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## Mechanisms regulating trophic transfer in the Humboldt Upwelling System differ across time scales

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## Abstract

The Humboldt Upwelling System hosts a highly productive ecosystem with central importance for global fisheries, yet with strong seasonal and interannual variability in the planktonic base of the food chain ultimately affecting fish yield. Understanding the variability in energy transfer within the plankton community in the contemporary climate can provide valuable insights for future projections of planktonic dynamics. Therefore, we use a regional physical-biogeochemical ocean model simulation (CROCO-BioEBUS) from 1990 to 2010 to investigate the underlying mechanisms of seasonal and interannual variability of the trophic transfer. Our model simulations suggest that, on an interannual scale, variations in trophic transfer are governed by variations in the offshore surface flow that modulate the plankton cross-shore distribution. Weak offshore surface flow, as simulated during the El Niño period, allows the zooplankton to stay relatively close to the shore, leading to more efficient grazing and trophic transfer compared to years with strong offshore flow. This mechanism differs from the seasonal one, where the mixed layer depth is the primary driver of variations in plankton dynamics, including trophic transfer. Our results highlight that mechanisms controlling plankton trophic transfer differ across time scales, and thus stress that extrapolating solely from seasonal findings to understand long-term trophic transfer changes in the context of climate change may be insufficient.

## 1. Introduction

The Humboldt upwelling system has a strikingly efficient energy transfer from phytoplankton to fish, playing a vital role in global fisheries. The constant upwelling of nutrients supports high primary production and also exceptionally high fish production (Chavez *et al* 2008). Plankton, as the primary fuel for fisheries, both in terms of quantity (biomass) and quality (plankton composition), has long been believed to be one of the key factors driving changes in fish production (Ryther 1969, Pauly and Christensen 1995, Friedland *et al* 2012). Yet, even though the Humboldt system does not host the highest primary production compared to other major eastern boundary upwelling ecosystems, its fish catch is close to an order of magnitude higher than that of other major eastern boundary upwelling ecosystems (Bakun and Weeks 2008, Chavez *et al* 2008).

The Humboldt upwelling system exhibits strong interannual environmental fluctuations, including variability due to the widely-studied El Niño-Southern Oscillation (ENSO). Notably, several fish landing collapses happen to coincide with occurrences of El Niño events (Caviedes 1975, Barber and Chavez 1983, Ñiquen and Bouchon 2004). Barber and Chavez (1983) suggest that the anomalous physical conditions during El Niño, such as a deepened thermocline and mixed layer depth, along with reduced upwelling, could result in decreased planktonic production and consequently lower fish production. Ñiquen and Bouchon (2004) further extend the analysis of low planktonic biomass to potential changes in fish habitat and mortality. Tam *et al* (2008) find that during El Niño, omnivorous fish switch to a more zooplankton-dominated diet, resulting in less efficient trophic transfer from plankton to fish. Bakun and Weeks (2008) suggest that the

ENSO-related ecosystem perturbations described above (low plankton biomass and thereby low fish production) are not detrimental but, in fact, essential for the—ultimately—high fish production observed in the Humboldt system: that it is through these ENSO-related perturbations that the ecosystem can periodically ‘reset’ itself, preventing it from reaching mature states, and thereby excluding longer-lived apex predators. Consequently, small species like anchovy can experience rapid bottom-up driven growth and high fish production, benefiting from the pronounced interannual environmental fluctuations.

Apart from strong ENSO-related interannual fluctuations, the Humboldt system also reveals unique variability on a seasonal scale. Despite benefiting from continuously upwelled nutrients that drive high productivity, observed phytoplankton concentrations follow a seasonal cycle that runs counter to upwelling intensity. This is a unique seasonal pattern known as the ‘seasonal paradox’, with surface phytoplankton concentration peaking when upwelling intensity is weakest throughout the year (Calienes *et al* 1985, Chavez 1995) and has only been observed in the Humboldt system among the four major eastern boundary upwelling systems (Chavez and Messié 2009, Xue *et al* 2022b). Previous observational and modelling studies have pointed to the significant role of mixed layer depth, not only in the change of phytoplankton production as a result of changing light conditions (Echevin *et al* 2008, Messié and Chavez 2015, Xue *et al* 2022b), but also in how energy is transferred to the upper trophic level in the ecosystem (Xue *et al* 2022a). In the study, we assess whether the variability in energy transfer across the planktonic community on interannual time scales differs from what has been previously assessed on a seasonal scale (Xue *et al* 2022a).

Due to the great social and economic importance of the Humboldt ecosystem, its potential response to climate change is of considerable interest. Understanding the dynamics of temporal variations of the energy flow through the plankton ecosystem in the current climate can provide insights for projections into future climate states, e.g. using an emergent constraint on projections of phytoplankton biomass and production (Kwiatkowski *et al* 2017, Xue *et al* 2024), with ultimate implications for fish production. To better understand temporal variations of the plankton ecosystem energy flow, we use a model simulation from 1990 to 2010 to understand interannual energy transfer across plankton web, with a specific focus on the extreme conditions due to El Niño and La Niña, comparing them to seasonally extreme conditions in summer and winter. By examining both seasonal and interannual scales of trophic transfer within the same simulation, this study shows how the effects of physical drivers on marine ecosystems depend on the time scale considered, in particular, that for interannual time scales, variations of offshore

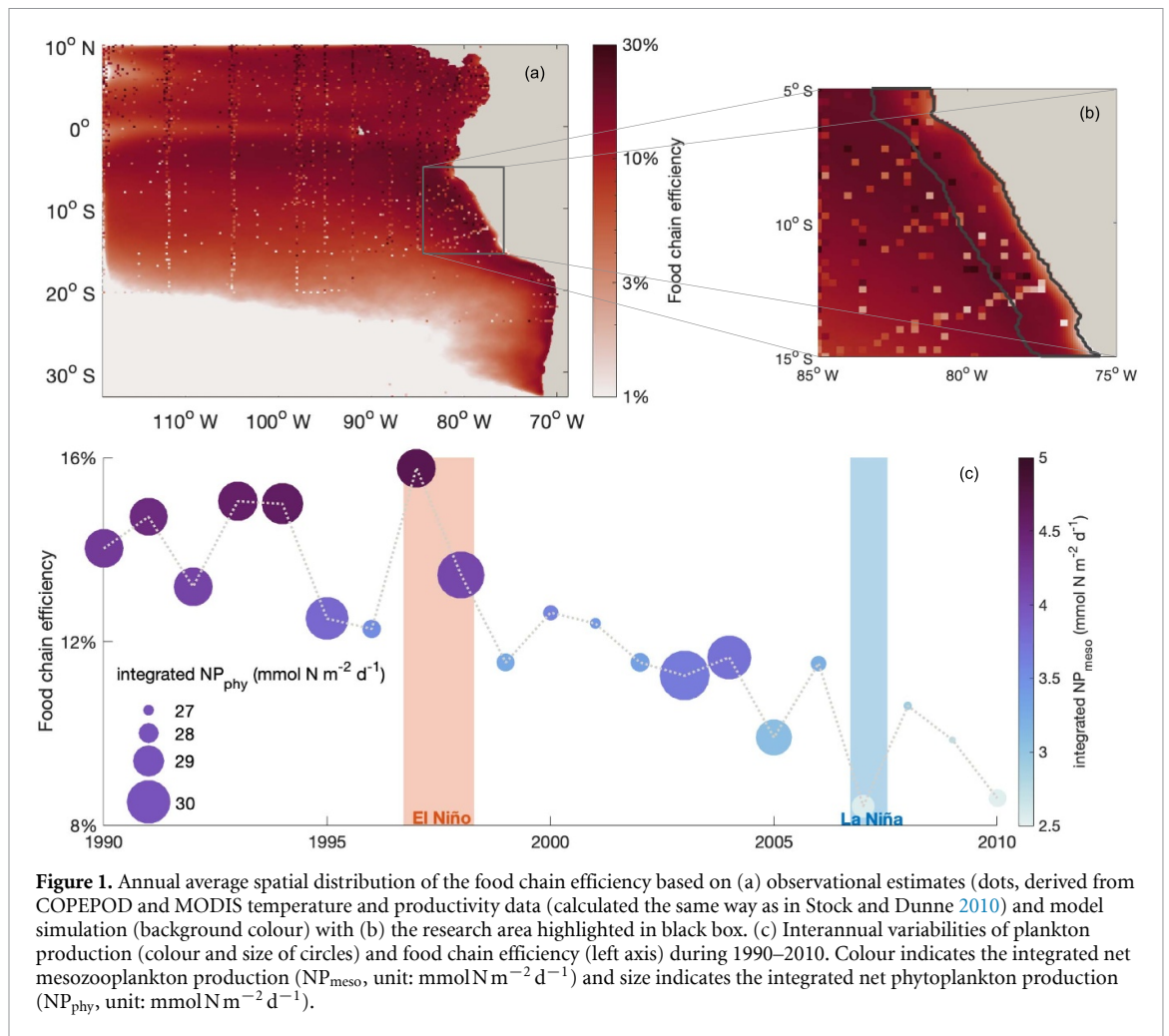
flow turn out to be more important than that of mixed layer depth. The results shed light on how the mechanisms of trophic transfer are sensitive to the time scale considered, with potential implications for how we interpret long-term changes in trophic transfer due to climate change.

## 2. Methods

### 2.1. Regional physical—biogeochemical model: CROCO-BioEBUS

We use a three-dimensional regional coupled physical-biogeochemical model: CROCO (Coastal and Regional Ocean COMMunity model) - BioEBUS (Biogeochemical model for the Eastern Boundary Upwelling Systems) to investigate the energy transfers within the planktonic community on seasonal to interannual time scales. CROCO is a split-explicit free-surface regional ocean circulation model (Shchepetkin and McWilliams 2005). It is able to resolve fine-scale physical processes in the coastal region along with larger-scale dynamics. BioEBUS is a nitrogen-based model with four plankton groups representing small and large phytoplankton, microzooplankton and mesozooplankton (Gutknecht *et al* 2013). The preferences of zooplankton for different prey are parameterised as constant factors.

To investigate the interannual variability of plankton dynamics, we used an interannual configuration of CROCO-BioEBUS (Xue *et al* 2023). The model domain extends from 10° N to 33° S and from 118° W to 69° W (figure 1(a)) with a horizontal resolution of 1/12°. It has 32 vertical sigma layers with a finer resolution towards the surface of 0.5–2 m in shallow waters. Surface forcing, including humidity, precipitation rates, and atmospheric and surface ocean temperature, is provided by Climate Forecast System Reanalysis (CFSR, Saha *et al* 2010) data with a 38 km spatial resolution. Wind forcing is provided by the Cross-Calibrated Multi-Platform (CCMP, Atlas *et al* 1996) product with a 1/4 degree spatial resolution. Both datasets have a 6-hourly temporal resolution. Initial and boundary conditions for CROCO, such as temperature, salinity, and current velocities, are derived from Simple Ocean Data Assimilation (SODA, Carton *et al* 2018), while initial and boundary conditions for BioEBUS, such as oxygen and nitrate, are obtained from the monthly climatology CARS (CSIRO—Commonwealth Scientific and Industrial Research Organisation Atlas of Regional Seas, Ridgway *et al* 2002). This configuration was initially set up by José *et al* (2019). For our study, we used the exact same configuration with calibrated plankton dynamics following Xue *et al* (2022b). The interannual simulation is spun up by repeating the forcing of year 1990 for 30 years (figure S1). After the spin-up, the model is forced by interannually-varying forcing during the period from 1990 to 2010, which is later used for analyses. In this study, we focus on the 200 km band off the Peruvian coast between



5° S–15° S (figure 1(b)) where high plankton production overlaps with the anchovy habitat (Bertrand *et al* 2004).

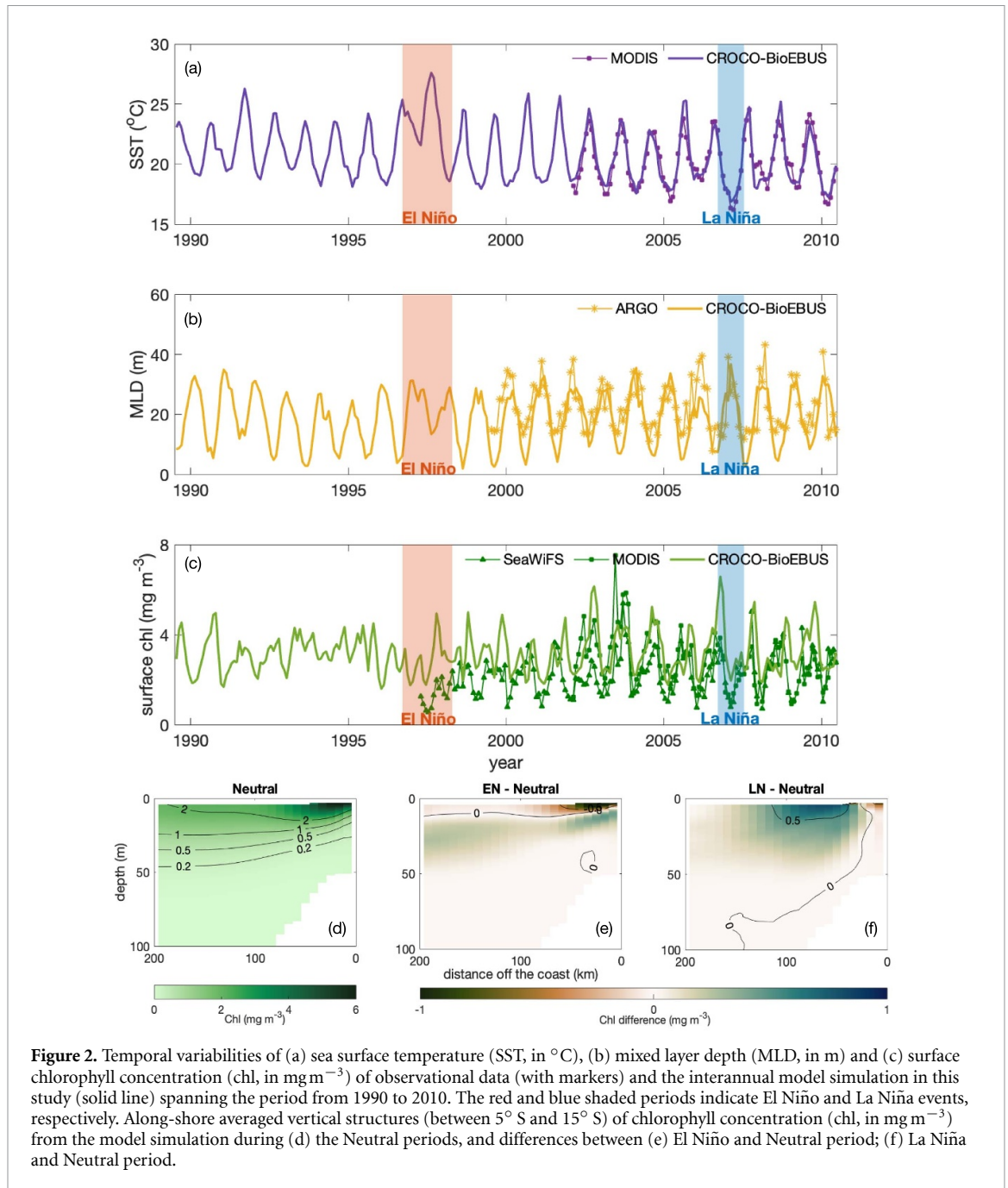
### 2.1.1. Model evaluation

Temporal variations of sea surface temperature (sst), mixed layer depth (MLD), and surface chlorophyll concentration (chl) from 1990–2010 (figure 2) have been evaluated against monthly satellite products (SeaWiFS & MODIS, NASA Ocean Biology Processing Group 2022a, 2022b, 2022c), Argo mixed layer database (Holte *et al* 2017), and compared against *in situ* measurements and model simulations in Espinoza-Morriberón *et al* (2017). The interannual time series captures the anomalous warming of sst during the El Niño period around the years 1997–1998 (figure 2(a)), along with a significant deepening of the summer MLD (figure 2(b)) as previously also reported in Espinoza-Morriberón *et al* (2017). During the year 2007, the interannual simulation exhibits an anomalous cold signal that coincides with the reported La Niña event in 2007 (Lavado-Casimiro and Espinoza 2014). Overall, despite the slight underestimation of the MLD compared to observations, the model simulation reasonably fits the observed data, reproducing the seasonal cycle of the MLD. While the time series of simulated surface chlorophyll does

not always match satellite estimates, particularly the drop of chlorophyll during the El Niño period which is underestimated by the model (figure 2(c)), the spatial pattern of the simulated phytoplankton biomass closely resembles the drop in chlorophyll during El Niño apparent in *in situ* measurements (figures 2(d) and (e)), see figure 3 in Espinoza-Morriberón *et al* (2017). Chlorophyll is a proxy for phytoplankton biomass and can have biases, for instance, due to the extensive cloud coverage over the region and different spatio-temporal coverage by the satellites (22% in monthly composites) in the coastal band that constitutes our study area. During winter, the cloud coverage is even more pronounced, reaching up to 60%. A detailed evaluation can be found in the supplementary materials. Additionally, food chain efficiency (FCE), the main focus of this study, roughly aligns with observational estimates, particularly in terms of magnitude (figures 1(a) and (b), for a definition and calculation details of FCE, see section 2.3). However, due to the sparsity of observational data, it is not possible to evaluate the temporal variability.

### 2.2. Definitions of El Niño and La Niña

The El Niño and La Niña periods are defined in the model simulation using the same method as



Espinoza-Morriberón *et al* (2017), which is based on a 3-month running mean of the SST anomaly in the Niño 1 + 2 region ( $0^{\circ}\text{S}$ – $10^{\circ}\text{S}$  and  $90^{\circ}\text{W}$ – $80^{\circ}\text{W}$ ). An El Niño event is defined as a period during which the SST anomaly is greater than  $0.5^{\circ}\text{C}$  for more than 5 months. A La Niña event, on the other hand, is defined as a time period in which the SST anomaly is consistently less than  $-0.5^{\circ}\text{C}$  for more than 5 months. In figure 1(c), we highlighted the two major El Niño and La Niña events that occurred during the simulated time period of 1997–1998 and 2007 in red and blue shades, respectively.

### 2.3. Diagnostics to assess trophic transfer

To disentangle the complexity of plankton interactions, we calculate the food chain efficiency (FCE) and food chain length (FCL) based on the energy transferred within the food web, following the formulations in Xue *et al* (2022a) modified from Ulanowicz (1995). FCE indicates the energy transfer from the primary producer to the top of the food chain, in the model here expressed as the ratio of net mesozooplankton production ( $\text{NP}_{\text{meso}}$ ) to net phytoplankton production ( $\text{NP}_{\text{phy}}$ , equation (1)). Net phytoplankton production ( $\text{NP}_{\text{phy}}$ ) is computed as the nutrient uptake subtracting exudation, while net mesozo-

oplankton production ( $NP_{\text{meso}}$ , also for microzooplankton) is the grazing minus faecal pellets and metabolic loss.

$$FCE = \frac{NP_{\text{meso}}}{NP_{\text{phy}}}. \quad (1)$$

FCL is defined as the trophic level of the top of the food chain, which in our model is the mesozooplankton. The trophic level of mesozooplankton depends on how it allocates its diet between phytoplankton (trophic level 1) and microzooplankton (trophic level 2). As a result, the trophic level of mesozooplankton, and thus the FCL, ranges between 2 and 3 in the model. A value of 2 indicates that mesozooplankton is completely herbivorous; a value of 2.5 indicates that it feeds 50% herbivorously and 50% carnivorously; and a value of 3 indicates that it is completely carnivorous. A short food chain typically indicates a system dominated by large-sized plankton, promoting more efficient energy transfer. Conversely, longer food chains indicate a shift towards small-sized plankton dominance, which would negatively influence FCE.

The FCE derived from observations is calculated following Stock and Dunne (2010), as the ratio of mesozooplankton production to primary production, consistent with the modelled FCE. Observationally estimated mesozooplankton production is calculated using biomass from the Coastal & Oceanic Plankton Ecology, Production, & Observation Database (COPEPOD; O'Brien 2007) and growth rates from Hirst and Bunker (2003), which are based on temperature and chlorophyll data from MODIS (NASA Ocean Biology Processing Group 2022a, 2022b). Phytoplankton production is from Vertically Generalized Production Model (VGPM; Behrenfeld and Falkowski 1997).

### 3. Results and discussion

#### 3.1. Interannual variability of planktonic trophic transfer

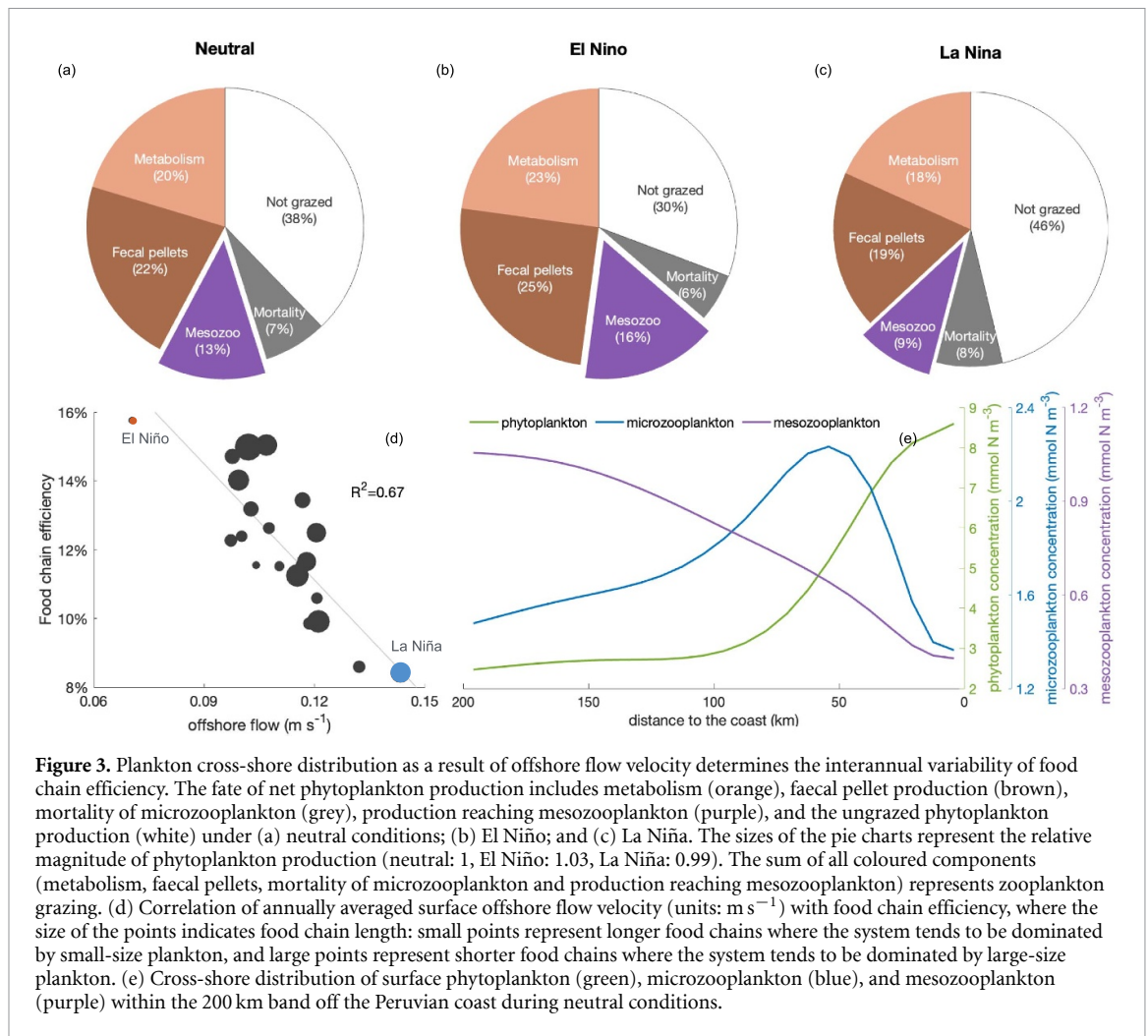
FCE reveals a stronger interannual variation than integrated net phytoplankton production, making it the key factor for interannual integrated net mesozooplankton production variation in the model. From 1990 to 2010, the annual mean integrated phytoplankton production shows a 7% variance relative to its mean over the period, while mesozooplankton production exhibits a 33% variance (figure 1(c)), thus a much stronger interannual variation. The energy reaching mesozooplankton is largely determined by grazing (purple within the coloured components in figures 3(a)–(c)), which is controlled not only by primary production but also by the efficiency of energy transfer up the food chain, i.e. FCE. In the model, the fate of phytoplankton

production is either grazing by zooplankton (subsequently used for metabolism, egested as faecal pellets, lost as non-grazed microzooplankton mortality, or eventually reaching mesozooplankton) or remaining unconsumed by zooplankton. Under neutral conditions, 62% of phytoplankton production is grazed, with 13% reaching mesozooplankton. Comparatively, during El Niño conditions, a larger fraction of phytoplankton is grazed (70%), with 16% reaching mesozooplankton. During La Niña conditions, a smaller fraction of phytoplankton is grazed (54%), with only 9% reaching mesozooplankton. As shown in figure 1(c), mesozooplankton production tends to follow the same interannual trend as FCE. Indeed, on an interannual basis, FCE appears to be the primary driver of total mesozooplankton production ( $R^2 = 0.96$ ,  $p$ -value  $< 0.0001$ ), while the influence of primary production is much smaller ( $R^2 = 0.44$ ,  $p$ -value  $< 0.002$ ).

The interannual variation in FCE, which represents how well energy is transferred from phytoplankton to mesozooplankton, relates to the offshore flow (figure 3(d)) that influences plankton spatial distributions. Generally, offshore flow pushes plankton away from the coast during their growth. As illustrated by the zonal pattern of different plankton groups under neutral conditions, the distributions of the three plankton groups are distinct (figure 3(e)): phytoplankton peak close to the coast, the microzooplankton's peak is shifted offshore, and mesozooplankton peak even further offshore. Phytoplankton have fast growth rates and can accumulate biomass close to the coast, where upwelling brings freshly upwelled nutrients. Zooplankton, however, their distribution depends not only on the availability of phytoplankton as prey but also on physical transport processes. The temporal lag between prey and predator growth, combined with the offshore flow, leads to spatial decoupling, explaining why higher trophic levels accumulate their biomass further offshore. This spatial decoupling between predator and prey, due to the slower growth rates of higher trophic levels (Grémillet *et al* 2008), affects grazing efficiency.

#### 3.2. 1997 El Niño and 2007 La Niña years as examples of extremes in trophic transfer

The occurrences of El Niño in 1997 and La Niña in 2007 coincide with the largest positive and negative anomalies in offshore flow velocity (figure 3(d)), influencing FCE, which ranges from a minimum of 9% in 2007 to a maximum of 16% in 1997. This can be illustrated by the trophic transfer from phytoplankton to microzooplankton (but similarly is reflected in the energy transfer further up to mesozooplankton, as shown in figure S5). As shown in figures 4(a) and (b), average phytoplankton within the research area are lower during El Niño ( $69 \text{ mmol N m}^{-2}$ ) compared to La Niña ( $85 \text{ mmol N m}^{-2}$ ), with similar zonal

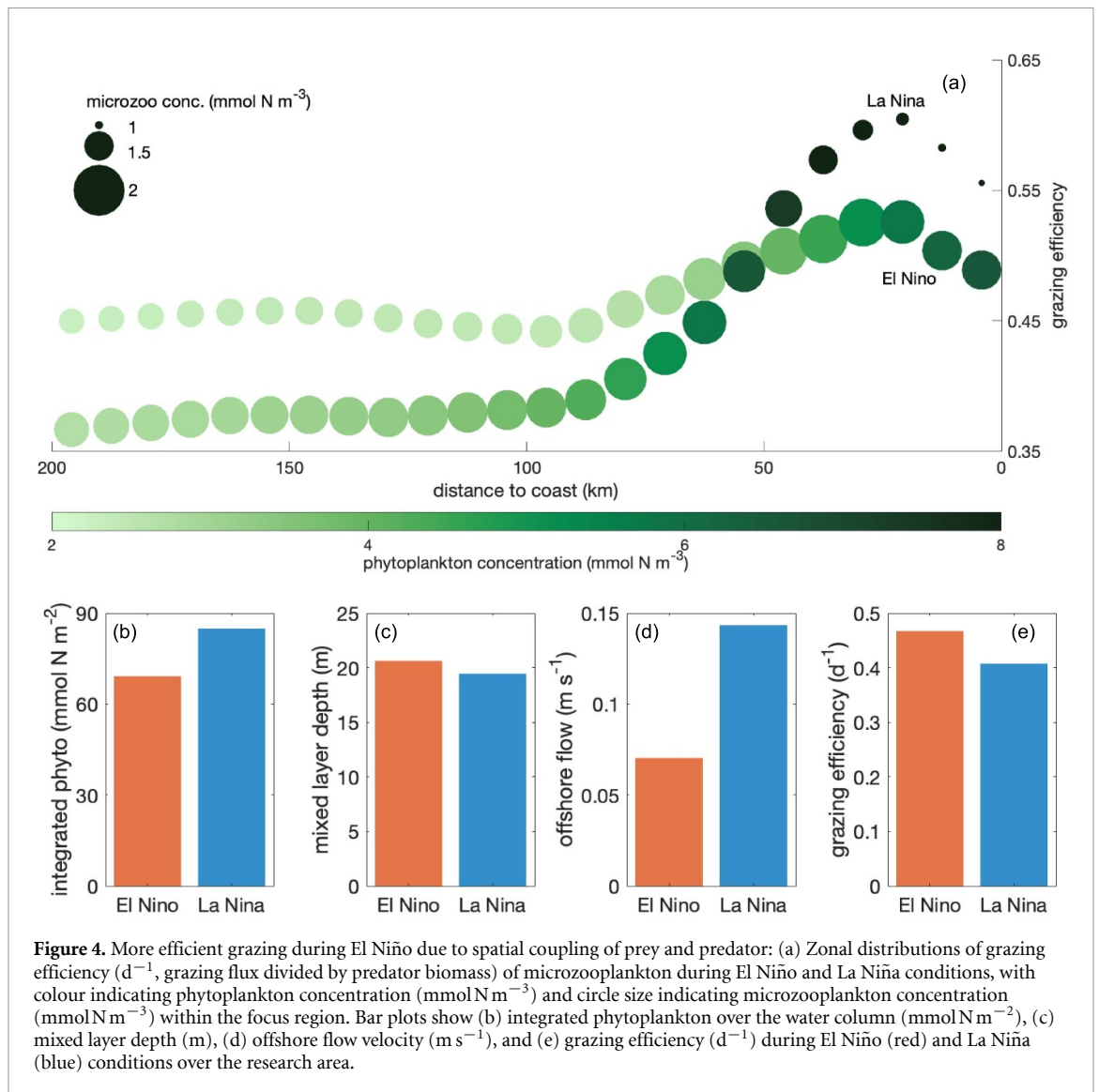


**Figure 3.** Plankton cross-shore distribution as a result of offshore flow velocity determines the interannual variability of food chain efficiency. The fate of net phytoplankton production includes metabolism (orange), faecal pellet production (brown), mortality of microzooplankton (grey), production reaching mesozooplankton (purple), and the ungrazed phytoplankton production (white) under (a) neutral conditions; (b) El Niño; and (c) La Niña. The sizes of the pie charts represent the relative magnitude of phytoplankton production (neutral: 1, El Niño: 1.03, La Niña: 0.99). The sum of all coloured components (metabolism, faecal pellets, mortality of microzooplankton and production reaching mesozooplankton) represents zooplankton grazing. (d) Correlation of annually averaged surface offshore flow velocity (units:  $\text{m s}^{-1}$ ) with food chain efficiency, where the size of the points indicates food chain length: small points represent longer food chains where the system tends to be dominated by small-size plankton, and large points represent shorter food chains where the system tends to be dominated by large-size plankton. (e) Cross-shore distribution of surface phytoplankton (green), microzooplankton (blue), and mesozooplankton (purple) within the 200 km band off the Peruvian coast during neutral conditions.

distributions showing high coastal and low offshore concentrations. The offshore flow velocity during El Niño ( $0.7 \text{ m s}^{-1}$ ) is much weaker than during La Niña ( $1.4 \text{ m s}^{-1}$ ). During El Niño, the weak offshore flow allows microzooplankton to stay relatively close to the coast despite their comparatively slow growth, thus benefiting more from the high coastal phytoplankton concentration and on average over the focus region graze more efficiently on phytoplankton ( $0.47 \text{ d}^{-1}$ ), despite overall lower phytoplankton biomass. At the same time, MLD, which affects grazing efficiency on a seasonal scale (Xue *et al* 2022a), does not change substantially and even works in the opposite direction, as the slightly deeper MLD during El Niño would negatively affect grazing efficiency. Conversely, during La Niña, the strong offshore flow pushes microzooplankton further offshore, spatially decoupling them from the highly concentrated coastal phytoplankton and resulting in an overall less efficient grazing on phytoplankton ( $0.41 \text{ d}^{-1}$ ). Therefore, the spatial coupling or decoupling of predator and prey can result in different predator grazing efficiency, thereby affecting FCE.

The positive response of zooplankton grazing to El Niño is consistent with observation in northern

Chile by Ulloa *et al* (2001), where zooplankton biomass doubled during 1997 El Niño compared to the neutral period. In the northern Humboldt system, though Ayón *et al* (2008) and Aronés *et al* (2019) observed no obvious increase in zooplankton during El Niño, they found that minimum zooplankton abundance tended to coincide with prolonged strong La Niña conditions, consistent with unfavourable feeding conditions during La Niña. In addition to favourable changes in grazing, there is a small negative, opposing effect on FCE due to a longer food chain during El Niño in the simulation (figure 3(d)). This is consistent with the observed shift towards smaller-sized plankton species during El Niño (Ulloa *et al* 2001, Chavez *et al* 2002, Escribano *et al* 2004). Nonetheless, our model can only capture limited variations in the food web structure due to its simplified representation of complex real-world ecosystem dynamics, a characteristic shared with other biogeochemical models. This simplification includes limiting the model to a few generalised plankton groups and using simple formulations and parameterizations for zooplankton behaviour and physiology, such as zooplankton grazing and fixed prey preferences. A previous sensitivity study by Xue *et al* (2022a), which



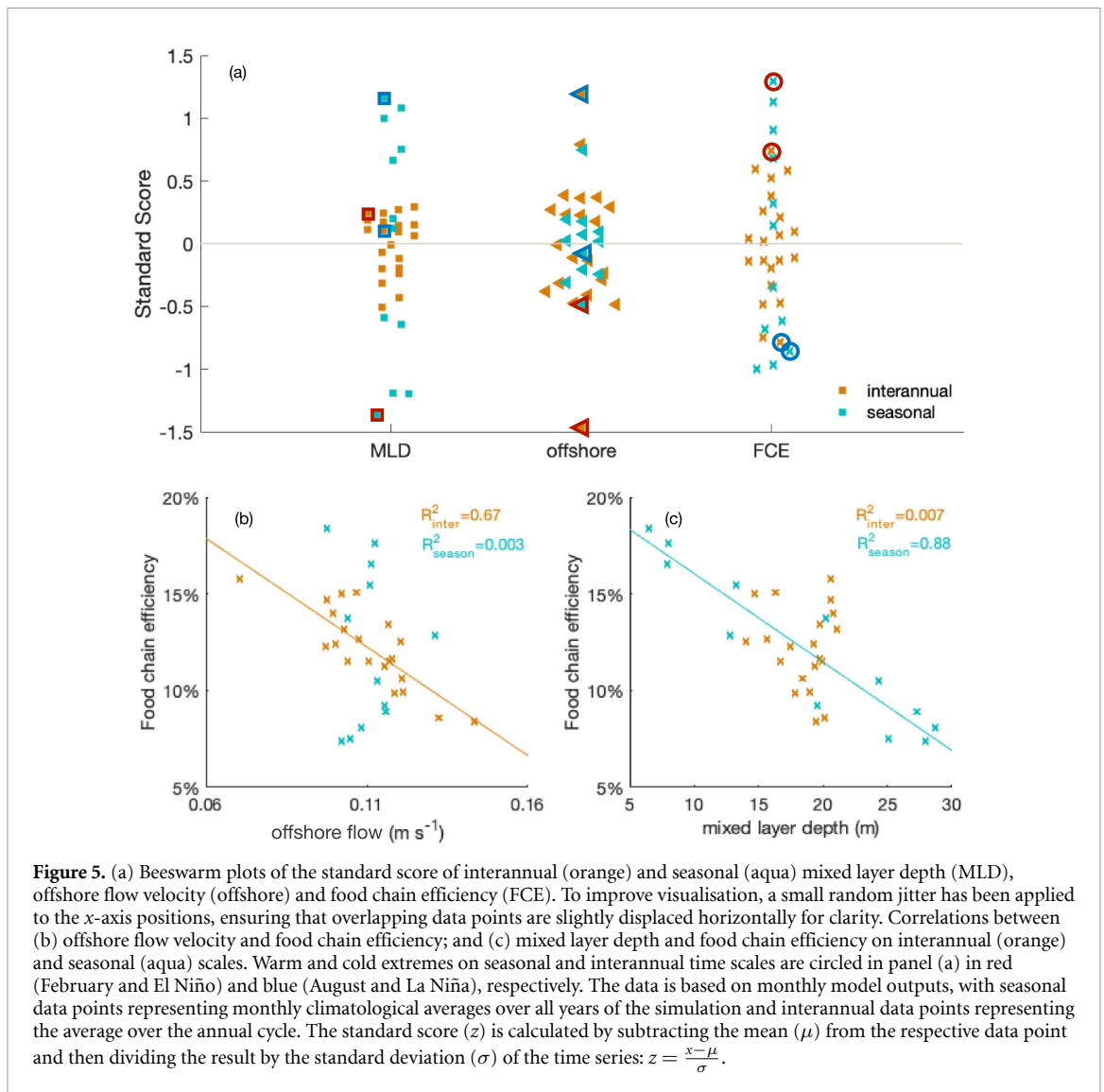
**Figure 4.** More efficient grazing during El Niño due to spatial coupling of prey and predator: (a) Zonal distributions of grazing efficiency ( $d^{-1}$ , grazing flux divided by predator biomass) of microzooplankton during El Niño and La Niña conditions, with colour indicating phytoplankton concentration ( $mmol\ N\ m^{-3}$ ) and circle size indicating microzooplankton concentration ( $mmol\ N\ m^{-3}$ ) within the focus region. Bar plots show (b) integrated phytoplankton over the water column ( $mmol\ N\ m^{-2}$ ), (c) mixed layer depth (m), (d) offshore flow velocity ( $m\ s^{-1}$ ), and (e) grazing efficiency ( $d^{-1}$ ) during El Niño (red) and La Niña (blue) conditions over the research area.

manipulated food web structure through changing prey preferences, indicated that capturing changes in the food web structure to a degree observed in real ecosystems is beyond the capability of typical biogeochemical models. While these models can help understand the role of food web structure changes in processes like trophic transfer, they can only simulate limited changes in food web structure and may therefore underestimate the impact of these changes.

Enhanced mesozooplankton production during El Niño would raise the expectation that there would be a positive effect on fisheries, contrasting observations: anchovy landings, which constitute the most important fishery of the Humboldt system, tend to collapse during El Niño events (Alheit and Niquen 2004). The canonical wisdom is that the strong inter-annual fluctuation of fish production is bottom-up driven (Barber and Chavez 1983), meaning it is determined by plankton biomass. This concept has been challenged by Iriarte *et al* (2000) and Ayón *et al* (2008), who found no clear decrease in either

phytoplankton or zooplankton during El Niño in the Humboldt system. Additionally, Espinoza and Bertrand (2008) found that enhanced production of zooplankton is a poor predictor of high fishing yield. Bertrand *et al* (2004) argue that various factors need to be taken into consideration when explaining the change in fish production, such as multi-timescale oceanographic conditions or fishing pressure. A recent study by Hill *et al* (2022) utilised an end-to-end model, which included environmental components, plankton, and fish, to examine the sensitivity of fish production to different factors. They found that the survival rate of fish larvae has a greater impact on fish production than changes in prey biomass. Also, Carrasco and Santander (1987) emphasised the significance of the survival rate of fish larvae, observing a notable increase in carnivorous and omnivorous copepod species during El Niño period that primarily feed on anchovy and sardine larvae, in addition to changes in zooplankton biomass. Hence, an El Niño increase in mesozooplankton may in turn negatively affect fish.





**Figure 5.** (a) Beeswarm plots of the standard score of interannual (orange) and seasonal (aqua) mixed layer depth (MLD), offshore flow velocity (offshore) and food chain efficiency (FCE). To improve visualisation, a small random jitter has been applied to the  $x$ -axis positions, ensuring that overlapping data points are slightly displaced horizontally for clarity. Correlations between (b) offshore flow velocity and food chain efficiency; and (c) mixed layer depth and food chain efficiency on interannual (orange) and seasonal (aqua) scales. Warm and cold extremes on seasonal and interannual time scales are circled in panel (a) in red (February and El Niño) and blue (August and La Niña), respectively. The data is based on monthly model outputs, with seasonal data points representing monthly climatological averages over all years of the simulation and interannual data points representing the average over the annual cycle. The standard score ( $z$ ) is calculated by subtracting the mean ( $\mu$ ) from the respective data point and then dividing the result by the standard deviation ( $\sigma$ ) of the time series:  $z = \frac{x - \mu}{\sigma}$ .

### 3.3. Mechanisms regulating plankton dynamics on interannual time scales differ from mechanisms previously found for seasonal timescales

On a seasonal scale, the planktonic trophic transfer is governed by changing MLD (figure 5(c)), different to what we found on an interannual scale. MLD exhibits much higher variation on a seasonal scale with a standard score range of  $[-1.4 \ 1.2]$  compared to that on the interannual scale (a standard score range of  $[-0.5 \ 0.3]$ , figure 5(a)). Changing the MLD will not only affect the ‘top-down’ process as it controls zooplankton grazing due to dilution (Xue *et al* 2022a), but it is also considered a first-order mechanism to determine phytoplankton production through light limitation (Echevin *et al* 2008, Xue *et al* 2022b).

On an interannual scale, the variability in offshore flow explains most of the variation of the trophic transfer within the ecosystem. The variability of the offshore flow surpasses the relative variation simulated in the MLD during 1990–2010 (standard scores range of  $[-1.2 \ 1.5]$  versus  $[-0.5 \ 0.3]$ , respectively,

figure 5(a)). Changes in offshore flow have been observed not only during the 1997 El Niño event (figure 3(d), Espinoza-Morriberón *et al* 2017), but also by Echevin *et al* (2018) for the 2017 El Niño, and by Cane (1983) and Barber and Chavez (1983) for the 1982–1983 El Niño, which showed inshore warm current anomalies. MLD, which has been previously found to play a significant role in plankton dynamics on a seasonal scale (Xue *et al* 2022a), appears to be less relevant on the interannual scale (figure 5(c)).

Besides interannual and seasonal variability, our model captures a trend over the two decades of the historical simulation. Prior to 1999, the ecosystem shows high FCE and mesozooplankton production. Post-1999, despite fluctuating phytoplankton production, there is a shift towards less efficient trophic transfer and lower mesozooplankton production, likely due to changes in offshore flow and MLD. During the simulated period (figure S3), the MLD shows a very subtle deepening signal ( $p$ -value = 0.8), while there is a significant trend towards stronger

offshore flow velocity ( $p$ -value = 0.003). The stronger offshore flow could result from intensified upwelling (Bonino *et al* 2019) due to stronger along-shore winds (Gutiérrez *et al* 2011), which can spatially decouple phytoplankton and zooplankton and thereby lower FCE. However, we cannot conclude here if the trend from 1990 to 2010 is a signal of decadal variability or changes on longer timescales, e.g. due to climate change (figure 1(c), more details in supplementary materials).

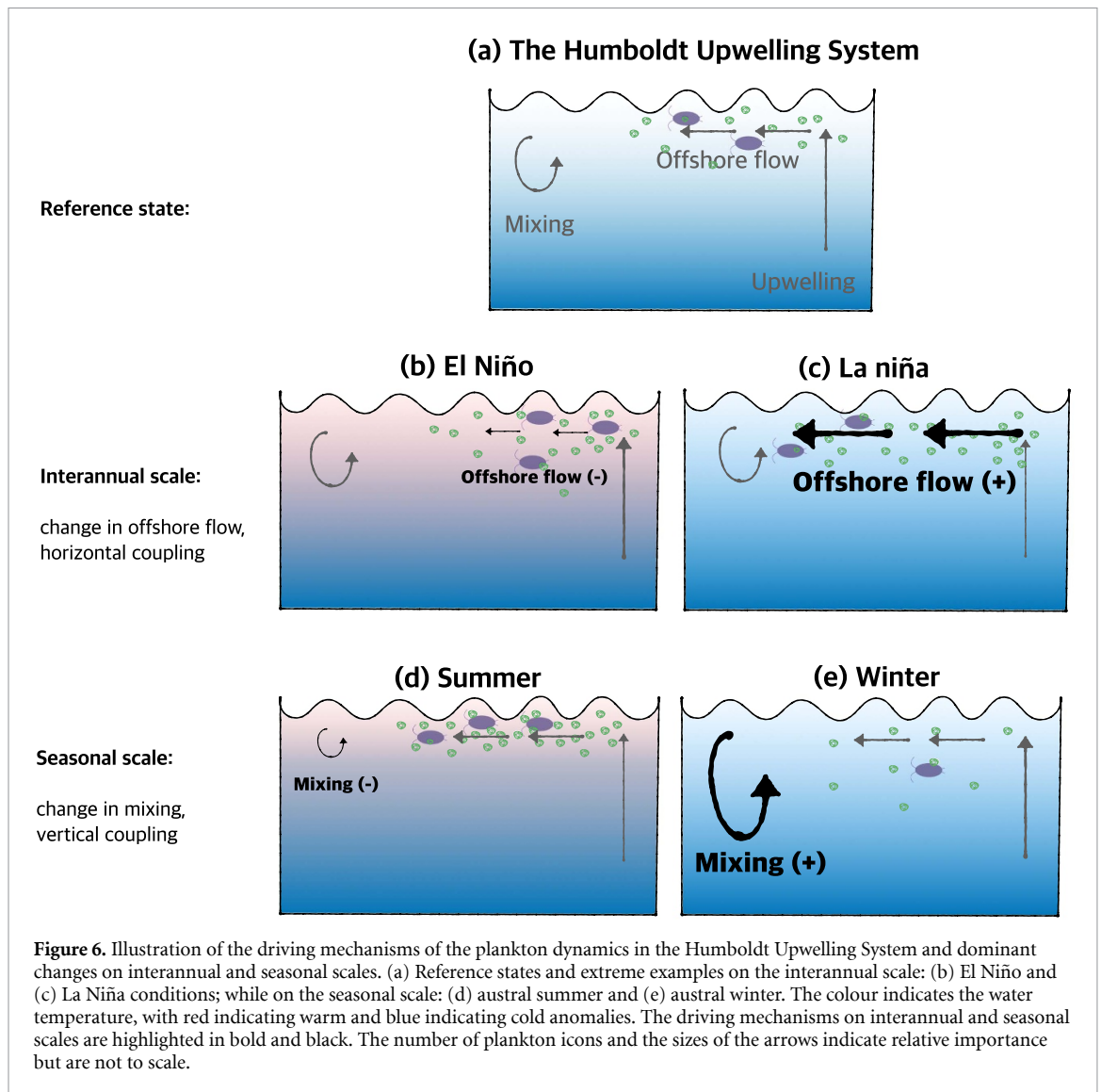
Note that the variations of oceanographic conditions we find on interannual and seasonal scales are larger than the previously reported long-term changes projected until the end of the century due to climate change: the mean states of offshore flow and MLD are projected to decrease 0%–25% and 16%–26% (the absolute value of the coefficient of variation for offshore flow and MLD in our simulation are 25% and 48%), respectively, under the high emission scenarios until the end of the century in CMIP5 and CMIP6 models (Echevin *et al* 2020, Bograd *et al* 2023). As both environmental variables are projected to change with similar magnitudes, they should both be taken into consideration when investigating how future plankton dynamics will evolve. Our results suggest that the simulated long-term mean change by the end of the century will not exceed background natural variability on seasonal to interannual time scales (figure 5). This indicates that the projected long-term change is potentially already being experienced by the system under current seasonal and interannual variability, suggesting that the plankton system may be able to cope with the potential upcoming changes under global warming. However, beyond long-term mean changes, the skill of models to project future extreme conditions, such as El Niño events, appears limited (Wittenberg 2009). Despite the potentially significant ecosystem impacts, the projections of future El Niño remain uncertain (Timmermann *et al* 1999, Kohyama and Hartmann 2017, Cai *et al* 2018, Wengel *et al* 2021).

#### 4. Conclusions and implications

We here emphasise that the mechanisms that affect trophic transfer within the plankton community in the Humboldt upwelling system differ on time scales varying from months to years (figure 6). On an interannual scale, we determine offshore flow velocity as the driver of trophic transfer within the plankton community. Strong offshore surface flow leads to horizontal spatial decoupling of zooplankton and phytoplankton, deteriorating grazing conditions, and consequently low FCE. In comparison, on a seasonal scale, MLD plays a significant role in trophic transfer by changing the vertical distributions of zooplankton and phytoplankton, similarly affecting grazing conditions and driving changes in FCE.

The above findings are subject to certain limitations. For instance, the model is designed to be bottom-up forced by environmental conditions, with zooplankton used as a closure term, lacking the ability to respond to dynamics from higher trophic levels, such as fish. In ecosystems like the Humboldt system, which experience strong fluctuations in fish populations, neglecting these variations in top-down controls can induce deficiencies in the simulation of lower trophic levels, such as plankton (Hill *et al* 2021). Additionally, the model's limited trophic complexity does not fully capture the intricate trophic interactions of a real ecosystem (Stock *et al* 2014). Choices of formulation and parameterization of zooplankton behaviour and physiology, such as zooplankton grazing and prey preferences, are often simplified in biogeochemical models, leading to substantial uncertainties in the simulation results (Prowse *et al* 2019, Rohr *et al* 2023). While models with limited trophic complexity, like ours, have limited capability to capture the complex trophic interactions of a real ecosystem, adding complexity does not necessarily make the results more realistic. Higher model complexity with more species can increase the spread of possible ecosystem responses, potentially providing a broader understanding of ecological dynamics. However, this complexity requires a systematic understanding of trophic dynamics and extensive experimental observations to constrain a large number of model parameters. Due to the limited availability of observational constraints targeting ecological variables like zooplankton biomass, especially the continuous observations necessary to study temporal variability, most biogeochemical models lack sufficient data for calibration, hindering their ability to capture the plankton dynamics (Stock *et al* 2014). Despite the considerable simplifications inherent in our model, it demonstrates reasonable agreement with observations on both seasonal and interannual timescales. Nevertheless, it is important to acknowledge that other configurations or parameterizations of the ecosystem model may exhibit varying sensitivities to bottom-up versus top-down forcings.

Notwithstanding the limitations, our analysis across time scales reveals that the driving mechanisms of plankton dynamics within the Humboldt system are sensitive to the specific time scales considered. The ecosystem responds differently to varying oceanographic conditions on different timescales, emphasising the need to disentangle the effects of various drivers by using model sensitivity studies (e.g. changes in offshore flow and MLD), as these drivers will be affected by climate change. Extrapolating solely from findings on seasonal or interannual scales to draw conclusions about the mechanisms governing trophic transfer on long-term scales in the context of climate change may be inadequate.



### Data availability statement

The data that support the findings of this study are openly available at the following URL/DOI: <https://hdl.handle.net/20.500.12085/b4d40ba5-48ad-48c8-99c4-fc422aa3cebd>.

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### Conflict of interest

The authors declare that they have no conflict of interest.

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