0.111**	0.002	2.22	9.6	0.231
	9	*Auxis rochei rochei*	Bullet tuna	1.302	1.269	0.568	0.065	0.151	**0.201**	4.8	10.6	0.453
Small pelagic fish	10	*Etrumeus micropus*	Pacific round herring	2.898	1.910	**3.778**	0.366	0.125	**0.610**	4.2	14.04	0.299
	11	*Sardinella* spp.	*Sardinella* spp.	3.699	**19.140**	2.149	**0.605**	0.100	0.457	5.1	11.6	0.440
	12	*Decapterus maruadsi*	Round scad	8.381	**10.317**	1.239	**0.823**	0.072	0.104	3.1	9.08	0.341
Benthic and Reef fish	13	*Seriola dumerili*	Amberjack	2.177	**3.188**	1.946	0.219	0.023	**0.280**	1.2	3.3	0.364
	14	*Mene maculata*	Moonfish	**8.099**	5.739	2.188	**4.574**	0.472	2.965	2.64	6.7	0.394
	15	*Decapterus kurroides*	Mackerel scad	**5.306**	1.967	2.004	**0.369**	0.078	0.112	1.97	7.1	0.277
	16	*Polydactylus sextarius*	Polynemid fish	0.444	0.368	**0.718**	**0.117**	0.052	0.025	2.34	11.1	0.211
Cephalopod	17	*Uroteuthis chinensis*	Mitre squid	1.248	**1.872**	1.322	0.207	0.207	**0.328**	4.7	11.64	0.404
	18	Loliginidae	Squids	0.355	0.202	**1.279**	0.123	0.007	**0.422**	4.7	11.64	0.404
Crustaceans	19	*Portunus sanguinolentus*	*Portunus sanguinolentus*	**0.127**	0.051	0.038	0.040	0.050	**0.072**	4.93	14.5	0.340
	20	*Penaeus japonicus*	*Penaeus japonicus*	**0.046**	0.038	0.033	0.045	**0.066**	0.065	8.6	15.6	0.551
	21	*Penaeus penicillatus*	*Penaeus penicillatus*	**0.158**	0.086	0.097	0.008	**0.094**	0.058	8.6	15.6	0.551
	22	*Metapenaeopsis barbata*	*Metapenaeopsis barbata*	**0.269**	0.184	0.159	**0.316**	0.115	0.131	7.6	12.22	0.622
	23	*Metanephrops thomsoni*	*Metanephrops thomsoni*	**0.597**	0.323	0.293	0.001	0.163	**0.250**	5.65	14.2	0.398
Zooplankton	24	Zooplankton_P	Zooplankton_P	10	10	10	0	0	0	25	180	0.139
	25	Zooplankton_B	Zooplankton_B	10	10	10	0	0	0	25	180	0.139
Phytoplankton	26	Phytoplankton_P	Phytoplankton_P	22.1	22	21.5	0	0	0	106.52		
	27	Phytoplankton_B	Phytoplankton_B	22.1	22	21.5	0	0	0	106.52		
Detritus	28	Detritus	Detritus	163.5	163.5	163.5	0	0	0			
Sum				277.418	300.78	251.458	12.425	5.473	10.569			

Grey highlight represents the Benthic groups, also Bolt highlight the highest within 3 events.

2.4. Model Balancing and Verification

Because *DC* is more uncertain than other parameters, the *DC* of each group was used as the main adjustment parameter in the model-balancing process. The rationality of the model was judged by examining the *EE* of each group. The gross food conversion efficiency was expected to correspond to P/Q. First, because the basic assumption of the model is that the system is in a steady state with constant biomass during the study period, the *EE* of each group must not be >1; in other words, the amount of each group consumed in the ecosystem (feeding and catching) must not exceed the amount of production [36].

Most groups have a P/Q between 0.05 and 0.3 [45]. Top predators have a lower P/Q, whereas smaller species have a higher P/Q; for instance, crustaceans have a $P/Q \leq 0.5$ [56]. The respiration of the groups was also examined for positive values and for whether *P/Q* was lower than the net transfer efficiency (production/assimilated) to ensure the rationality of the model [36,57].

2.5. Ecosystem Assessment and Statistical Analysis

2.5.1. Basic Ecosystem Indices

Total trophic flow comprises respiration, consumption, flow to detritus, export, and import. The total system throughput (TST), defined as the sum of the flows, is an indirect indicator of ecosystem size [58]. Lindeman [21] provided a means for estimating the flows and biomass transferred through trophic levels (TLs) and for calculating the transfer efficiency. A TL is defined as the position of a group within the food web. Transfer efficiency is defined as the ratio of the production of each TL passed on to the next TL.

Several indices and indicators represent ecosystem structure, function, development, and maturity, and can be derived using EwE based on trophic energy transfer pathways [35,45]. The Shannon diversity index represents the biodiversity of species in a community. The system omnivory index (SOI) and connectance index (CI) reflect the complexity of inner linkages within an ecosystem [36]. Finn's cycling index (FCI)—calculated as recycled total flow divided by TST—quantifies the relative importance of cycling to TST and reflects stress and structural differences [59].

2.5.2. Mixed Trophic Impact Analysis

Mixed trophic impact (MTI) analysis was used to quantify the negative or positive effects that an increase in a group's biomass had on the other groups in the ecosystem, as follows:

$$\varepsilon_i = \sqrt{\sum_{j=1}^{n} m_{ij}^2}, \quad (4)$$

where ε_i is the overall effect for the groups from the ecological model and m_{ij} denotes the relative impact of a slight increase in group i's biomass on the biomass of impacted group j, which could be positive (if the impacted group's biomass increases) or negative (if the impacted group's biomass decreases) [60].

The MTI routine depicts the relative impact measurement (direct or indirect) between the groups and is based on a sensitivity analysis [61]. The impacts are relative but comparable, and they were calculated with values ranging from -1 to 1. Two types of value were calculated: a positive value when two groups mutually benefited from each other and a negative value when two groups did not mutually benefit from each other. The groups with lower TL components (detritus, zooplankton, and phytoplankton) demonstrated a strong positive impact on the other groups [62].

2.5.3. Keystoneness Index

Keystone species are species with a relatively low biomass that take on a structuring role in the ecosystem and its food webs [55]. Keystone species can be identified by plotting the relative overall effect (ε_i) against the keystoneness index (KS_i) [60]. Mean trophic efficiency describes the effectiveness of energy transfer between TLs. Trophic interactions

within the food web were analyzed through MTI analysis to obtain trophic impact (ε_i) and relative biomass (p_i), and thus estimate KS_i:

$$KS_i = \log[\varepsilon_i(1 - p_i)], \quad (5)$$

where p_i is the contribution of group i to the total biomass of the food web.

$$p_i = \frac{B_i}{\sum_{i=1}^{n} B_i}, \quad (6)$$

where B is the biomass of group i.

2.5.4. Top–Down and Bottom–Up Effects

TD and BU effects can be estimated using the negative and positive elements in the MTI matrix, respectively [60]. The TD effect of group i was estimated as having a negative contribution to the overall effect, and BU = 1 − TD [60]. The TD effect can be calculated as follows:

$$\mathrm{TD} = \frac{\sum_{j \neq i}^{n} m_{ij}^2 (m_{ij} < 0)}{\sum_{j \neq i}^{n} m_{ij}^2}, \quad (7)$$

where m_{ij} is the element of the MTI matrix that represents the relative impact of the impacting group i on the impacted group j.

3. Results

3.1. TB Marine Ecosystem

In total, 28 groups were selected and balanced in the three Ecopath models: normal years, El Niño events, and La Niña events (Tables A4–A6). The TST was 10,556.3 t km^{-2} year^{-1}, and energy transfer efficiency from the first TL to the next TL up was 12.26% in normal years (Table 3). In terms of ecosystem structure, the total number and mean length of the pathways were 2108 and 7.757, respectively. The SOI, Shannon diversity index, and CI values were 0.247, 2.313, and 0.269, respectively; the maximum TL was 3.75 for skipjack tuna, and the mean TL of catch was 2.73.

Table 3. Summary of TB Ecopath model—statistics and attributes. Grey highlights the highest value of the three models.

	Parameter	La Niña	Normal	El Niño	Unit
Ecosystem Structure	Total number of pathways	824	2108	345	
	Mean length of pathways	7.217	7.757	6.774	
	System omnivory index	0.333	0.247	0.264	
	Shannon diversity index	2.462	2.313	2.557	
	Connectance Index	0.267	0.269	0.265	
	Maximum trophic level	3.866	3.751	3.782	
Ecosystem productivity	Total system throughput	11,121.62	10,556.30	10,957.02	t/km^2/year
Cycles and Flows	Transfer efficiency	15.69%	12.26%	13.40%	
	Cycling index (Finn's)	0.555	0.152	0.288	% of throughput
Consumption and Respiration	Sum of all consumption	4315.664	3853.056	4057.582	t/km^2/year
	Sum of all export	1989.309	2091.331	2127.226	t/km^2/year
	Sum of all respiratory	2697.572	2489.028	2580.958	t/km^2/year
	Sum of all flows into detritus	2119.073	2122.888	2191.254	t/km^2/year
Fishery	Landing	5.473	10.569	12.425	t/km^2/year
	Mean trophic level of catch	2.995	2.730	2.663	

The mass-balanced diagrams of the food web components and energy flows revealed that the biomass of pelagic species, particularly pelagic and small pelagic fish, was higher than that of the other group species (Figure 2 and Table 2).

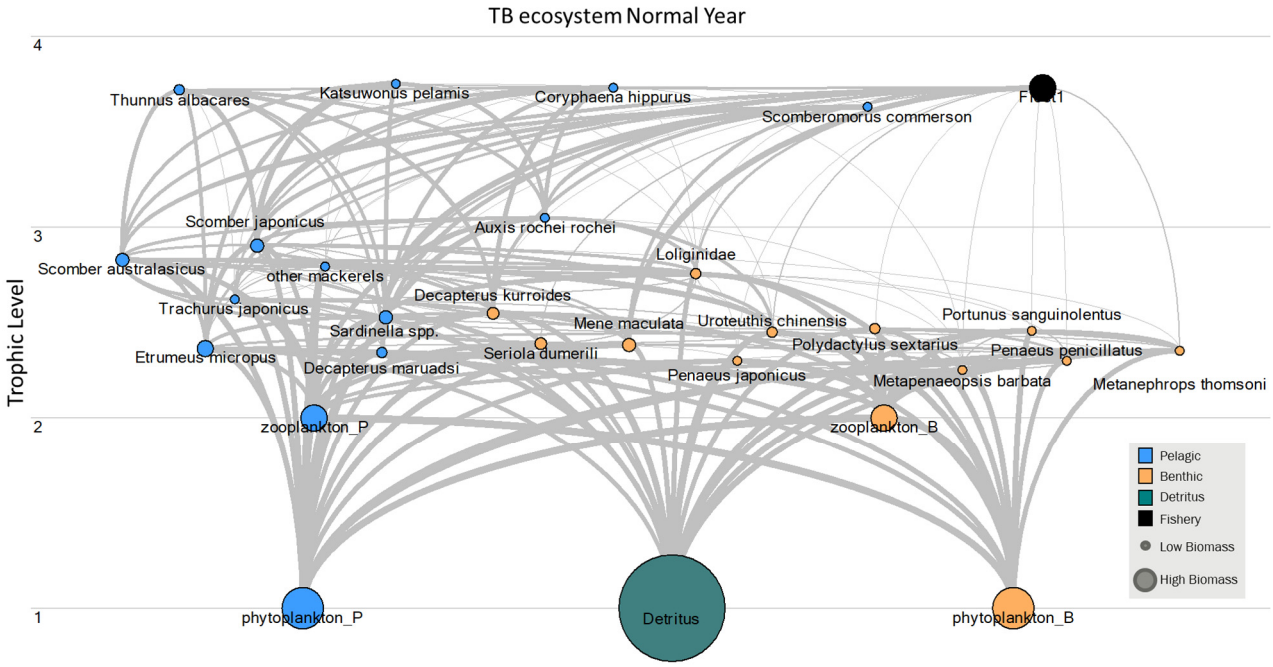


Figure 2. Trophic relationships between groups in the TB ecosystem in normal years. Circle size denotes biomass volume of each group.

Among the benthic and reef group, benthic and reef fish had a higher biomass than cephalopods and crustaceans did. The groups were mainly in TL 2 and TL 3, with 36% TST (Figure A1). The top predators (TL 4) in the TB ecosystem were *Thunnus albacares*, *Katsuwonus pelamis*, *Coryphaena hippurus*, and *Scomberomorus commerson*, which had low *EE* values (Figure 2 and Table A4). However, commercial species such as mackerel and *Mene maculata*, and prey species, including shrimps and crabs, had high *EE* values.

Regarding consumption and respiration, total consumption was 3853.056, total export was 2091.311, total respiration was 2489.028, total flow into detritus was 2122.888, and FCI value was 0.152% of the throughput (Table 3).

3.2. Interspecies Relationships

The interspecies relationships between groups in the TB ecosystem revealed that the MTI of pelagic species was considerably higher (Figure 3, area I) than that of benthic and reef species (Figure 3, area II); pelagic species also had mostly negative impacts due to their role as the top–down controllers of predation. However, the predator fish *C. hippurus* had a lower influence than *T. albacares* and *K. pelamis* did. The pelagic fish were mainly positively influenced by plankton and cephalopods but negatively influenced by predator fish, other pelagic species, and benthic species. Small pelagic fish generally had a negative impact on benthic species.

Most benthic species had a relatively low and negative impact, and they were mainly influenced by other benthic species (Figure 3, area II). However, benthic–pelagic coupling mainly occurred for the four benthic groups of *Uroteuthis chinensis*, Loliginidae, *M. maculata*, and *Decapterus kurroides*, with a high impact on both pelagic and other benthic species (Figure 3, groups 14–15, 17–18). Crustaceans (Figure 3, groups 19–23) had a low impact on the TB ecosystem, whereas fishing had a direct negative impact on commercial and target species. Moreover, all group species had a negative impact on themselves and their prey because of intraspecific competition and predation, respectively.

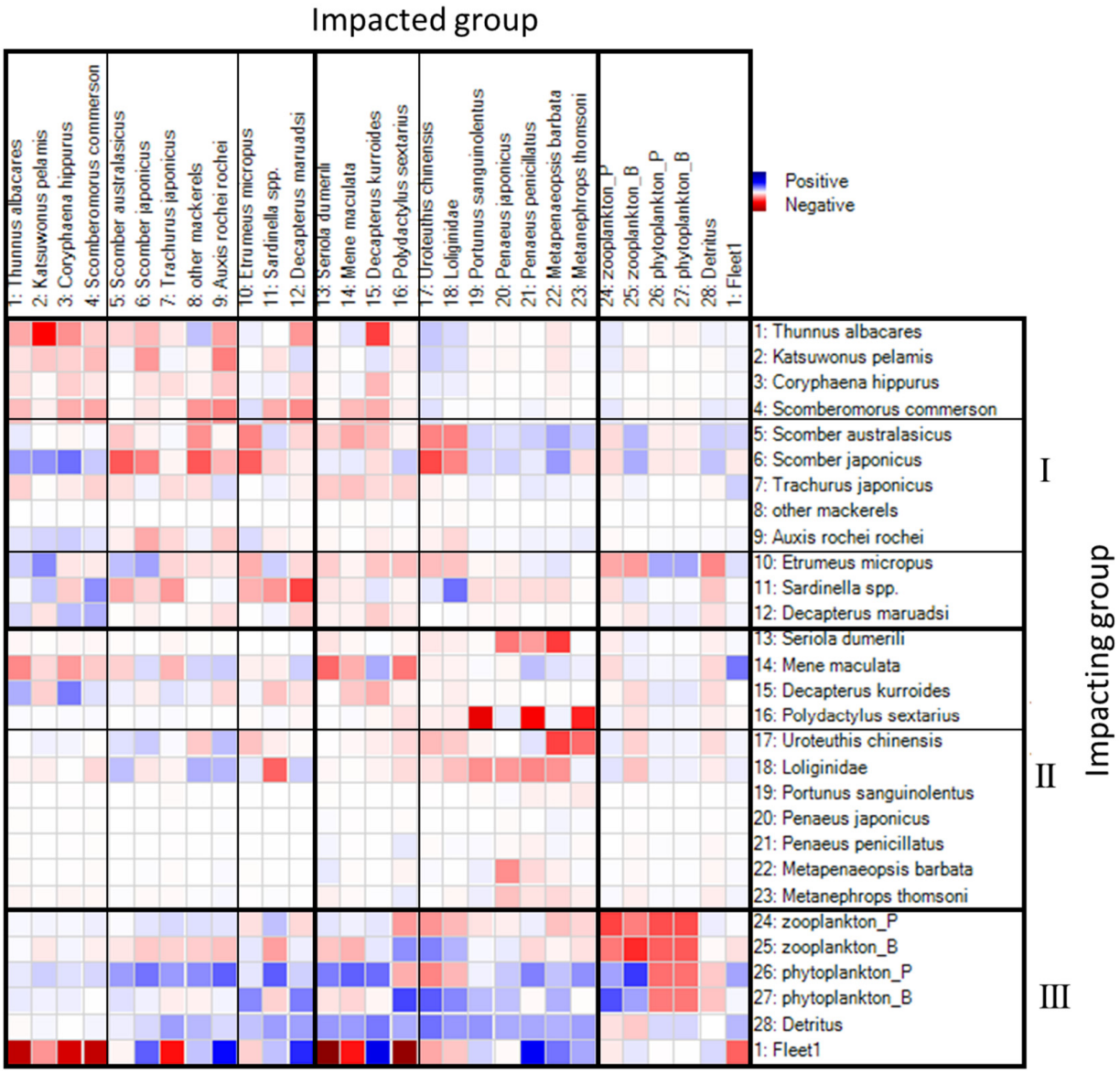


Figure 3. MTI relationships between groups and fisheries in the TB ecosystem. Positive (blue) and negative (red) values indicate positive and negative impacts, respectively; the colors cannot be interpreted in an absolute sense because the impact is relative but comparable between groups.

Zooplankton and phytoplankton had the largest positive impact on the ecosystem due to their role as bottom–up providers of prey (Figure 3, area III).

Fishing negatively affected most benthic species and all predators, but it positively affected pelagic fish and small pelagic fish. The overall TD and BU values were 0.699 and 0.301, respectively (Table 4), indicating that top–down control has a relatively high impact on the TB ecosystem.

Based on their KS_i and relative total impact, *Polydactylus sextarius*, *Scomber japonicus*, and pelagic phytoplankton were the top-three potential keystone species (Figure 4).

Table 4. Control effects in TB ecosystem model (TD, top–down effect; BU, bottom–up effect). Grey highlight represents Benthic groups.

	No.	Group Name	El Niño TD	La Niña TD	Normal TD	El Niño BU	La Niña BU	Normal BU
Predator fish	1	*Thunnus albacares*	0.866	0.847	0.939	0.134	0.153	0.061
	2	*Katsuwonus pelamis*	0.896	0.956	0.871	0.104	0.044	0.129
	3	*Coryphaena hippurus*	0.935	0.975	0.936	0.065	0.025	0.064
	4	*Scomberomorus commerson*	0.774	0.972	0.957	0.226	0.028	0.043
Pelagic fish	5	*Scomber australasicus*	0.756	0.697	0.752	0.244	0.303	0.248
	6	*Scomber japonicus*	0.692	0.371	0.684	0.308	0.629	0.316
	7	*Trachurus japonicus*	0.628	0.600	0.788	0.372	0.400	0.212
	8	other mackerels	0.803	0.475	0.783	0.197	0.525	0.217
	9	*Auxis rochei rochei*	0.728	0.568	0.642	0.272	0.432	0.358
Small pelagic fish	10	*Etrumeus micropus*	0.599	0.620	0.565	0.401	0.380	0.435
	11	*Sardinella* spp.	0.912	0.766	0.688	0.088	0.234	0.312
	12	*Decapterus maruadsi*	0.549	0.682	0.425	0.451	0.318	0.575
Benthic and Reef fish	13	*Seriola dumerili*	0.998	0.996	0.996	0.002	0.004	0.004
	14	*Mene maculata*	0.707	0.518	0.685	0.293	0.482	0.315
	15	*Decapterus kurroides*	0.629	0.355	0.439	0.371	0.645	0.561
	16	*Polydactylus sextarius*	0.982	0.998	0.995	0.018	0.002	0.005
Cephalopod	17	*Uroteuthis chinensis*	0.884	0.963	0.887	0.116	0.037	0.113
	18	Loliginidae	0.950	0.970	0.812	0.050	0.030	0.188
Crustaceans	19	*Portunus sanguinolentus*	0.948	0.913	0.968	0.052	0.087	0.032
	20	*Penaeus japonicus*	0.304	0.293	0.297	0.696	0.707	0.703
	21	*Penaeus penicillatus*	0.329	0.298	0.385	0.671	0.702	0.615
	22	*Metapenaeopsis barbata*	0.977	0.956	0.940	0.023	0.044	0.060
	23	*Metanephrops thomsoni*	0.856	0.817	0.886	0.144	0.183	0.114
Zooplankton	24	Zooplankton_P	0.946	0.909	0.934	0.054	0.091	0.066
	25	Zooplankton_B	0.790	0.819	0.808	0.210	0.181	0.192
Phytoplankton	26	Phytoplankton_P	0.240	0.212	0.209	0.760	0.788	0.791
	27	Phytoplankton_B	0.181	0.174	0.212	0.819	0.826	0.788
Detritus	28	Detritus	0.025	0.038	0.023	0.975	0.962	0.977
Fleet		Fleet	0.739	0.790	0.763	0.261	0.210	0.237
Mean		Mean	0.711	0.674	0.699	0.289	0.326	0.301

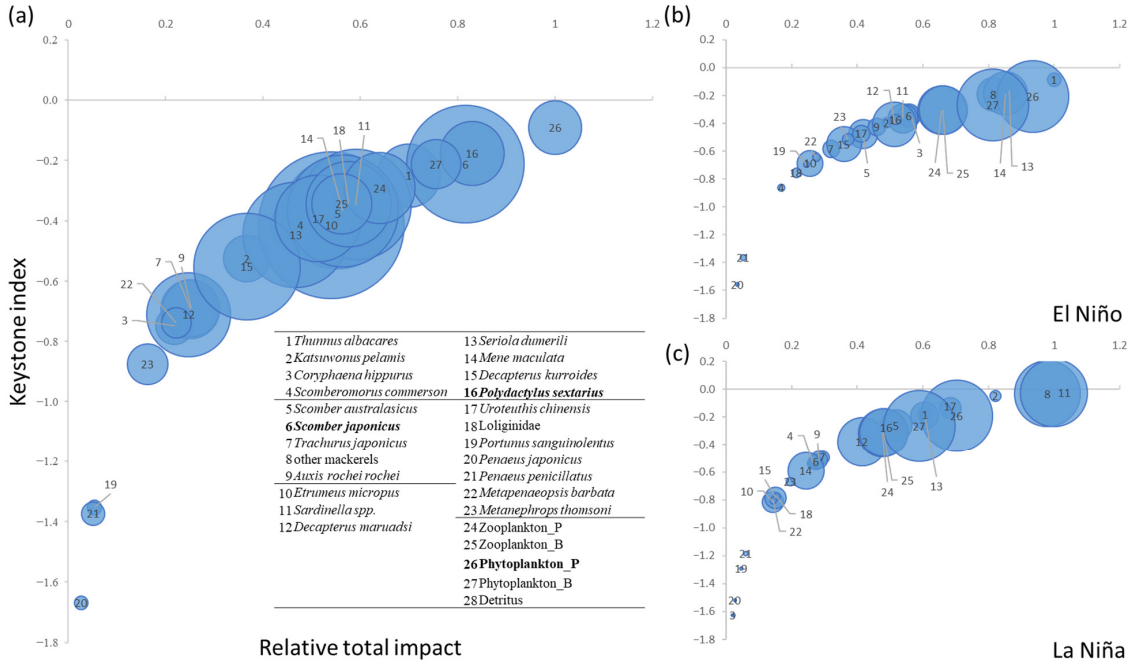


Figure 4. KS_i and relative total impact on the groups from the TB ecosystem model during (**a**) normal years, (**b**) El Niño events, and (**c**) La Niña events. Top-3 species with high KS_i shown in bold.

3.3. Climate-Induced Species Variation in TB Ecosystem

During El Niño events, the ecosystem structure, transfer efficiency, and fishing trophic levels were smaller than in normal years and during La Niña events (Table 3). However, TST, consumption, respiration, and transfer efficiency were higher in both El Niño and La Niña events, with the highest values during La Niña events. Moreover, during La Niña events, the biomass of most pelagic and small pelagic fish was higher than that of other species.

The pelagic and small pelagic fish that demonstrated a relatively high biomass in La Niña events included *Scomber australasicus*, *S. japonicus*, other mackerels, *Etrumeus micropus*, *Sardinella* spp., and *Decapterus maruadsi*. By contrast, the biomass of almost all benthic and reef species (including cephalopods and crustaceans) was relatively high during El Niño events but relatively low during La Niña events, especially for *M. maculata* and *D. kurroides* (Table 2). During El Niño events, the Shannon diversity index was relatively high but the SOI, CI, catch TL, and TST were relatively low (Table 3).

Our MTI analysis results demonstrated similar trends: during El Niño and La Niña events, zooplankton and phytoplankton positively affect other species, serving as bottom–up providers, while predator fish, especially yellowfin and skipjack tuna, negatively affect other species as top–down controls (Figure 5).

However, based on the changes in MTI for each group, during El Niño events, the impact percentages of *C. hippurus*, *M. maculate*, and *D. kurroides* increased from 0. 15%, 2.31%, and 1.13%, respectively, to 3.47%, 6.65%, and 2.64%, respectively, whereas those of *Saddnella* spp., other mackerels, and *S. australasicus* decreased from 9.68%, 8.81%, and 5.12% to 3.06%, 5.14%, and 2.28%, respectively (Figure 6).

Moreover, during El Niño events, pelagic phytoplankton (7.46%) was the most influential species, followed by *M. maculate* and plankton, whereas *C. hippurus* negatively affected most pelagic species. Fishing had the greatest influence during El Niño events, followed by normal years, and finally, by La Niña events. The influence of fisheries on benthic species gradually changed from negative to positive during El Niño events.

According to their KS_i and RTI, *P. sextarius*, *S. japonicus*, and pelagic phytoplankton were the top-three groups in TB's normal years (Figure 4, Table A7). We assume the main keystone species are *P. sextarius* and *S. japonicus* due to their low biomass and significant BU and TD impact. During El Niño events, *T. albacares*, *Seriola dumerili*, and *M. maculata* were the top-three groups in terms of *KSi*; phytoplankton and other mackerels also had high values. We suggest that the main keystone species during El Niño events is *T. albacares*. Although *Sardinella* spp., other mackerels, and *K. pelamis* had high *KSi* levels during La Niña events, we estimate that the keystone species is *K. pelamis*. *C. hippurus* and *Portunus sanguinolentus* revealed lowered KS_i levels during La Niña events (Figure 7).

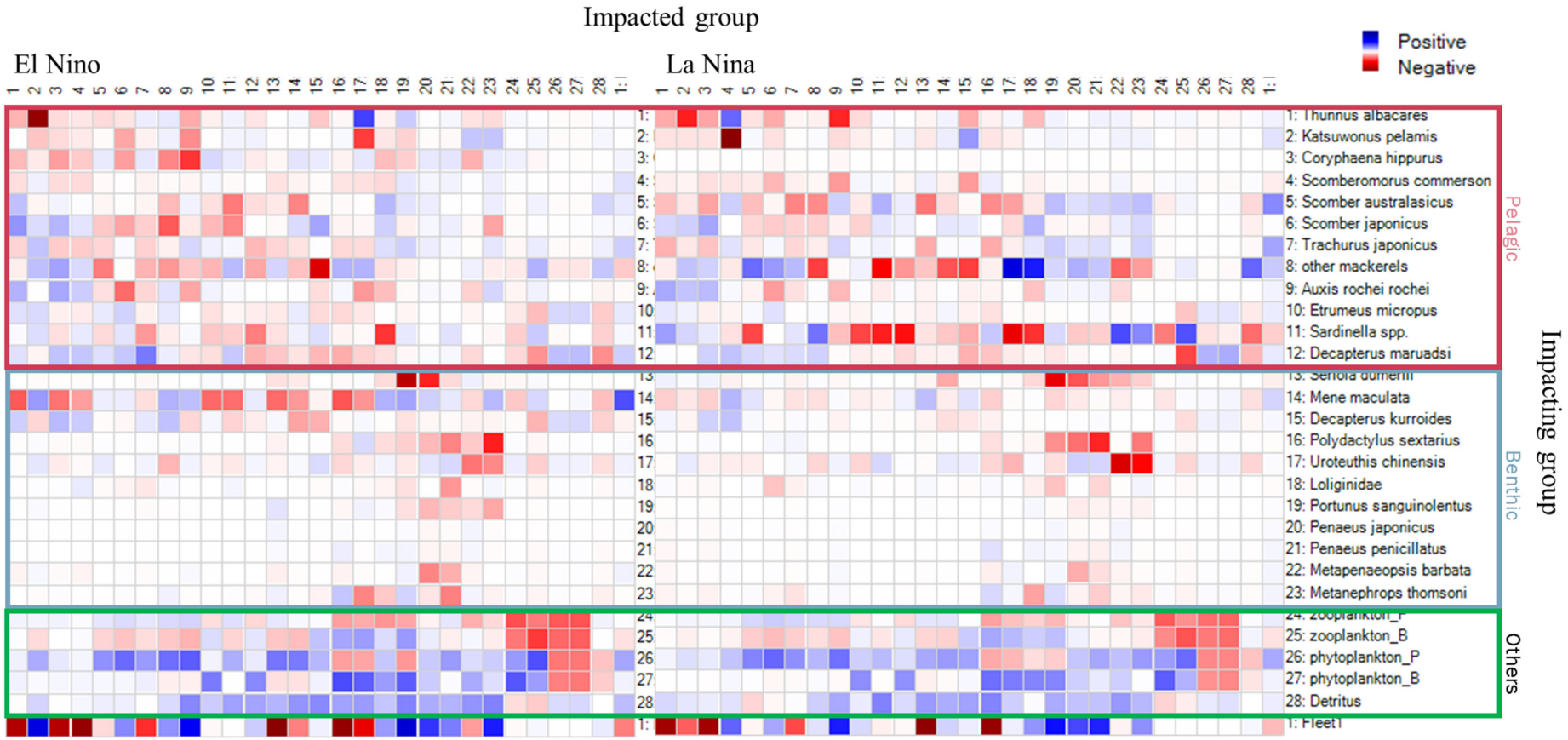


Figure 5. MTI in the TB ecosystem during El Niño and La Niña events. Impacted and impacting groups are arranged along the horizontal and vertical axes, respectively.

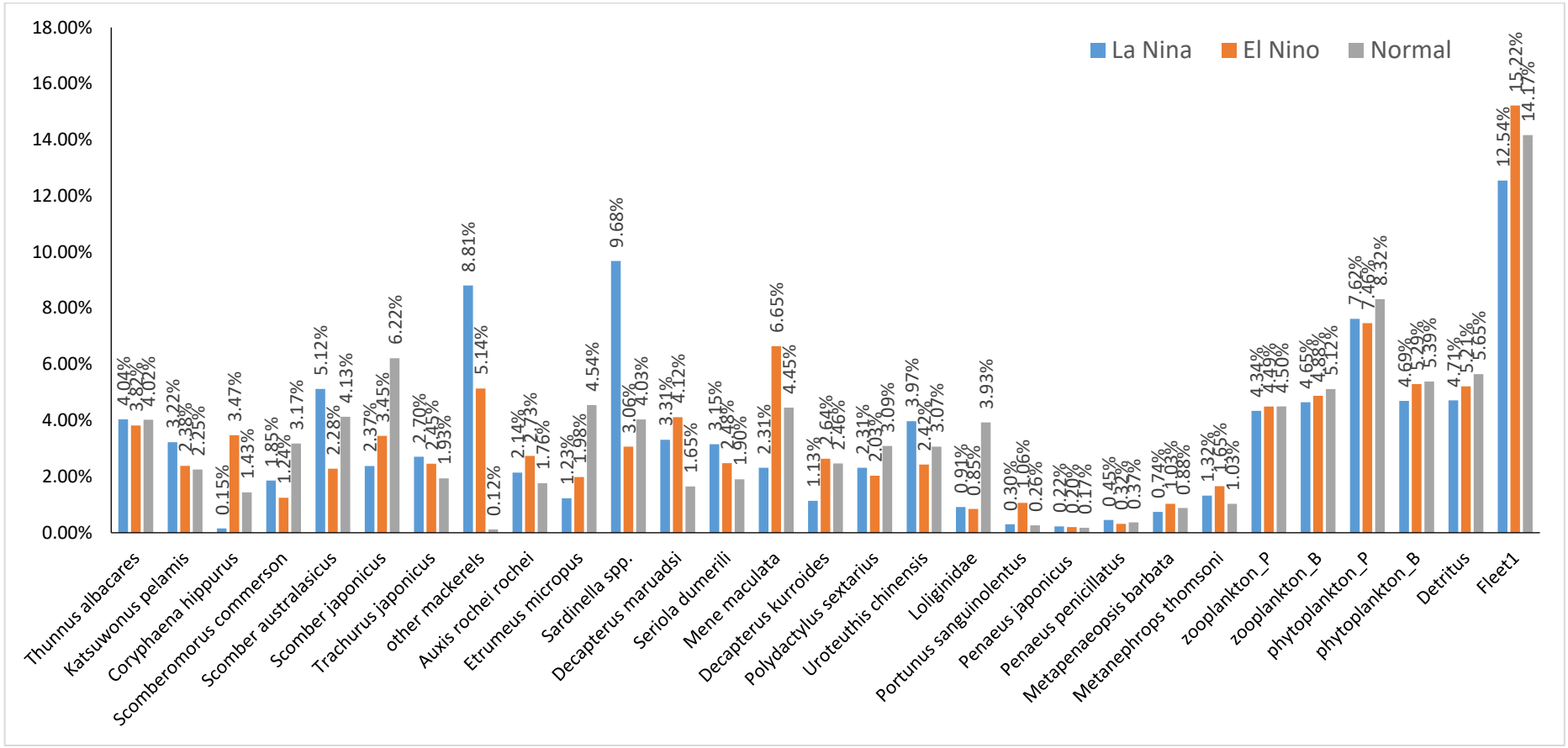


Figure 6. Overall trophic impact percentage variation in groups in the TB ecosystem during normal years and ENSO and La Niña events.

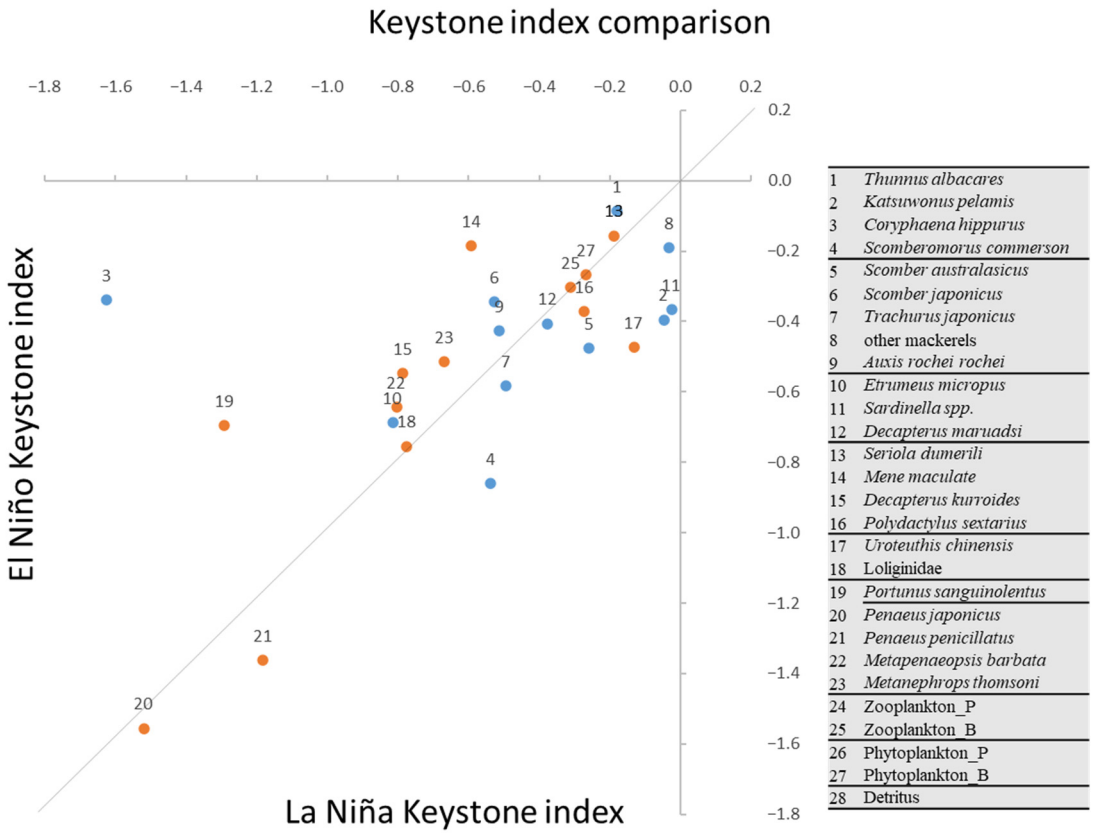


Figure 7. Comparison of KS_i values between El Niño and La Niña events in the TB ecosystem. Blue and orange represent pelagic and benthic respectively.

Moreover, the influence of the TD effect had a relatively high impact on the ecosystem across all three periods (Table 4).

4. Discussion

4.1. TB Ecosystem Structure

Our food web energy flow diagram indicates that TB ecosystems in three periods contain nearly four TLs, with each consumer group concentrated between TLs 2 and 3. The highest group in terms of TL was the predator fish group; moreover, most species, except for a few pelagic predators, had a high *EE*; these species may be essential food sources for predators due to their high *EE* [56]. Detritus had an *EE* of 0.215, indicating that detritus utilization in the TB ecosystem is low compared with production, but there is still some detritus utilization.

The results of our Lindeman's spine analysis demonstrated that the energy flow of the TB ecosystem in each period was mainly concentrated on the basic producers in TL 1 and on the primary consumers in TL 2 (Figure 2, Tables A1–A3). This inference was drawn based on the substantial biomass of large primary consumers and the flattened composition within the ecosystem. Additionally, it highlights that the upwelling ecosystem exhibits high productivity [63]. Across the entire study period, the energy flow of detritus accounted for a relatively low proportion of the total energy flow of TL 1. This result is similar to that for the proportion of producers and detritus during El Niño and La Niña events, indicating that the structural differences among the TLs of the ecosystem are nonsignificant under ENSO events.

In all three TB ecosystem models, a proportion of primary production was not used by organisms and flowed into the detritus stock, which benefited detritus-feeding groups [64]. Other unused detritus in the system may have been decomposed by microorganisms, buried to form sediment, or exported outside the system [56,65]. In the TB ecosystem,

although the transfer efficiency (12.26–15.69%) between each TL was higher than the global ecosystem average (10%) [66,67], the transfer efficiency decreased as TL increased. This result is generally consistent with the results of Lindeman [21] and Ju [20]—the transfer efficiency between nutrient classes decreases as nutrient classes increase—and it is also similar to nearby ecosystems, such as those in the East China Sea, South China Sea, and southern TS (Table 5) [20,68,69].

Table 5. Ecosystem indicators across regions.

Parameters	La Niña	Normal	El Niño	East China Sea	South China Sea	Southern TS
System omnivory index	0.33	0.25	0.26	0.2	0.18	0.21
Shannon diversity index	2.46	2.31	2.56	-	-	-
Connectance index	0.27	0.27	0.26	0.19	0.30	0.22
Total system throughput	11,121.62	10,556.30	10,957.02	-	262,118	18,832.08
Transfer efficiency	15.69%	12.26%	13.40%	14.6%	10.2%	15.57%
Cycling index (Finn's)	0.555	0.152	0.288	0.18	-	0.12
Sum of all consumption/TST (Q/TST)	0.39	0.37	0.37	-	0.01	0.5
Sum of all exports/TST (Ex/TST)	0.18	0.20	0.19	-	0.49	0.03
Sum of all respiratory flows/TST (R/TST)	0.24	0.24	0.24	-	0.01	0.32
Sum of all flows into detritus/TST (FD/TST)	0.19	0.20	0.20	-	0.50	0.16
Mean trophic level of catch	3.00	2.73	2.66	2.71	2.85	3.49
Reference				Jiang et al. [68]	Cheung [69]	Ju et al. [20]

The EE of TB is shown in Tables A4–A6. The top predators in the TB ecosystem had low EE because less mortality occurred due to predation [20]. Commercial species such as *S. australasicus* and *M. maculate* had high EE due to experiencing heavy exploitation and high consumption (i.e., high mortality due to predation), respectively [70]. Prey species such as shrimps and crabs demonstrated high EE due to a high proportion of their production being consumed within the ecosystem [71].

Comparing the results with the East China Sea [68], this study shows higher SOI and lower TE values in the TB. In contrast, compared with the South China Sea [69], TB exhibits higher SOI and TE values, although the mean trophic level of the catch is slightly higher in the South China Sea. The southern TS generally shows similar results; the SOI and CI values in our study are slightly higher than those found by [20], with the major difference being in FCI and the mean trophic level of the catch. The biomass observed in this study is relatively high when compared to the East China Sea and South China Sea, but similar to the southern TS [20]. The high fishing efficiency of Taiwanese seining [6,72], which contributes to over 50% of total catch, leads to a significant increase in biomass. Different fishing methods have varying gear selectivity, leading to the capture of different species. We considered the utilization of multiple fishing methods to integrate the calculation of biomass for different species inhabiting various depths, in order to avoid sampling errors caused by relying on a single fishing method for investigation [73,74]. La Peyre et al. [75] also state that differences in species-specific catch due to gear selectivity could have large consequences for constructing and calibrating fish and ecosystem models that remain difficult to reconcile.

4.2. Trophic Interactions in TB Ecosystem

In an ecosystem, various groups of organisms are affected by the interactions of other groups of organisms. The BU effect is a result of changes in the abundance of organisms at lower TLs, resulting in changes in predator abundance at higher TLs [76]. By contrast, the TD effect is caused by changes in the number of predators at higher TLs, and these effects can be transmitted from top to bottom through the trophic linkage [77,78]. Plankton groups were noted to have the largest positive impact on several groups, including zooplankton and benthic crustaceans, confirming their BU effect in the TB ecosystem [79,80]. The current results demonstrate that phytoplankton had a negative effect on zooplankton, and detritus had a positive effect on all species, except zooplankton. They also reveal that pelagic phytoplankton had a high biomass, *KSi*, and MTI; thus, we consider phytoplankton a dominant species or structure species [20]. Plankton communities are responsible for most of the BU effects in an ecosystem [20,81]. Being an upwelling ecosystem, all plankton groups exhibit high biomass, consistent with the norm [20,63,82];. Due to their higher *KSi*, *P. sextarius* and *S. japonicus* are selected as the two keystone species.

T. albacares and *K. pelamis* had a higher *KSi* with a high and negative MTI during the study period, indicating that an increase in their biomass negatively affects their prey species (small pelagic fishes; this is an example of TD). Predators mainly affect the ecosystem through TD control, as indicated by their negative effects on other groups [83]. Pelagic fish negatively affect small pelagic fish, as well as benthic and reef fish, but they have a positive impact on predators and crustaceans, as indicated by the wasp-waist control and TD control [63,84]. Small pelagic fish demonstrated negative effects on benthic species in general, indicating the presence of predation [70]. Furthermore, the high TD value (70%) demonstrated that the ecosystem is mainly subject to top–down control; this result is consistent with the neighboring ecosystem (TD, 64%) in the northern South China Sea [20]. In the East and South China Seas, top predators such as tuna and mackerel have been identified as keystone species in many ecosystem models [20,60,80]. These high-impact groups tend to exert a strong TD effect.

All crustaceans demonstrated a low influence on the TB ecosystem. *M. maculate*, *D. kurroides*, and cephalopods demonstrated pelagic–benthic coupling with negative effects on the benthic species and positive effects on the pelagic fish; this result indicates the presence of a bridge between pelagic fish and crustaceans in the mesopelagic layer [85]. Pelagic fish move to the mesopelagic layer during the daytime in search of predator refuge and ascend to the surface layer at nighttime for feeding after the nightly ascension of zooplankton [86,87]. Furthermore, small pelagic fish (e.g., *Sardinella* spp. and *E. micropus*) are part of a major mid-TL node in the food web and participate in complex interactions between predators, prey, and competitors [10,88]. Moreover, the relatively high trophic efficiencies in the East China Sea ecosystem highlight a favorable coupling of benthic and pelagic invertebrates with their predators [60,89].

4.3. Climate Impact on TB Ecosystem

During ENSO events, significant changes occurred in terms of biomass, ecosystem structure, productivity, consumption, and respiration in the TB ecosystem. In particular, changes in the marine environment during ENSO events led to an increase in the abundance of specific species, which attracted more organisms to inhabit and forage in the area [6,8,90]. During La Niña events, the SST in the eastern and central tropical Pacific is lower than normal, whereas it is higher than normal during El Niño events [91].

ENSO events have been reported to have various positive and negative effects on the species population in the TS [8,42,90]. Ecosystem structure, transfer efficiency, and mean trophic levels of catch were all smaller during El Niño events than during La Niña events. Benthic and reef species demonstrated a relatively high abundance during El Niño events, which possibly increased the complexity and diversity of pelagic species' diet composition [92]. In general, groups of the pelagic domain tended to have a higher omnivory index than those in the non-pelagic domain [63].

Pelagic fish and small pelagic fish with high biomass and energy consumption led to an increase in TST, consumption, respiration, and mean fishing TL during La Niña events. Because small pelagic fish contain a high calorie content, they are the prey of top predators but the predator of benthic invertebrates [93]. The increase in TST during La Niña events reflects changes in the overall flow of energy within the ecosystem [58]. Similar phenomena have also been observed along the Pacific coast of Central and South America [94,95]). During El Niño events, TB had a low SST and a high NPP in winter, creating a suitable habitat for benthic and reef species [96]. However, in the summer, TB's low SST and high NPP during La Niña events attracts top predators and pelagic species [97]. This is also evident in species interactions. During El Niño years, the keystone species transition from *S. japonicus* and *P. sextarius* to yellowfin tuna, and during La Niña events the keystone species is skipjack tuna. The increased abundance of pelagic fish and small pelagic fish during La Niña events intensifies the impact on the ecosystem, reflected in the values of RTI and MTI. In El Niño years, there is an increase in benthic species abundance, particularly for *M. maculata*. Simultaneously, across the three periods, phytoplankton shows high values for both RTI and MTI indices, especially during normal years, indicating characteristics of an upwelling ecosystem and a bottom–up effect. However, the TD index suggests that TD control remains dominant in ecological control throughout the three periods. The TD index is lowest during La Niña events and highest during El Niño years, possibly due to the negative correlation between upwelling intensity and ENSO [98].

As an ecosystem grows larger, its biodiversity increases, and the linkage between organisms and their food habits changes from a simple chain structure to a more complex network structure [99]. During ENSO events, the La Niña model, with a higher TST, also provided a higher SOI and CI, but a lower system omnivory index due to the increase in the number of pelagic species, such as mackerels and *Sardinella* spp., which carry large amounts of energy. By contrast, in the El Niño model, an increase in the number of benthic species led to the diversification of the food composition of all species and to an increase in the degree of food web linkage with a high SOI, resulting in the development of a highly complex ecosystem [100].

The impact of fisheries on benthic species changed from negative to positive during El Niño events, revealing that fishing leads to composition changes and system ecological effects. The high exploitation of small pelagic fish and benthic predators (i.e., *M. maculate*) has positive effects on benthic invertebrates in terms of reduced predation. Fishing had a negative effect on all top predators, except *K. pelamis*; a positive effect on pelagic and small pelagic fish; and a negative effect on most benthic species. Because of the high exploitation of top predators and benthic species through the TD effect, the number of small pelagic species increased [19,45,67,101,102]

Nevertheless, one limitation of our study that should be acknowledged is the lack of explicit consideration of water temperature effects on biological processes. Temperature plays a crucial role in regulating biological rates, including primary production, metabolic rates (respiration), and consumption [103–105]. While we recognize that environmental factors such as temperature significantly affect these biological rates, we did not use a forcing function to dynamically modify them because Ecopath is a static snapshot mass-balance model that does not account for temporal dynamics. To capture these environmental effects, models like Ecosim, which incorporate time dynamics, are required. Future research could address this limitation by integrating environmental variables into dynamic models to better understand their influence on energy flow and trophic interactions in the TB ecosystem.

5. Conclusions

In the TB ecosystem, the biomass of pelagic species, including pelagic and small pelagic fish, was found to be higher than that of other group species. Moreover, benthic fish and reef species demonstrated a higher biomass than cephalopods and crustaceans did. The keystone species demonstrating the TD effect were *P. sextarius* and *S. japonicus* in normal years. Moreover, El Niño and La Niña events led to different variations in ecosystem structure. During La Niña events, total biomass, TST, consumption, respiration, SOI, and CI were higher, whereas the Shannon diversity index were lower. As such, the biomass of pelagic species was relatively high during La Niña events, and that of almost all benthic species was relatively high during El Niño events. The keystone species also shifted to the predator fish *T. albacares* and *K. pelamis* during El Niño and La Niña events, respectively.

When used for marine resource assessment and management, ecological modeling enables the inclusion of trophic interaction dynamics, allowing for the development of precautionary approaches and adaptive management processes. The current Ecopath model provides a basis for the further development of dynamic simulations to understand the extent to which fishing activities, the environment, and other anthropogenic factors drive marine resources and elucidate the configuration of trophic interactions in study areas.

Deficiencies in available biological and fisheries data might influence the quality of ecosystem-based studies. Additional studies on further characterizing the key elements of ecosystems, such as the ecological efficiency of specific groups, the aspect ratio of some fish, and the biomass of some fish groups and detritus, are warranted for the improvement of model input data and ecosystem characterization [36,106,107]. One of the most direct ways to improve the collection of species biomass parameters in a study area is through the direct sampling of field data. Furthermore, Free et al. [108] have developed resource assessment models that rely solely on catch data. Lin et al. [109] have incorporated fishing mortality rates into their considerations for biomass calculations. Moreover, incorporating fishing efficiency [110] as a reference factor can contribute to the computation of more reliable biomass estimates.

Author Contributions: Conceptualization, K.-W.L.; methodology, N.-J.S.; resources, C.-H.L.; data curation, P.-Y.H., W.-H.L. and T.-Y.L.; writing—original draft preparation, P.-Y.H.; writing—review and editing, P.-Y.H. and K.-W.L.; supervision, K.-W.L. All authors have read and agreed to the published version of the manuscript.

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Conflicts of Interest: The authors declare no conflict of interest.

Appendix A

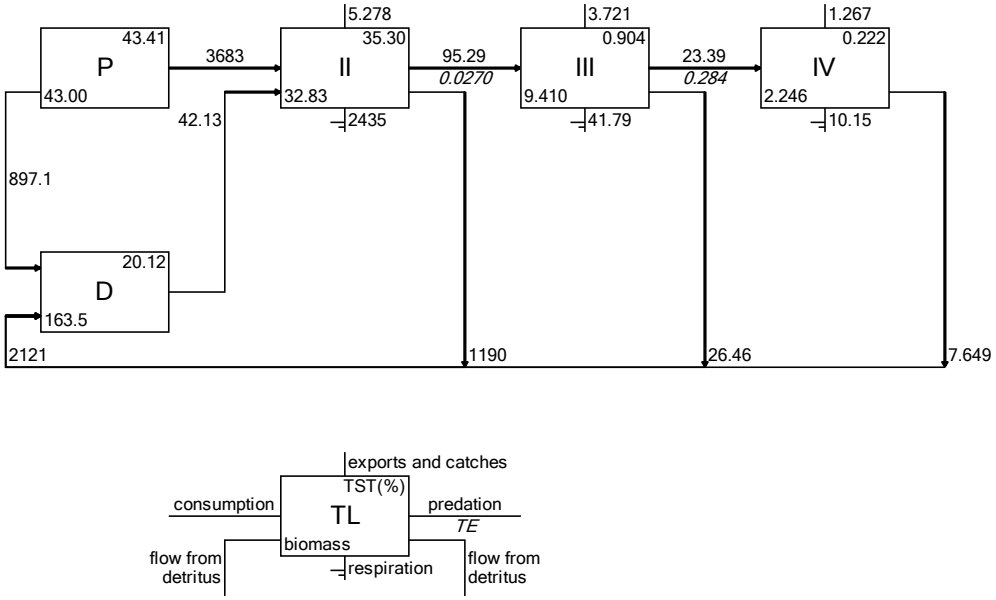


Figure A1. Lindeman's spine diagram for the TB ecosystem during normal years. Lindeman spine showing trophic flows among integer trophic levels (TL). Primary producer (P); detritus (D); Total system throughput (TST); Transfer efficiency (TE).

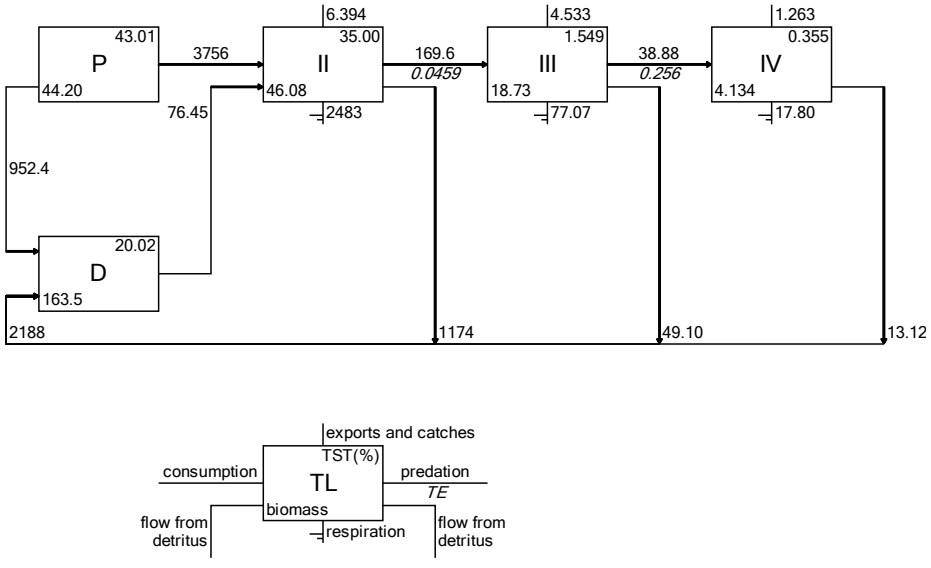


Figure A2. Lindeman's spine diagram for the TB ecosystem during El Niño events. Lindeman spine showing trophic flows among integer trophic levels (TL). Primary producer (P); detritus (D); Total system throughput (TST); Transfer efficiency (TE).

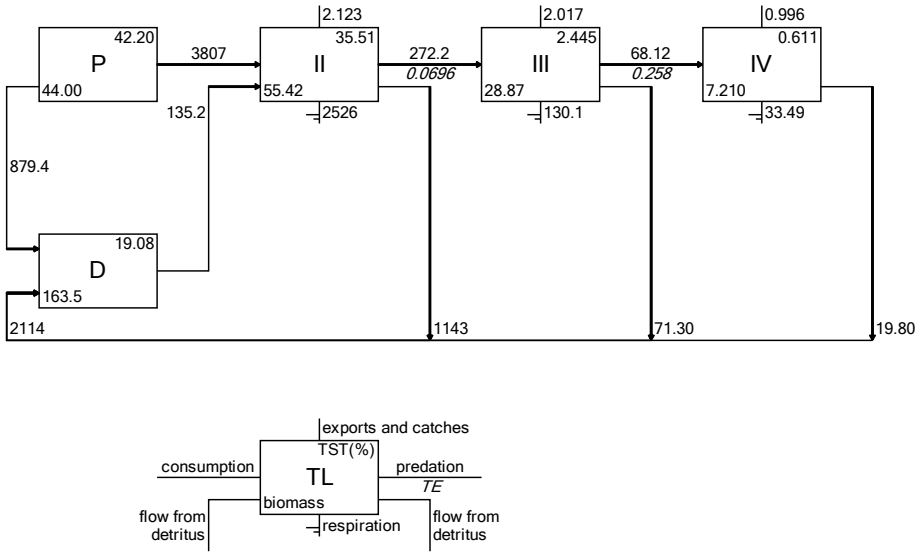


Figure A3. Lindeman's spine diagram for the TB ecosystem during La Niña events. Lindeman spine showing trophic flows among integer trophic levels (TL). Primary producer (P); detritus (D); Total system throughput (TST); Transfer efficiency (TE).

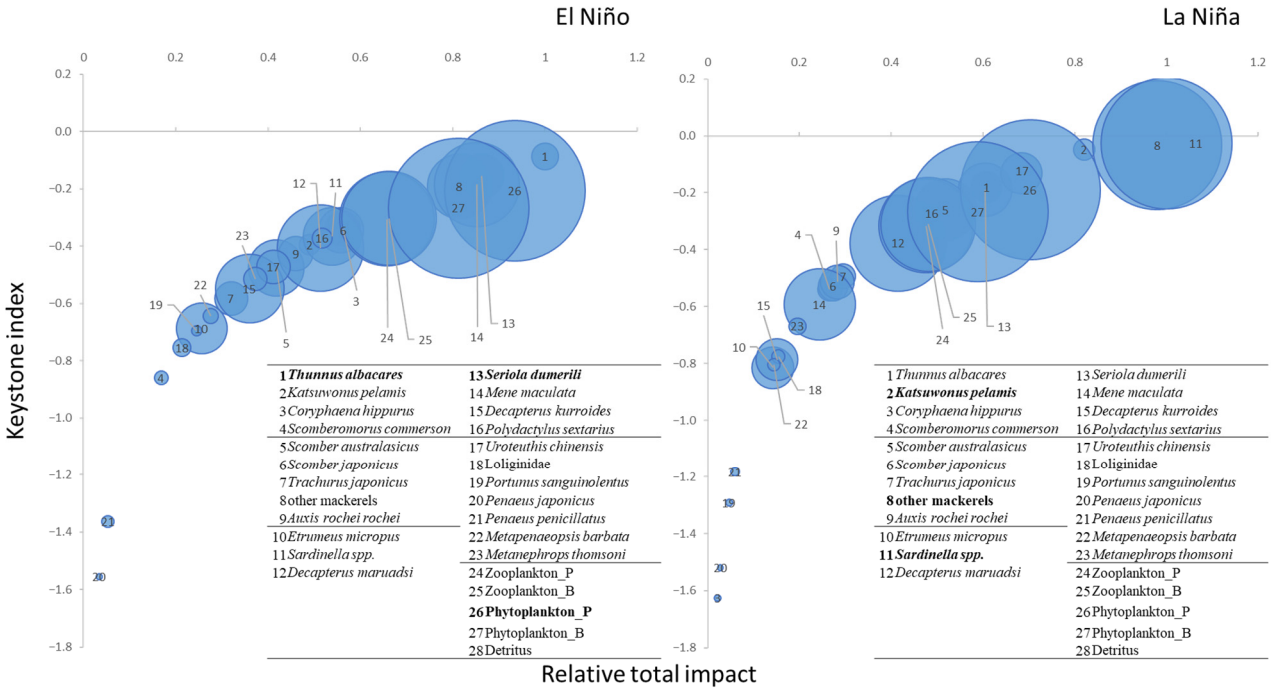


Figure A4. KSi and relative total impact on the groups from TB ecosystem model during El Niño and La Niña events. Top-3 species with high KSi shown in bold.

Table A1. Diet composition matrix for the TB ecosystem during normal years.

	Prey\Predator	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
1	Yellow fin tuna	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	Skipjack tuna	0.02	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3	Dolphinfish	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4	Spanish mackerel	0	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5	Spotted mackerel	0.15	0.1	0.1	0.1	0	0.05	0.07	0.04	0.06	0	0.05	0	0	0.07	0	0	0	0.02	0	0	0	0	0	0	0
6	Chub mackerel	0.25	0.363	0.292	0.147	0	0	0	0	0.133	0	0	0	0	0	0	0	0	0.073	0	0	0	0	0.055	0	0
7	Japanese jack mackerel	0.01	0.005	0.05	0.01	0.001	0.001	0	0.005	0.02	0	0.01	0	0	0.01	0	0	0	0.01	0.02	0	0	0	0	0	0
8	other mackerels	0	0.002	0.002	0.003	0.001	0.001	0.001	0	0	0	0	0	0	0	0	0	0.001	0	0	0	0	0	0	0	0
9	Bullet tuna	0.1	0.14	0.15	0.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10	Pacific round herring	0.1	0.19	0	0	0.168	0.197	0	0.03	0	0	0.1	0	0	0.02	0	0	0.048	0	0	0	0	0	0	0	0
11	*Sardinella* spp.	0.1	0.17	0	0.28	0.02	0.03	0	0	0.086	0	0	0	0	0.01	0.07	0	0.03	0.2	0	0	0	0	0	0	0
12	Round scad	0.1	0	0.15	0.15	0.01	0	0.032	0.01	0	0	0.04	0	0	0	0	0	0	0	0	0	0	0	0	0	0
13	Amberjack	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
14	Moonfish	0	0	0	0.1	0.05	0	0.07	0.055	0	0	0	0	0	0	0.03	0	0	0	0	0	0	0	0	0	0
15	Mackerel scad	0.16	0	0.243	0.1	0.02	0	0.057	0.04	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
16	Polynemid fish	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
17	Mitre squid	0	0.01	0	0	0.08	0.1	0.02	0.1	0.1	0	0.01	0	0.03	0	0	0	0	0	0	0	0	0	0.006	0	0
18	Squids	0.01	0.01	0.01	0.01	0.08	0.08	0.02	0.1	0.1	0	0	0	0.02	0	0	0.01	0	0	0	0	0	0	0.005	0	0
19	*Portunus sanguinolentus*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.01	0	0.002	0	0	0	0	0.001	0	0
20	*Penaeus japonicus*	0	0	0	0	0	0	0	0	0	0	0	0	0.01	0	0	0	0.001	0.003	0	0	0	0.02	0.006	0	0
21	*Penaeus penicillatus*	0	0	0	0	0	0	0	0	0	0	0	0	0.02	0	0	0.04	0	0.011	0.03	0	0	0.02	0.005	0	0
22	*Metapenaeopsis barbata*	0	0	0.003	0	0	0	0	0	0.001	0	0	0	0.047	0	0	0	0.02	0.011	0.03	0	0	0	0.012	0	0
23	*Metanephrops thomsoni*	0	0	0	0	0	0.01	0	0	0	0	0	0	0	0	0	0.06	0.02	0	0.08	0	0	0	0	0	0
24	Zooplankton_P	0	0	0	0	0.2	0.2	0.2	0.2	0.2	0.18	0.22	0.17	0.214	0.2	0.2	0	0	0	0	0.1	0.1	0	0	0	0
25	Zooplankton_B	0	0	0	0	0	0	0	0	0	0.18	0	0.17	0	0	0.2	0.3	0.28	0.22	0.24	0.2	0.2	0.2	0.2	0	0
26	Phytoplankton_P	0	0	0	0	0.33	0.3	0.3	0.3	0.3	0.23	0.33	0.22	0.4	0.44	0.25	0	0	0	0	0.2	0.2	0.16	0.19	0.5	0.5
27	Phytoplankton_B	0	0	0	0	0	0	0	0	0	0.23	0	0.22	0	0	0	0.33	0.3	0.25	0.3	0.2	0.2	0.3	0.23	0.5	0.5
28	Detritus	0	0	0	0	0.04	0.031	0.23	0.12	0	0.18	0.24	0.22	0.259	0.25	0.25	0.25	0.3	0.2	0.3	0.3	0.3	0.3	0.29	0	0
	Import	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Sum	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

Table A2. Diet composition matrix for the TB ecosystem during El Niño events.

	Prey\Predator	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**
1	Yellow fin tuna	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	Skipjack tuna	0.07	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3	Dolphinfish	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4	Spanish mackerel	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5	Spotted mackerel	0.15	0.1	0.08	0.1	0	0.07	0.07	0.07	0.06	0	0.052	0	0	0.01	0	0	0	0.04	0	0	0	0	0	0	0
6	Chub mackerel	0.225	0.3	0.2	0.1	0	0	0	0	0.11	0	0	0	0	0	0	0	0	0.04	0	0	0	0	0.01	0	0
7	Japanese jack mackerel	0.01	0.05	0.01	0.02	0.01	0.02	0	0.01	0.03	0	0.01	0	0.01	0.001	0	0	0	0.04	0.02	0	0	0	0	0	0
8	other mackerels	0	0.12	0.2	0.1	0.04	0.09	0.03	0	0	0	0	0	0	0	0	0	0.08	0	0	0	0	0	0	0	0
9	Bullet tuna	0.2	0.2	0.2	0.12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10	Pacific round herring	0.07	0.08	0	0	0.05	0.08	0	0.05	0.015	0	0.02	0	0	0.05	0	0	0.02	0	0	0	0	0	0	0	0
11	*Sardinella* spp.	0.05	0.08	0	0.1	0.13	0.1	0	0	0.05	0	0	0	0	0.049	0.04	0	0.02	0	0	0	0	0	0	0	0
12	Round scad	0.125	0	0.18	0.18	0.1	0.1	0.27	0.1	0.015	0	0.128	0	0	0	0	0	0	0	0	0	0	0	0	0	0
13	Amberjack	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
14	Moonfish	0	0	0	0.13	0.12	0	0.07	0.1	0	0	0	0	0.08	0	0.06	0	0	0	0	0	0	0	0	0	0
15	Mackerel scad	0.09	0	0.1	0.1	0.02	0	0.03	0.14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
16	Polynemid fish	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
17	Mitre squid	0	0.05	0	0.01	0	0	0	0	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0.02	0	0
18	Squids	0.01	0.01	0.015	0.04	0	0	0	0	0.005	0	0.01	0	0.01	0	0	0.02	0	0	0	0	0	0	0.01	0	0
19	*Portunus sanguinolentus*	0	0.01	0.005	0	0	0	0	0	0	0	0	0	0.05	0	0	0.005	0	0.005	0	0	0	0	0	0	0
20	*Penaeus japonicus*	0	0	0	0	0	0	0	0	0	0	0	0	0.02	0	0	0.01	0	0	0.02	0	0	0.02	0	0	0
21	*Penaeus penicillatus*	0	0	0	0	0	0	0	0	0	0	0	0	0.01	0	0	0.03	0	0.02	0.03	0	0	0.02	0.01	0	0
22	*Metapenaeopsis barbata*	0	0	0.01	0	0	0	0	0	0.005	0	0	0	0	0	0	0.01	0.01	0	0.02	0	0	0	0	0	0
23	*Metanephrops thomsoni*	0	0	0	0	0	0.01	0	0	0	0	0	0	0.02	0	0	0.1	0.02	0	0.1	0	0	0	0	0	0
24	Zooplankton_P	0	0	0	0	0.2	0.2	0.2	0.2	0.2	0.18	0.22	0.17	0.2	0.2	0.2	0	0	0	0	0.1	0.1	0	0	0	0
25	Zooplankton_B	0	0	0	0	0	0	0	0	0	0.18	0	0.17	0	0	0.2	0.245	0.25	0.2	0.24	0.2	0.2	0.2	0.2	0	0
26	Phytoplankton_P	0	0	0	0	0.3	0.3	0.3	0.3	0.3	0.23	0.33	0.22	0.4	0.44	0.25	0	0	0.205	0	0.2	0.2	0.16	0.1	0.5	0.5
27	Phytoplankton_B	0	0	0	0	0	0	0	0	0	0.23	0	0.22	0	0	0	0.33	0.3	0.25	0.27	0.2	0.2	0.3	0.3	0.5	0.5
28	Detritus	0	0	0	0	0.03	0.03	0.03	0.03	0.2	0.18	0.23	0.22	0.2	0.25	0.25	0.25	0.3	0.2	0.3	0.3	0.3	0.3	0.35	0	0
	Import	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Sum	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

Table A3. Diet composition matrix for the TB ecosystem during La Niña events.

	Prey\Predator	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
1	Yellow fin tuna	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	Skipjack tuna	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3	Dolphinfish	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4	Spanish mackerel	0	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5	Spotted mackerel	0.1	0.1	0.1	0.1	0	0.05	0.07	0.01	0.04	0	0.04	0	0	0.01	0	0	0	0.04	0	0	0	0	0	0	0
6	Chub mackerel	0.1	0.15	0.2	0.1	0	0	0	0	0.04	0	0	0	0	0	0	0	0	0.2	0	0	0	0	0.05	0	0
7	Japanese jack mackerel	0.01	0.02	0.05	0.02	0.01	0.01	0	0	0.01	0	0	0	0.01	0.004	0	0	0	0.04	0.02	0	0	0	0.03	0	0
8	other mackerels	0.19	0.228	0.237	0.22	0.26	0.329	0.29	0	0	0	0.012	0	0	0.06	0	0	0.165	0.04	0	0	0	0	0	0	0
9	Bullet tuna	0.22	0.22	0.2	0.15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10	Pacific round herring	0.07	0.05	0	0	0.01	0.05	0	0.01	0	0	0.014	0	0	0.01	0	0	0.02	0	0	0	0	0	0	0	0
11	*Sardinella* spp.	0.22	0.17	0	0.109	0.09	0.04	0	0.41	0.18	0	0	0	0	0.096	0.04	0	0	0	0	0	0	0	0	0	0
12	Round scad	0.03	0	0.1	0.1	0.02	0	0.03	0.1	0	0	0.05	0	0	0	0	0	0	0	0	0	0	0	0	0	0
13	Amberjack	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
14	Moonfish	0	0	0	0.1	0.08	0	0.07	0.04	0	0	0	0	0.21	0	0.06	0	0	0	0	0	0	0	0	0	0
15	Mackerel scad	0.04	0	0.1	0.1	0.01	0	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
16	Polynemid fish	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
17	Mitre squid	0	0.05	0	0	0	0	0	0	0.02	0	0.032	0	0.01	0	0	0	0	0	0	0	0	0	0.04	0	0
18	Squids	0.01	0.001	0.001	0.001	0	0	0	0	0.005	0	0.002	0	0.006	0	0	0.01	0	0	0	0	0	0	0.03	0	0
19	*Portunus sanguinolentus*	0	0	0.001	0	0	0	0	0	0	0	0	0	0.012	0	0	0.01	0	0.01	0	0	0	0	0	0	0
20	*Penaeus japonicus*	0	0	0	0	0	0	0	0	0	0	0	0	0.01	0	0	0.02	0	0	0.02	0	0	0.02	0	0	0
21	*Penaeus penicillatus*	0	0.001	0.001	0	0	0	0	0	0	0	0	0	0.014	0	0	0.07	0	0.02	0.03	0	0	0.02	0.01	0	0
22	*Metapenaeopsis barbata*	0	0	0.01	0	0	0	0	0	0.005	0	0	0	0.012	0	0	0	0.025	0	0.02	0	0	0	0	0	0
23	*Metanephrops thomsoni*	0	0	0	0	0	0.001	0	0	0	0	0	0	0.016	0	0	0.1	0.04	0	0.07	0	0	0	0	0	0
24	Zooplankton_P	0	0	0	0	0.2	0.2	0.21	0.2	0.2	0.18	0.2	0.17	0.2	0.25	0.2	0	0	0	0	0.1	0.1	0	0	0	0
25	Zooplankton_B	0	0	0	0	0	0	0	0	0	0.18	0	0.17	0	0	0.2	0.24	0.2	0.2	0.24	0.2	0.2	0.2	0.2	0	0
26	Phytoplankton_P	0	0	0	0	0.3	0.3	0.3	0.2	0.3	0.23	0.3	0.22	0.3	0.35	0.25	0	0	0	0	0.2	0.2	0.16	0.14	0.5	0.5
27	Phytoplankton_B	0	0	0	0	0	0	0	0	0	0.23	0	0.22	0	0	0	0.3	0.25	0.25	0.3	0.2	0.2	0.3	0.23	0.5	0.5
28	Detritus	0	0	0	0	0.02	0.02	0.02	0.02	0.2	0.18	0.35	0.22	0.2	0.22	0.25	0.25	0.3	0.2	0.3	0.3	0.3	0.3	0.27	0	0
	Import	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Sum	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

Table A4. Input and output parameters of the TB Ecopath model during normal years.

	No.	Group Name	Group Name	Trophic Level	Biomass (t/km^2)	*P/B* (/Year)	*Q/B* (/Year)	*EE*	*P/Q* (/Year)
Predator fish	1	*Thunnus albacares*	Yellow fin tuna	3.716	0.704	2.65	11.64	0.241	0.228
	2	*Katsuwonus pelamis*	Skipjack tuna	3.751	0.380	2.62	12.53	0.459	0.209
	3	*Coryphaena hippurus*	Dolphinfish	3.731	0.248	3.71	8.48	0.229	0.438
	4	*Scomberomorus commerson*	Spanish mackerel	3.631	0.598	4.5	11.4	0.338	0.395
Pelagic fish	5	*Scomber australasicus*	Spotted mackerel	2.832	2.136	4.3	8.8	0.953	0.489
	6	*Scomber japonicus*	Chub mackerel	2.907	2.423	4.8	11.7	0.651	0.410
	7	*Trachurus japonicus*	Japanese jack mackerel	2.622	0.607	4.11	10	0.903	0.411
	8	other mackerels	other mackerels	2.794	0.052	2.22	9.6	0.907	0.231
	9	*Auxis rochei rochei*	Bullet tuna	3.049	0.568	4.8	10.6	0.985	0.453
Small pelagic fish	10	*Etrumeus micropus*	Pacific round herring	2.360	3.778	4.2	14.04	0.921	0.299
	11	*Sardinella* spp.	*Sardinella* spp.	2.532	2.149	5.1	11.6	0.942	0.440
	12	*Decapterus maruadsi*	Round scad	2.340	1.239	3.1	9.08	0.949	0.341
Benthic and Reef fish	13	*Seriola dumerili*	Amberjack	2.390	1.946	1.2	3.3	0.120	0.364
	14	*Mene maculata*	Moonfish	2.387	2.188	2.64	6.7	0.946	0.394
	15	*Decapterus kurroides*	Mackerel scad	2.549	2.004	1.97	7.1	0.850	0.277
	16	*Polydactylus sextarius*	Polynemid fish	2.465	0.718	2.34	11.1	0.015	0.211
Cephalopod	17	*Uroteuthis chinensis*	Mitre squid	2.446	1.322	4.7	11.64	0.958	0.404
	18	Loliginidae	Squids	2.753	1.279	4.7	11.64	0.901	0.404
Crustaceans	19	*Portunus sanguinolentus*	*Portunus sanguinolentus*	2.457	0.038	4.93	14.5	0.979	0.340
	20	*Penaeus japonicus*	*Penaeus japonicus*	2.300	0.033	8.6	15.6	0.902	0.551
	21	*Penaeus penicillatus*	*Penaeus penicillatus*	2.300	0.097	8.6	15.6	0.898	0.551
	22	*Metapenaeopsis barbata*	*Metapenaeopsis barbata*	2.252	0.159	7.6	12.22	0.813	0.622
	23	*Metanephrops thomsoni*	*Metanephrops thomsoni*	2.353	0.293	5.65	14.2	0.825	0.398
Zooplankton	24	Zooplankton_P	Zooplankton_P	2.000	10	25	180	0.145	0.139
	25	Zooplankton_B	Zooplankton_B	2.000	10	25	180	0.104	0.139
Phytoplankton	26	Phytoplankton_P	Phytoplankton_P	1.000	21.5	106.52		0.810	
	27	Phytoplankton_B	Phytoplankton_B	1.000	21.5	106.52		0.800	
Detritus	28	Detritus	Detritus	1.000	163.5			0.215	

Table A5. Input and output parameters of the TB Ecopath model during El Niño events.

	No.	Group Name	Group Name	Trophic Level	Biomass (t/km^2)	*P/B* (/Year)	*Q/B* (/Year)	*EE*	*P/Q* (/Year)
Predator fish	1	*Thunnus albacares*	Yellow fin tuna	3.777	0.822	2.65	11.64	0.132	0.228
	2	*Katsuwonus pelamis*	Skipjack tuna	3.782	0.455	2.62	12.53	0.695	0.209
	3	*Coryphaena hippurus*	Dolphinfish	3.726	1.366	3.71	8.48	0.023	0.438
	4	*Scomberomorus commerson*	Spanish mackerel	3.622	0.212	4.5	11.4	0.835	0.395
Pelagic fish	5	*Scomber australasicus*	Spotted mackerel	2.893	3.519	4.3	8.8	0.946	0.489
	6	*Scomber japonicus*	Chub mackerel	2.953	2.275	4.8	11.7	0.765	0.410
	7	*Trachurus japonicus*	Japanese jack mackerel	2.893	1.240	4.11	10	0.884	0.411
	8	other mackerels	other mackerels	2.906	4.724	2.22	9.6	0.808	0.231
	9	*Auxis rochei rochei*	Bullet tuna	2.732	1.302	4.8	10.6	0.916	0.453
Small pelagic fish	10	*Etrumeus micropus*	Pacific round herring	2.360	2.898	4.2	14.04	0.945	0.299
	11	*Sardinella* spp.	*Sardinella* spp.	2.551	3.699	5.1	11.6	0.722	0.440
	12	*Decapterus maruadsi*	Round scad	2.340	8.381	3.1	9.08	0.919	0.341

Table A5. *Cont.*

	No.	Group Name	Group Name	Trophic Level	Biomass (t/km^2)	*P/B* (/Year)	*Q/B* (/Year)	*EE*	*P/Q* (/Year)
Benthic and Reef fish	13	*Seriola dumerili*	Amberjack	2.482	2.177	1.2	3.3	0.084	0.364
	14	*Mene maculata*	Moonfish	2.365	8.099	2.64	6.7	0.788	0.394
	15	*Decapterus kurroides*	Mackerel scad	2.544	5.306	1.97	7.1	0.954	0.277
	16	*Polydactylus sextarius*	Polynemid fish	2.474	0.444	2.34	11.1	0.113	0.211
Cephalopod	17	*Uroteuthis chinensis*	Mitre squid	2.499	1.248	4.7	11.64	0.140	0.404
	18	Loliginidae	Squids	2.463	0.355	4.7	11.64	0.777	0.404
Crustaceans	19	*Portunus sanguinolentus*	*Portunus sanguinolentus*	2.496	0.127	4.93	14.5	0.890	0.340
	20	*Penaeus japonicus*	*Penaeus japonicus*	2.300	0.046	8.6	15.6	0.864	0.551
	21	*Penaeus penicillatus*	*Penaeus penicillatus*	2.300	0.158	8.6	15.6	0.381	0.551
	22	*Metapenaeopsis barbata*	*Metapenaeopsis barbata*	2.252	0.269	7.6	12.22	0.358	0.622
	23	*Metanephrops thomsoni*	*Metanephrops thomsoni*	2.277	0.597	5.65	14.2	0.409	0.398
Zooplankton	24	Zooplankton_P	Zooplankton_P	2.000	10	25	180	0.409	0.139
	25	Zooplankton_B	Zooplankton_B	2.000	10	25	180	0.303	0.139
Phytoplankton	26	Phytoplankton_P	Phytoplankton_P	1.000	22.1	106.52		0.815	
	27	Phytoplankton_B	Phytoplankton_B	1.000	22.1	106.52		0.781	
Detritus	28	Detritus	Detritus	1.000	163.5			0.21	

Table A6. Input and output parameters of the TB Ecopath model during La Niña events.

	No.	Group Name	Group Name	Trophic Level	Biomass (t/km^2)	*P/B* (/Year)	*Q/B* (/Year)	*EE*	*P/Q* (/Year)
Predator fish	1	*Thunnus albacares*	Yellow fin tuna	3.765	1.019	2.65	11.64	0.183	0.228
	2	*Katsuwonus pelamis*	Skipjack tuna	3.834	0.518	2.62	12.53	0.294	0.209
	3	*Coryphaena hippurus*	Dolphinfish	3.866	0.046	3.71	8.48	0.005	0.438
	4	*Scomberomorus commerson*	Spanish mackerel	3.769	0.615	4.5	11.4	0.025	0.395
Pelagic fish	5	*Scomber australasicus*	Spotted mackerel	3.062	4.187	4.3	8.8	0.940	0.489
	6	*Scomber japonicus*	Chub mackerel	3.123	0.980	4.8	11.7	0.921	0.410
	7	*Trachurus japonicus*	Japanese jack mackerel	3.111	0.684	4.11	10	0.911	0.411
	8	other mackerels	other mackerels	3.040	18.574	2.22	9.6	0.715	0.231
	9	*Auxis rochei rochei*	Bullet tuna	2.698	1.269	4.8	10.6	0.873	0.453
Small pelagic fish	10	*Etrumeus micropus*	Pacific round herring	2.360	1.910	4.2	14.04	0.989	0.299
	11	*Sardinella* spp.	*Sardinella* spp.	2.450	19.140	5.1	11.6	0.903	0.440
	12	*Decapterus maruadsi*	Round scad	2.340	10.317	3.1	9.08	0.971	0.341
Benthic and Reef fish	13	*Seriola dumerili*	Amberjack	2.664	3.188	1.2	3.3	0.006	0.364
	14	*Mene maculata*	Moonfish	2.554	5.739	2.64	6.7	0.976	0.394
	15	*Decapterus kurroides*	Mackerel scad	2.551	1.967	1.97	7.1	0.907	0.277
	16	*Polydactylus sextarius*	Polynemid fish	2.542	0.368	2.34	11.1	0.060	0.211
Cephalopod	17	*Uroteuthis chinensis*	Mitre squid	2.655	1.872	4.7	11.64	0.931	0.404
	18	Loliginidae	Squids	2.914	0.202	4.7	11.64	0.938	0.404
Crustaceans	19	*Portunus sanguinolentus*	*Portunus sanguinolentus*	2.478	0.051	4.93	14.5	0.959	0.340
	20	*Penaeus japonicus*	*Penaeus japonicus*	2.300	0.038	8.6	15.6	0.932	0.551
	21	*Penaeus penicillatus*	*Penaeus penicillatus*	2.300	0.086	8.6	15.6	0.928	0.551
	22	*Metapenaeopsis barbata*	*Metapenaeopsis barbata*	2.252	0.184	7.6	12.22	0.983	0.622
	23	*Metanephrops thomsoni*	*Metanephrops thomsoni*	2.506	0.323	5.65	14.2	0.910	0.398
Zooplankton	24	Zooplankton_P	Zooplankton_P	2.000	10	25	180	0.517	0.139
	25	Zooplankton_B	Zooplankton_B	2.000	10	25	180	0.125	0.139
Phytoplankton	26	Phytoplankton_P	Phytoplankton_P	1.000	22	106.52		0.841	
	27	Phytoplankton_B	Phytoplankton_B	1.000	22	106.52		0.784	
Detritus	28	Detritus	Detritus	1.000	163.5	0.266		0.215	

Table A7. Keystoneness index and relative total impact.

	No.	Group Name	El Niño KSi	El Niño RTI	La Niña KSi	La Niña RTI	Normal KSi	Normal RTI
Predator fish	1	*Thunnus albacares*	−0.087	1.000	−0.180	0.608	−0.240	0.713
	2	*Katsuwonus pelamis*	−0.395	0.490	−0.048	0.821	−0.519	0.373
	3	*Coryphaena hippurus*	−0.339	0.562	−1.626	0.022	−0.742	0.223
	4	*Scomberomorus commerson*	−0.860	0.168	−0.538	0.266	−0.402	0.489
Pelagic fish	5	*Scomber australasicus*	−0.476	0.418	−0.259	0.519	−0.345	0.568
	6	*Scomber japonicus*	−0.345	0.558	−0.527	0.274	−0.181	0.833
	7	*Trachurus japonicus*	−0.583	0.320	−0.494	0.295	−0.686	0.255
	8	other mackerels	−0.191	0.815	−0.033	0.980	−1.844	0.018
	9	*Auxis rochei rochei*	−0.426	0.460	−0.513	0.283	−0.686	0.255
Small pelagic fish	10	*Etrumeus micropus*	−0.687	0.256	−0.815	0.142	−0.376	0.539
	11	*Sardinella* spp.	−0.366	0.539	−0.026	1.000	−0.324	0.597
	12	*Decapterus maruadsi*	−0.406	0.514	−0.377	0.415	−0.703	0.246
Benthic and Reef fish	13	*Seriola dumerili*	−0.156	0.863	−0.189	0.605	−0.424	0.473
	14	*Mene maculata*	−0.185	0.852	−0.592	0.244	−0.342	0.573
	15	*Decapterus kurroides*	−0.548	0.360	−0.787	0.151	−0.533	0.369
	16	*Polydactylus sextarius*	−0.372	0.517	−0.272	0.489	−0.170	0.837
Cephalopod	17	*Uroteuthis chinensis*	−0.473	0.412	−0.132	0.684	−0.383	0.516
	18	Loliginidae	−0.755	0.214	−0.775	0.154	−0.333	0.579
Crustaceans	19	*Portunus sanguinolentus*	−0.695	0.245	−1.292	0.047	−1.353	0.055
	20	*Penaeus japonicus*	−1.556	0.034	−1.520	0.028	−1.665	0.027
	21	*Penaeus penicillatus*	−1.363	0.053	−1.183	0.060	−1.369	0.053
	22	*Metapenaeopsis barbata*	−0.644	0.276	−0.804	0.144	−0.739	0.224
	23	*Metanephrops thomsoni*	−0.515	0.372	−0.669	0.196	−0.880	0.162
Zooplankton	24	Zooplankton_P	−0.305	0.658	−0.316	0.476	−0.335	0.640
	25	Zooplankton_B	−0.303	0.662	−0.311	0.481	−0.311	0.676
Phytoplankton	26	Phytoplankton_P	−0.207	0.935	−0.189	0.703	−0.211	1.000
	27	Phytoplankton_B	−0.267	0.813	−0.267	0.589	−0.319	0.779

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