**Abiotic forcing in allometric trophic network models**

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**Abstract**

Current ecological research and ecosystem management call for improved understanding of the abiotic drivers of community dynamics, including temperature effects on species interactions and biomass accumulation. Allometric trophic network (ATN) models provide an attractive framework to study consumer-resource interactions from organisms to ecosystems, but they rarely consider changes in some key abiotic drivers that affect e.g. consumer metabolism and producer growth. Here we investigate how seasonal changes in carrying capacity and light-dependent growth rate of producers and temperature-dependent mass-specific metabolic rate of consumers affect ATN model dynamics, namely seasonal biomass accumulation, productivity and standing stock biomass of different trophic guilds, including age-structured fish communities. Our simulations of the complex Lake Constance (LC) food web indicated marked effects of seasonal abiotic drivers on seasonal biomass accumulation of different guild groups, particularly among the lowest trophic levels (autotrophs and invertebrates). While the adjustment of irradiance level had minor effect, increasing metabolic rate associated with 1–2˚C temperature increase lead to a marked decline of larval (0-year age) fish biomass, but to a substantial biomass increase of 2- and 3-year-old fish that were not predated by ≥4-year-old perch. A gradual temperature increase of 0.037˚C year–1 observed in LC increased the productivity of highest trophic levels (i.e., juvenile and adult fish) by ca. 40–50% over the 100-year simulation period. However, when looking at biomass distribution and transfer between trophic guilds in the LC food web, inclusion of seasonal abiotic drivers caused only minor changes in average standing stock biomasses and productivity of different trophic guild groups. Our results demonstrate the potential of introducing seasonal variation in abiotic ATN model parameters to simulate within-year fluctuations in community dynamics, as well as to assess potential future community-level responses to ongoing environmental changes.

**Keywords**: Abiotic forcing; allometric trophic network model; food web; Lake Constance; seasonality

**Introduction**

Abiotic environmental drivers, such as temperature, light and nutrient availability, are key factors affecting the structure, function and productivity of terrestrial and aquatic ecosystems, with the impacts ranging across different levels of biological organization (e.g. from individual’s physiology to species population density and to trophic and competitive interactions between coexisting species; Dunson and Travis 1991; Brown et al. 2004; Gårdmark and Huss 2020). In lakes, water temperature, nutrients and light availability commonly shape the productivity and energy source of consumers, including zooplankton, benthic invertebrates and fish, via complex top-down and bottom-up control of benthic and pelagic food-web compartments (e.g. Shurin et al. 2012; van Dorst et al. 2020). Although these abiotic drivers are increasingly modified by human impacts, such as climate change, land use and eutrophication (e.g. Woodward et al. 2010; Kovalenko 2019), their potential effects on seasonal biomass development and standing stocks of different trophic guilds have seldom been accounted for in allometric trophic network models (Martinez 2020).

Understanding the mechanisms of how abiotic environmental conditions influence species’ abundance and interactions is critical for conservation and ecosystem management. Allometric trophic network (ATN) models that build upon predator-prey interactions and population dynamics depending on species’ body size and metabolic type (Yodzis and Innes 1992; Brose et al. 2006; Kath et al. 2018; Martinez 2020) can help to simulate ecosystem responses to environmental variation and various disturbances, such as harvesting (Kuparinen et al. 2016). The simplicity and generality of ATN models makes them attractive tools for evaluating human impacts on ecosystems, as well as for testing various ecological theories, such as coexistence theory (Brose 2008) and biodiversity-ecosystem functioning relationships (Schneider et al. 2016). Some parameters in ATN models, such as the growth rate of primary producers and the metabolic rate of consumers, are often set as temporally invariant constants. However, these abiotic drivers can show large seasonal fluctuations and be strongly influenced by ongoing environmental changes, with potential complex ecosystem-level impacts (e.g. McMeans et al. 2015; Woolway et al. 2020). Considering seasonal variation in abiotic environmental factors, such as temperature and irradiance, would likely produce ATN simulation results that correspond better with the abundance of and interactions between various trophic levels in real food webs.

Indeed, the study by Boit et al. (2012) illustrates how inclusion of abiotic forcing, i.e., seasonal changes in carrying capacity, temperature, and irradiance, increases the ATN model fit to observed seasonal dynamics and size-abundance distribution of the plankton community. However, Boit et al. (2012) did not effectively study or disentangle the mechanisms shaping the impacts of abiotic forcing on various trophic guilds, including age-structured fish communities. Yet, factors affecting the magnitude, timing, and seasonal variation of biomass production and trophic interactions between different guilds have fundamental implications for the general ecosystem structure and function (e.g. McMeans et al. 2015).

Here, we studied how inclusion of seasonality affects ATN model dynamics, using an existing ATN model parametrized for Lake Constance (LC) as an example. Although our study does not aim to simulate empirical data of community dynamics, the recent ATN model for LC food web provides arguably more realistic insights than randomly generated food webs and it also accounts for life-history structuring for fishes (Kuparinen et al. 2016). More specifically, we tested how the inclusion of seasonal variation in autotrophs’ carrying capacity, light-dependent growth rate of producers, and temperature-dependent mass-specific metabolic rate of consumers affects seasonal biomass development, productivity (i.e., producer growth or invertebrate and fish consumer consumption gains) and standing stock biomass of different trophic guilds, including age-structured fish communities. To simulate ongoing environmental changes in lakes (namely warming and reduced light penetration due to browning or eutrophication; e.g. Woodward et al. 2010; Kritzberg et al. 2019; Blanchet et al. 2022), we also investigated how adjustment of temperature and irradiance level, as well as a gradual temperature increase of 0.037 °C year–1 observed in LC (Adrian et al. 2009) over a 100-year simulation period affect the biomass dynamics of producer, invertebrate and fish guilds in the ATN model.

**Material and methods**

*Lake Constance ATN model*

We studied the effect of varying autotrophs’ carrying capacity, temperature, and light availability (irradiance) on ATN model dynamics. We utilized the ATN model parametrized by the observed complex food-web structure in LC (Martinez 2020) and accounting for abiotic environmental drivers (cf. Boit et al. 2012) and age-structured fish communities (cf. Kuparinen et al. 2016). The modelled network consists of 133 feeding links among 30 functionally distinct guilds (i.e., species or groups of functionally similar species), including basal producers (n=6 guilds), heterotrophic microbes (n=7), invertebrates (n=7), and five life-history stages of two fish species (n=10 guilds). The fish guilds include larvae, juveniles, 2 years, 3 years, and 4 years or older planktivorous European whitefish (*Coregonus lavaretus*, hereafter whitefish) and omnivorous European perch (*Perca fluviatilis*, hereafter perch) which are the most common and commercially fished species in the pelagic fish community of LC (Kuparinen et al. 2016).

The biomass dynamics of the food web (see Table S1–S2 for details) within the growing season of year are described by a set of ordinary differential equations (ODEs). We denote the carbon biomass density (hereafter ‘biomass’) of guild by ( and its derivative with respect to time (days) by , where . The vector of all guild biomasses is denoted by **.** Following Boit et al. (2012), the length of the growing season is set to 240 days, and thus we set and . To simplify the presentation, year and time are omitted from the description of the growing season dynamics. The following ODEs describe the biomass dynamics for (1) producers and (2) consumers:

(1)

(2)

where is the intrinsic growth rate of producer and it is calculated based on allometric scaling

(3)

where the allometric scaling exponent , is the body mass of the reference producer guild (Alg1) and is the body mass of producer guild , both expressed in terms of their dry carbon weight (Boit et al. 2012). is the limiting factor in the producers’ logistic growth model where denotes the vector of ones and is the carrying capacity shared by all autotrophs. The matrix , where the matrix consists of the producer competition coefficients , is used to normalize the competition coefficients such that equals the realized carrying capacity of the autotrophs. Here denotes the matrix transpose and the matrix inverse. The fraction of new producer biomass lost to exudation is .

The metabolic rate of consumer is and it is based on allometric scaling

(4)

where the allometric scaling constant and the allometric scaling exponent are 0.314 and 0.15 for invertebrates and 0.88 and 0.11 for fish, respectively (Boit et al. 2012). The maximum consumption rate scaling factor of guild feeding on guild is . The inefficiencies in the biomass transfer are accounted for by assimilation efficiency parameter . is the maintenance respiration coefficient and is the fraction of consumers’ assimilated carbon used for production of new biomass under activity, including locomotion, foraging (food handling and digestion), ontogenetic processes, and reproduction (Boit et al. 2012; Kath et al. 2018). The consumer and fish species’ normalized functional response to prey species densities is:

 (5)

where is the prey preference for consumer species feeding on resource species , is the Holling exponent, is the half saturation density describing the biomass of the prey at which the predator achieves half of its maximum feeding rate when consuming only prey and in the absence of feeding interference, and is the coefficient of intraspecific feeding interference. The feeding link specific parameters and are determined by the type of the predator and its prey, and possibly their body mass ratio (Bland et al. 2019). The list of all aforementioned parameters, their units, value ranges, descriptions and references are provided in Table S2, whereas the guild specific intrinsic growth rates and average metabolic rates are presented in Table S1.

The adult fish guilds allocate a portion of their consumed biomass to reproduction. The amount of biomass allocated depends on the total consumption gains and the maintenance losses . We use a piecewise defined model for the rate of biomass allocation to reproduction by adult fish guild during the growing season:

(6)

where denotes the age-dependent proportion of mature biomass in adult fish guild , and is an age-dependent parameter controlling reproductive investment. This model has three desirable properties: 1) it ensures that reproduction is zero when consumption gains are zero, 2) it enforces impaired reproduction when the maintenance losses are greater than the consumption gains, and 3) when the consumption gains exceed the maintenance losses, reproduction increases linearly as a function of the consumption gains. The biomass allocated to reproduction is unavailable for growth and is thus subtracted from the rate of biomass gained by consumption by adult fish guild :

(7)

Furthermore, the amount of accumulated biomass allocated to reproduction by adult fish guild during the growing season is solved by adding Equation 4 to the system of ODEs.

At the end of the growing season of year , the fish biomass is moved up one age class to become the initial biomass of the one-year older age class for year

(8)

with the exception that for the final age class of ≥4-year-old fish, the initial biomass is the sum of the end biomasses of the 3-year and 4-year-old age classes

(9)

The larvae biomass (age 0) is calculated as the sum of the biomasses allocated to reproduction by all adult age classes (ages 2–4)

(10)

For the other guilds, biomass in the end of the growing season becomes the initial biomass for the next year’s growing season.

*Abiotic forcing in ATN*

We introduced seasonal variation in the parameters for autotrophs’ carrying capacity (*K*), mass-specific growth rates of autotrophs (), and metabolic rates of consumers () to elucidate their effects on the ATN model dynamics (Figure 1; Table 1). We largely followed the approach and used the same parameter values as described in Supporting Information of Boit et al. (2012) but made some adjustments to the seasonal models. Essentially, we assumed that the constant model is a lower resolution approximation of the seasonally varying models that corresponds to the seasonally varying model on average in some meaningful way. Thus, we decided to normalize the seasonal models such that the average total producer biomasses are equal in each model. This way we were able to test how the seasonally varying parameter values affect the biomass dynamics. We then also tested the effects of adjusting the magnitudes of the parameters.

Firstly, we modelled seasonal changes in carrying capacity of primary producers with an adjusted version of Boit et al. (2012):

(11)

where is the original constant carrying capacity, is a decay component and equaling to the middle of the 240-day growing season (Figure 1a). This abiotic forcing simulates the high production capacity of autotrophs when nutrients are highly available during the early-season water column mixing period, followed by decreasing production capacity due to increasing nutrient limitation towards the mid growing season stratification period. By adjusting the seasonal carrying capacity model of Boit et al. (2012) this way, we can interpret the constant carrying capacity model as the average of the seasonally changing carrying capacity model and thus be better able to compare the two models.

Secondly, we modelled seasonal changes in producers’ growth by multiplying the constant autotroph growth rate with a time-varying light coefficient , i.e., where

(12)

The half-saturation constant for irradiance, , was set to 20% of the maximum irradiance (Wallace et al. 1996), whereas is the epilimnion depth and is a typical value for the bulk attenuation coefficient (Wallace et al. 1996). The scaling factor was chosen so that average yearly total producer biomass was equal to the average total producer biomass of the constant model. The irradiance at time is expressed in unit of W m–2 and modelled as a half sine function which gives the maximum amount of radiation in the middle of the growing season and less towards the beginning and end of the season, thus mimicking the seasonally changing day length (Figure 1b):

(13)

Here () was used to adjust the mean irradiance level in the simulations.

Thirdly, we modelled abiotic forcing of higher trophic levels by multiplying the consumers’ constant metabolic rate with a time-varying temperature dependent coefficient , i.e., where

(14)

Here is the standard temperature and is a temperature-dependency coefficient. The time-varying temperature was modelled as a half sine function to have the warmest temperature in the middle of the growing season and colder temperatures at the beginning and the end of the season (Figure 1c):

(15)

where is as a free parameter used to make small adjustments to temperatures. With °C, the temperatures range between 7°C and 17°C. The used by Boit et al. (2012) produces values typically exceeding the seasonally invariant . Hence, to make the model outputs more comparable, we added a scaling coefficient , which was chosen again so that the yearly average total producer biomass equals the yearly average total producer biomass of the constant model.

To further test for the effects of abiotic drivers, we run the ATN model after adjusting the levels of temperature and irradiance that affect the mass-specific metabolic rate of consumers (eqn 12) and the light-dependent autotroph growth rate (eqn 9), respectively. For this, the level of was decreased or increased by 1 °C and 2 °C (), whereas the level of was decreased or increased by 25 W m–2 or 50 W m–2 (). To test for potential interacting effects of increased and decreased associated with predicted impacts of ongoing global warming and brownification of freshwater ecosystems (Woolway et al. 2020; Blanchet et al. 2022), we run the ATN model after increasing by 2 °C –which is a conservative estimate of the average temperature increase of summer surface waters in large Austrian lakes by 2050 (Dokulil 2014)– and decreasing by 50 Wm–2. Finally, to study the effects of warming climate on the food web productivity, a gradual 0.037 °C year–1 increase in as observed in LC (Adrian et al. 2009) was simulated by incrementing by 0.037 °C each year for 100 years, starting from and ending up with °C.

*Visualization of simulation results*

The effects of seasonal variation in carrying capacity (), mass-specific growth rates of autotrophs (), and metabolic rates of consumers () on ATN model dynamics were illustrated as relative differences in the standing stock biomasses (relative to the biomass at the beginning of the growing season) and productivity or consumption gains of the following trophic guild groups (see Supporting Information Table S1 for guild abbreviations): (i) phytoplankton (Alg1–5, APP), (ii) ciliates (Cil1–5), (iii) rotifers (Rot1–3, Asp), (iv) herbivorous crustaceans (Cru), (v) carnivorous crustaceans (Cyc, Lep), (vi) larval and juvenile whitefish (Whi0–1), (vii) adult whitefish (Whi2–4), (viii) larval and juvenile perch (Per0–1), and (ix) adult perch (Per2–4). For each ATN model configuration, the biomasses and productivities of each guild were simulated over 250 years (240-day long growing seasons), but the first 150 years were omitted to allow the system to settle into its dynamic equilibrium.

The effects of ATN model configuration and adjusted levels of and on seasonal (i.e., within-year) biomass dynamics were visualized for each trophic guild group as relative biomass differences over the last simulation year, calculated by subtracting the initial biomass at from the biomass at time . This allows direct comparison of the relative effects of ATN model configuration on the degree and timing of seasonal biomass fluctuations. Secondly, the effects of ATN model configuration on standing stock biomasses and productivities of trophic guild groups were calculated and visualized. Standing stock biomasses of different guilds were measured as mean biomasses calculated over the last 100 simulation years. The productivity of different consumer guild groups was estimated to evaluate the potential effect of ATN model configuration on biomass flow in LC food web. While standing stock biomasses reflect the amount of carbon retained in each trophic guild group (determined by the balance of biomass gain through photosynthesis or consumption of prey guilds and loss through consumption by predator guilds; see equations 1–3), the productivity reveals how much carbon is taken up by each consumer guild. The productivity of each consumer guild group was measured as sum of consumption gains (see “gain from resources (*j*)” in equation 2) in the last 100 simulation years. The standing stock biomasses and productivities were further standardized by dividing the trophic guild group specific mean biomasses and sum of consumption gains by the sum of biomasses and gains over all guilds except DOC, POC and bacteria. These standardized measures of standing stock biomasses and productivities allow direct visual inspection of biomass distribution across different trophic levels (functional guild groups) and of energy flow patterns in LC food web. All ATN simulations were run in Matlab version R2021a.

**Results**

*Seasonal biomass dynamics*

Inclusion of seasonal variation in the *K*, and parameters in the ATN model strongly influenced the simulated seasonal patterns in biomass development of primary producers and consumers in the LC food web (Figure 2). While using constant *K*, and parameters produced nearly seasonally invariable biomasses, the seasonally varying *K* (following a reverse sigmoid curve; Figure 1) induced ca. 50–100% increase in biomass of phytoplankton, ciliates and rotifers as well as of herbivorous and carnivorous crustaceans, associated with the simulated high carrying capacity of autotrophs early in the growing season. For these functional groups, the inclusion of seasonally varying hump-shaped and (Figure 1) had somewhat opposite impacts on simulated biomass dynamics, with varying inducing an increased biomass maximum, whereas caused a deeper biomass minimum for phytoplankton and ciliates in mid and late growing season, respectively (Figure 2).

The simultaneous inclusion of seasonal variation in *K*, and parameters in the ATN model induced an early-season biomass boost for phytoplankton and ciliates, followed by a late-season biomass bust associated with the declining *K* and heavy consumption by higher trophic levels. For rotifers, herbivorous and carnivorous crustaceans, the seasonally varying *K*, and parameters induced a broad biomass peak from early to middle growing season. For fish, seasonal changes in these ATN model parameters introduced a hump-shaped biomass peak of 0-year-old whitefish and perch in the mid growing season, whereas 2- and 3-year-old fish showed an increased biomass peak later in the growing season (Figure 2). The contrasting patterns in simulated seasonal biomass dynamics arise from fact that 0- and 1-year-old fish are heavily consumed by older perch (thus biomass declines towards late growing season), unlike the larger 2- and 3-year-old fish that are not predated (thus biomass increases towards the late growing season; Figure 2). The ≥4-year-old fish, including the 3-year-old fish from the previous year, are already at their maximum carrying capacity at the beginning of the growing season, therefore showing a drastic biomass decline over the growing season.

Adjustment of the temperature level (coefficient of seasonal ) in the ATN model configuration had marked impacts on the simulated biomasses of fish guilds. While the simulated temperature increase by +1 °C or +2 °C slightly reduced the biomass of 0-year-old fish with a high metabolic rate and consumption by older perch (Table S1), it drastically increased the biomass of 2-year-old whitefish and perch, and less of 1- and 3-year-old fish (Figure 3). In contrast, adjustment of the irradiance level (coefficient of seasonal ) in the ATN model configuration had only minor if any effect on the seasonal biomass dynamics of producers and consumers (Supporting Information Figure S1).

*Biomass distribution among trophic levels and consumer gains*

Despite the effects on seasonal biomass dynamics, the ATN-model configuration had no marked effects on distribution of standing stock biomass among trophic levels (Figure 4) or on relative productivity (i.e., consumption gains) of consumer guilds(Figure 5). However, simultaneous adjustment of the temperature (+2 °C) and irradiance (-50 W m–2) levels had more evident effects on biomass distribution (Figure 4) and consumer productivity (Figure 5) by reducing the relative biomass and production of ciliates but increasing the relative biomass of adult fish and the productivity of rotifers. These shifts are apparently associated with the reduced productivity of light-dependent autotrophs, which reduces the relative biomass of herbivorous ciliates. These primary consumers are, in turn, heavily predated by secondary consumers (i.e., large rotifers, cladocerans and cyclopoids; Figure 4, Table S1) under increasing metabolic rate in warmer temperatures, which further support increasing relative biomass accumulation to top predator fish. Despite some effects on standing stock biomasses and productivity, the biomass (carbon) flows in the food web, illustrated as proportional consumption gains (Supporting Information Figure S2), were nearly constant regardless of the ATN model configuration.

*Effect of gradual temperature increase*

The simulated gradual temperature increase of 0.037 °C year–1 observed in Lake Constance (cf. Adrian et al. 2009) changed the ATN model output so that the relative productivity (i.e., consumption gains) of all consumer guild groups increased, except that of ciliates (Figure 6). While the simulated phytoplankton productivity increased by 18%, the consumption gains of rotifers, herbivorous and carnivorous crustaceans increased by approx. 30% during the 100-year simulation period. The juvenile and adult whitefish and perch showed approx. 40–60% increase in consumption gains during the 100-year simulation period, indicating that the adjusted ATN model predicts cumulative positive effect of gradual temperature increase on the highest consumer levels.

**Discussion**

Allometric trophic network (ATN) models have many theoretical and applied applications (summarized by Martinez 2020), including simulation of community-level responses to fisheries (Kuparinen et al. 2016) and to environmental stochasticity (Kuparinen et al. 2019). However, the influence of abiotic forcing, such as seasonal changes in the carrying capacity and growth rate of producers and metabolic rate of consumers, on ATN modelling outcomes has remained largely unexplored, mainly because many ATN studies have rather focussed on theoretical analyses across randomly generated food webs as opposed to specific study systems. Here, we mechanistically integrated abiotic drivers to the consumer-resource dynamics described by the ATN model for the Lake Constance food web. The ATN model simulations demonstrated contrasting impacts of different abiotic drivers on the main functional groups. In general, adding seasonal variation in the producer carrying capacity () had stronger positive impact on seasonal biomass development of primary producers and invertebrate consumers as compared to temperature-dependent mass-specific metabolic rate of consumers () or seasonal light-dependent growth rate of autotrophs (). The simulated effect of abiotic forcing on seasonal biomass development diminished towards the highest consumers, i.e. juvenile and adult fish. However, adjustment of the temperature level by +1 °C or +2 °C in the seasonally varying ATN model suppressed the seasonal biomass peak of 0-year-old fish but increased the biomass peaks of adult (especially 2-year-old) perch and whitefish. Adjustment of the irradiance level had minor if any influence on the simulated seasonal biomass dynamics of the main trophic guilds in LC food web.

Introducing seasonal variation in the *K* or parameters in the ATN model had no effect on the simulated distribution of standing stock biomass and productivity (i.e., consumption gains) across trophic levels, whereas seasonality in the light-dependent growth rate of autotrophs () slightly increased the simulated biomass and productivity of rotifers. A more evident shift towards a more top-heavy food web was observed when all three abiotic drivers showed seasonal variation and the temperature level was simultaneously increased by +2 °C and the irradiance level was decreased by –50 W m2, thereby simulating environmental changes associated with global warming and reduced light availability due to water browning. The simulated gradual temperature increase of 0.037 °C per year (as observed in Lake Constance; Adrian et al. 2009) increased the relative productivity of primary producers by 18% but decreased that of ciliates by ca. 15%. The ATN model outputs suggested increased productivity for all higher consumer guild groups, including invertebrates (ca. +30%), larval and juvenile stages of fish (ca. +35–50%) and adult fish (ca. +40–60%). To summarize, our study illustrates the potential of introducing seasonal variation in the ATN model parameters to simulate temporal fluctuations in community dynamics. When it comes to the overall standing stock biomasses and productivities (consumption gains) of the main guild groups, our simulations suggest that the ATN model developed for the pelagic food web of Lake Constance seems relatively insensitive to the adjustment of abiotic drivers (, and ).

*Abiotic forcing of seasonal biomass dynamics*

Boit et al. (2012) found that adding minimal abiotic forcing markedly improved the ATN model fit with empirical data of seasonal dynamics and size-abundance distribution of the phytoplankton community in Lake Constance. This implies that, to make the simulations more realistic, ATN models should likely consider seasonal variation in some key parameters determining the biomass accumulation and transfer from producers up to top predators. We took the next step in analysing potential impacts of abiotic forcing in ATN models by looking separately at the responses of different trophic guild groups, including age-structured fish populations (cf. Kuparinen et al. 2016), to seasonally varying carrying capacity (*K*) and light-dependent growth rate () of producers and temperature-dependent mass-specific metabolic rate of consumers (). Adding seasonal variation in these key parameters, especially in *K* and , made the seasonal patterns in biomass development more realistic as compared to the outcomes of an ATN model where these parameters were constants, resulting into nearly constant seasonal biomasses of primary producers and invertebrate consumers. Including a seasonal decline in the autotrophs’ carrying capacity () induced development of a phytoplankton biomass peak early in the growing season, followed by a biomass peak of herbivorous and carnivorous pelagic invertebrates, a pattern observed also empirically in Lake Constance seasonal dynamics (Gaedke et al. 2002). These primary and secondary consumers subsequently declined following the phytoplankton biomass decline in the mid growing season. Adding seasonal variation in the temperature-dependent metabolic rate of consumers () induced a U-shaped pattern in phytoplankton biomass development likely due to increased consumption by ciliates in early growing season, followed by intense grazing by rotifers and herbivorous crustaceans towards mid growing season when the consumer metabolic rates were at the highest level. Although we here did not use empirical abiotic or temporal community data from Lake Constance to validate our simulations, our findings indicate the potential of using seasonally varying parameters in ATN models to better reflect temporal fluctuations in abiotic drivers that influence e.g. community dynamics, consumers’ energetic demands and seasonal changes in resource availability (e.g., McMeans et al. 2015; Gårdmark and Huss 2020; Kharouba and Wolkovich 2020).

*Adjusted temperature and irradiance level*

Climate change, together with intensive land use (e.g. agriculture and forestry), is predicted to increase surface water temperatures (Gobiet et al. 2014), harmful algal blooms (Elliott 2012) and loading of nutrients and coloured dissolved organic carbon into lakes (Karlsson et al. 2009; Kritzberg et al. 2019; Blanchet et al. 2022). While higher surface water temperatures may increase the metabolic rate of consumers (Sheridan and Bockford 2011; Lindmark et al. 2017) and reduce nutrient and oxygen availability due to impaired water column mixing (Yankova et al. 2017; Woolway et al. 2020), changes in light availability associated with e.g. browning has also been shown to influence the growth and biomass of producers and consumers (Karlsson et al. 2009; van Dorst et al. 2020; Blanchet et al. 2022). We modified the abiotic forcing parameters developed by Boit et al. (2012) to test how the level of and seasonal changes in temperature and irradiance affect biomass dynamics in Lake Constance food web. Adjustment of the irradiance level had virtually no effect and the temperature adjustment had only minor effect on seasonal biomass development of the lowest (primary producers and consumers) and highest (≥4-year-old fish) trophic levels. In contrast, a temperature decrease of 1–2 °C increased the biomass peaks of 0-year-old fish, whereas a temperature increase of 1–2 °C increased the biomass peaks of 2-year-old fish and to a lesser extent of 1- and 3-year-old fish. The observed warming-induced decline of 0-year-old fish and increase of adult fish results from increased predation pressure on fish larvae associated with increased metabolic and thus consumption rates of large fish. We also found a gradual temperature increase of 0.037 °C year–1 to increase the productivity of producers and higher consumers (i.e. adult fish). Unlike other consumers, the gradual temperature increase showed a negative effect on the productivity of herbivorous ciliates, which have a relatively high metabolic rate and are eaten by several predatory invertebrates, including large ciliates, rotifers, cladocerans and copepods (Table S1). The observed decline in ciliate productivity is also supported by experimental studies indicating a high food demand of ciliates in high temperatures (cf. Weisse et al. 2002). Our findings partly contradict with previous modelling studies for Lake Constance suggesting that no strong mismatches should be expected with seasonally homogenous warming, but only when warming will be seasonally heterogeneous (Straile et al. 2015). Future studies could therefore test whether the outcomes of ATN simulations would depend more on the timing (e.g., peaks in temperature and irradiance) than on the degree of abiotic forcing.

In our study, adjustment of the irradiance level had minor if any impact on the seasonal biomass dynamics of the main trophic guilds in LC food web. Following largely Boit et al. (2012) approach, we simulated seasonal changes in light availability by adjusting the producer growth rate with a light coefficient based on simulated irradiance level at a given day during the growing season. However, this adjustment of irradiance level evidently caused only minor effects on the seasonal development of phytoplankton biomass and therefore also on seasonal dynamics of different consumer guilds (Supporting Information Figure S1). In nature, phytoplankton taxa show marked differences in light utilization efficiency, with harmful (toxins producing) and nonedible cyanobacteria being particularly adapted to low light conditions and green, more edible algae being adapted to higher light environments (e.g., Schwaderer et al. 2011). Such differences in light utilization efficiency among non-edible and edible phytoplankton taxa could be accounted for in future development of abiotic forcing in ATN models. Moreover, while our simulations of light availability effects on producer growth rate could indirectly influence consumer biomass and consumption gains, in nature light conditions can have strong direct impacts on feeding efficiency and thus growth of visual predators (e.g., van Dorst et al. 2020).

*Effects on biomass distribution*

Our ATN model simulations suggest that simultaneous warming and reduced light availability may induce a shift toward a slightly top-heavier food web in Lake Constance. While our findings contradict with some modelling studies of warming and eutrophication impacts on food webs (e.g. Binzer et al. 2012, 2016), they are partly supported by experimental studies indicating reduced producer but increased consumer biomass with warming (Shurin et al. 2012), particularly in environments where plentiful nutrients lead to increased biomass of higher trophic levels and strong top-down control of producer biomass (O’Connor et al. 2009). Although we found some support for altered biomass distribution among trophic levels, the impacts of abiotic forcing were generally minor. Thus, in terms of large-scale (i.e., biomass distribution among trophic levels) and long-term (i.e., across 100 simulation years) biomass dynamics, our ATN model for LC food web is evidently not sensitive to seasonally varying abiotic drivers. However, it should be noted that the model does not effectively account for potential seasonal or annual fluctuations in nutrient availability, which can be among the major drivers of bottom-up and top-down control in lake communities (Rogers et al. 2020) and thus should likely be incorporated in future ATN model developments.

*Study limitations*

Our study aimed to test the effects of seasonally varying abiotic drivers on ATN simulation results. The results indicate in general minor effects of seasonally varying abiotic drivers on biomass accumulation and transfer across main guild groups in the Lake Constance pelagic food web. Naturally, our findings are limited to one food web, but at the same time finely solved complex lake food webs remain rare, particularly such that include realistic life-history structuring. Use of stochastic, empirical data of environmental drivers in the ATN simulations, followed by comparison of simulation results with empirical data of community dynamics, would confirm the ATN model applicability to simulation and prediction of natural community- and ecosystem-level processes (cf. Boit et al. 2012), to support ecosystem-based environmental management. To test for the generality of food-web responses, abiotic forcing should also be accounted and tested for by using ATN models parametrized for other ecosystems or using random networks (cf. Williams and Martinez 2000). Moreover, while ATN models simulate biomass transfer and accumulation in food webs, stoichiometry (e.g. C:N:P balance) and food quality (e.g. fatty acid composition and quantity) are fundamental factors affecting trophic transfer efficiency as well as growth, survival and fitness of individuals, which ultimately modify community-level responses to abiotic drivers in natural ecosystems (Sardans et al. 2011; Glibert 2012; Twining et al. 2015).

*Conclusions*

Our study demonstrates the potential of using seasonally varying parameter values (abiotic drivers) in ATN models to incorporate within-year temporal fluctuations in community dynamics. When it comes to the long-term dynamics and biomass distribution among trophic guilds, our simulations of LC food web indicate that the developed ATN model is relatively insensitive to the adjustment of the abiotic drivers that were originally incorporated by Boit et al. (2012). Thus, we conclude that ATN approach can be considered a fairly robust tool to simulate food-web dynamics. However, abiotic drivers can be much more drastic and stochastic than those considered in our study. More research is needed to reveal how e.g. the timing, magnitude and frequency of fluctuations in abiotic drivers may shape complex food-web dynamics in various ecosystems. Such mechanistic models considering abiotic drivers of food-web dynamics are highly needed for sound management and mitigation of human impacts in aquatic ecosystems influenced by multiple stressors (Woodward et al. 2010; Kovalenko 2019).

**References**

Adrian, R., O´Reilly, C.M., Zagarese, H., Baines, S.B., Hessen, D.O., Keller, W., Livingstone, D.M., Sommaruga, R., Straile, D., Van Donk, E., Weyhenmeyer, G.A. & Winder, M. 2009. Lakes as sentinels of climate change. – Limnology and Oceanography 54: 2283–2297.

Bland, S., Valdovinos, F.S., Hutchings, J.A. & Kuparinen, A. 2019. The role of fish life histories in allometrically scaled food-web dynamics. – Ecology and Evolution 9: 3651–3660.

Boit, A., Martinez, N.D., Williams, R.J. & Gaedke, U. 2012. Mechanistic theory and modelling of complex food-web dynamics in Lake Constance. – Ecology Letters 15: 594–602.

Binzer, A., Guill, C., Brose, U. & Rall, B.C. 2012. The dynamics of food chains under climate change and nutrient enrichment. – Philosophical Transactions of the Royal Society B 367: 2935–2944.

Binzer, A., Guill, C., Rall, B.C. & Brose, U. 2016. Interactive effects of warming, eutrophication and size structure: impacts on biodiversity and food-web structure. – Global Change Biology 22: 220–227.

Blanchet, C.C., Arzel, C., Davranche, A., Kahilainen, K.K., Secondi, J., Taipale, S., Lindberg, H., Loehr, J., Manninen-Johansen, S., Sundell, J., Maanan, M. & Nummi, P. 2022. Ecology and extent of freshwater browning - What we know and what should be studied next in the context of global change. – Science of The Total Environment 812: 152420.

Brose, U., Williams, R.J. & Martinez, N.D. 2006. Allometric scaling enhances stability in complex food webs. – Ecology Letters 9: 1228–1236.

Brose, U. 2008. Complex food webs prevent competitive exclusion among producer species. – Proceedings of the Royal Society B 275: 2507–2514.

Brown, J.F., Allen, A.P., Savage, V.M. & West, G.B. 2004. Toward a metabolic theory of ecology. – Ecology 85: 1771–1789.

Dokulil, M.T. 2014. Predicting summer surface water temperatures for large Austrian lakes in 2050 under climate change scenarios. – Hydrobiologia 731: 19–29.

Dunson, W.A. & Travis, J. 1991. The role of abiotic factors in community organization. – The American Naturalist 138: 1067–1091.

Elliott, J.A. 2012. Is the future blue-green? A review of the current model predictions of how climate change could affect pelagic freshwater cyanobacteria. – Water Research 46: 1364–1371.

Gaedke, U., Hochstädter, S. & Straile, D. 2002. Interplay between energy limitation and nutritional deficiency: empirical data and food web models. – Ecological Monographs 72: 251–270.

Glibert, P.M. 2012. Ecological stoichiometry and its implications for aquatic ecosystem sustainability. Current Opinion in Environmental Sustainability 4: 272–277.

Gobiet, A., Kotlarski, S., Beniston, M., Heinrich, G., Rajczak, J. & Stoffel, M. 2014. 21st century climate change in the European Alps – a review. – Science of the Total Environment 493: 1138–1151.

Gårdmark, A. & Huss, M. 2020. Individual variation and interactions explain food web responses to global warming. – Philosophical Transactions of the Royal Society B 375: 20190449.

Karlsson, J., Byström, P., Ask, J., Persson, L. & Jansson, M. 2009. Light limitation of nutrient-poor lake ecosystems. – Nature 460: 506–509.

Kath, N.J., Boit, A., Guill, C. & Gaedke, U. 2018. Accounting for activity respiration results in realistic trophic transfer efficiencies in allometric trophic network (ATN) models. – Theoretical Ecology 11: 453–463.

Kharouba, H.M. & Wolkovich, E.M. 2020. Disconnects between ecological theory and data in phenological mismatch research. – Nature Climate Change 10: 406–415.

Kovalenko, K.E. 2019. Interactions among anthropogenic effects on aquatic food webs. –Hydrobiologia 841: 1–11.

Kritzberg, E.S., Hasselquist, E.M., Škerlep, M., Löfgren, S., Olsson, O., Stadmark, J., Valinia, S., Hansson, L.-A. & Laudon, H. 2019. Browning of freshwaters: consequences to ecosystem services, underlying drivers, and potential mitigation measures. – Ambio 49: 375–390.

Kuparinen, A., Boit, A., Valdovinos, F.S., Lassaux, H. & Martinez, N.D. 2016. Fishing-induced life-history changes degrade and destabilize harvested ecosystems. – Scientific Reports 6: 22245.

Kuparinen, A., Perälä, T., Martinez, N.D. & Valdovinos, F.S. 2019. Environmentally-induced noise dampens and reddens with increasing trophic level in a complex food web. – Oikos 128: 608–320.

Lindmark, M., Huss, M., Ohlberger, J. & Gårdmark, A. 2017. Temperature-dependent body size effects determine population responses to climate warming. – Ecology Letters 21: 181–189.

Martinez, N.D. 2020. Allometric trophic networks from individuals to socio-ecosystems: consumer–resource theory of the ecological elephant in the room. – Frontiers in Ecology and Evolution 8: 92.

McMeans, B.C., McCann, K.S., Humphries, M., Rooney, N. & Fisk, A.T. 2015. Food web structure in temporally-forced ecosystems. – Trends in Ecology & Evolution 30: 662–672.

O’Connor, M.I., Piehler, M.F., Leech, D.M., Anton, A. & Bruno, J.F. 2009. Warming and resource availability shift food web structure and metabolism. – PLOS Biology 7: e1000178.

Rogers, T.L., Munch, S.B., Stewart, S.D., Palkovacs, E.P., Giron-Nava, A., Matsuzaki, S.S. & Symons, C.C. 2020. Trophic control changes with season and nutrient loading in lakes. – Ecology Letters 23: 1287–1297.

Sardans, J., Rivas-Ubach, A. & Peñuelas J. 2012. The elemental stoichiometry of aquatic and terrestrial ecosystems and its relationships with organismic lifestyle and ecosystem structure and function: a review and perspectives. – Biogeochemistry 111: 1–39.

Schneider, F.D., Brose, U., Rall, B.C. & Guill, C. 2016. Animal diversity and ecosystem functioning in dynamic food webs. – Nature Communications 7: 12718.

Schwaderer, A.S., Yoshiyama, K., de Tezanos Pinto, P., Swenson, N.G., Klausmeier, C.A. & Litchman, E. 2011. Eco-evolutionary differences in light utilization traits and distributions of freshwater phytoplankton. – Limnology and Oceanography 56: 589–598.

Sheridan, J.A. & Bickford, D. 2011. Shrinking body size as an ecological response to climate change. – Nature Climate Change 1: 401406.

Shurin, J.B., Clasen, J.L., Greig, H.S., Kratina, P. & Thompson, P.L. 2012. Warming shifts top-down and bottom-up control of pond food web structure and function. – Philosophical Transactions of the Royal Society B 367: 3008–3017.

Straile, D., Kerimoglu, O. & Peeters, F. 2015. Trophic mismatch requires seasonal heterogeneity of warming. – Ecology 96: 2794–2805.

Twining, C.W., Brenna, T., Hairston Jr., N.G. & Flecker, A.S. 2015. Highly unsaturated fatty acids in nature: what we know and what we need to learn. – Oikos 125: 749–760.

van Dorst, R.M., Gårdmark, A., Svanbäck, R. & Huss, M. 2020. Does browning-induced light limitation reduce fish body growth through shifts in prey composition or reduced foraging rates? – Freshwater Biology 65: 947–959.

Wallace, B.B., Hamilton, D.P. & Patterson, J.C. 1996. Response of photosynthesis models to light limitation. – Internationale Revue der Gesamten Hydrobiologie 81: 315–324.

Weisse, T., Stadler, P., Lindström, E.S., Kimmance, S.A. & Montagnes, D.J.S. 2002. Interactive effects of temperature and food concentration on growth rate: a test case using the small freshwater ciliate *Urotricha farcta*. – Limnology and Oceanography 47: 1447–1455.

Williams, R.J. & Martinez, N.D. 2000. Simple rules yield complex food webs. – Nature 404: 180–183.

Woodward, G., Perkins, D.M. & Brown, L.E. 2010. Climate change and freshwater ecosystems: impacts across multiple levels of organization. – Philosophical Transactions of the Royal Society B 365: 2093–2106.

Woolway, R.I., Kraemer, B.M., Lenters, J.D., Merchant, C.J., O’Reilly, C.M. & Sharma, S. 2020. Global lake responses to climate change. – Nature Research Earth & Environment 1: 388–403.

Yankova, Y., Neuenschwander, S., Köster, O. & Posch, T. 2017. Abrupt stop of deep water turnover with lake warming: Drastic consequences for algal primary producers. – Scientific Reports 7: 13770.

Yodzis, P. & Innes, S. 1992. Body size and consumer-resource dynamics. – The American Naturalist 139: 1151–1175.

**Tables**

**Table 1.** An overview of the parameters used in different ATN simulation scenarios.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| Model name | Carrying capacity model | Autotroph growth rate model | Consumer metabolic rate model |  |  |
| Constant ATN | constant | constant | constant | N/A | N/A |
| Seasonal ATN | eq 7 | eq 8 | eq 10, 11 | 0 | 0 |
| Seasonal K | eq 7 | constant | constant | N/A | N/A |
| Seasonal r | constant | eq 8 | constant | N/A | 0 |
| Seasonal x | constant | constant | eq 10, 11 | 0 | N/A |
| Seasonal ATN –2°C | eq 7 | eq 8 | eq 10, 11 | –2°C | 0 |
| Seasonal ATN –1°C | eq 7 | eq 8 | eq 10, 11 | –1°C | 0 |
| Seasonal ATN +1°C | eq 7 | eq 8 | eq 10, 11 | +1°C | 0 |
| Seasonal ATN +2°C | eq 7 | eq 8 | eq 10, 11 | +2°C | 0 |
| Seasonal ATN T+I | eq 7 | eq 8 | eq 10, 11 | +2°C | –50Wm–2 |
| Seasonal ATN GradT | eq 7 | eq 8 | eq 10, 11 | -2°C…+1.7°C | 0 |
| Seasonal ATN –50Wm–2 | eq 7 | eq 8 | eq 10, 11 | 0 | –50Wm–2 |
| Seasonal ATN –25Wm–2 | eq 7 | eq 8 | eq 10, 11 | 0 | –25Wm–2 |
| Seasonal ATN +25Wm–2 | eq 7 | eq 8 | eq 10, 11 | 0 | 25Wm–2 |
| Seasonal ATN +50Wm–2 | eq 7 | eq 8 | eq 10, 11 | 0 | 50Wm–2 |

**Figure captions**

**Figure 1.** Illustrations of constant *versus* seasonally changing (a) autotroph carrying capacity (*K*), (b) light coefficient () and (c) temperature coefficient (). The light coefficient affects mass-specific growth rates of autotrophs () depending on simulated irradiance level at a given day during the growing season, whereas the temperature coefficient affects the metabolic rate of consumers that is simulated to be at the highest level during the warm-water mid-summer period.

**Figure 2**. Seasonal biomass development (i.e., relative biomass density difference from the start of the growing season) of the main trophic guilds simulated using different ATN-model configurations. Abbreviations: *K* = autotroph carrying capacity, = light-dependent growth rate of autotrophs, and = temperature-dependent mass-specific metabolic rate of consumers. Seasonal ATN refers to the model configuration where all three abiotic parameters are set to follow the given seasonal patterns (see Figure 1).

**Figure 3**. Seasonal biomass development (i.e., relative biomass density difference from the start of the growing season) of the main trophic guilds simulated using the seasonal ATN model with adjusted temperature level ().

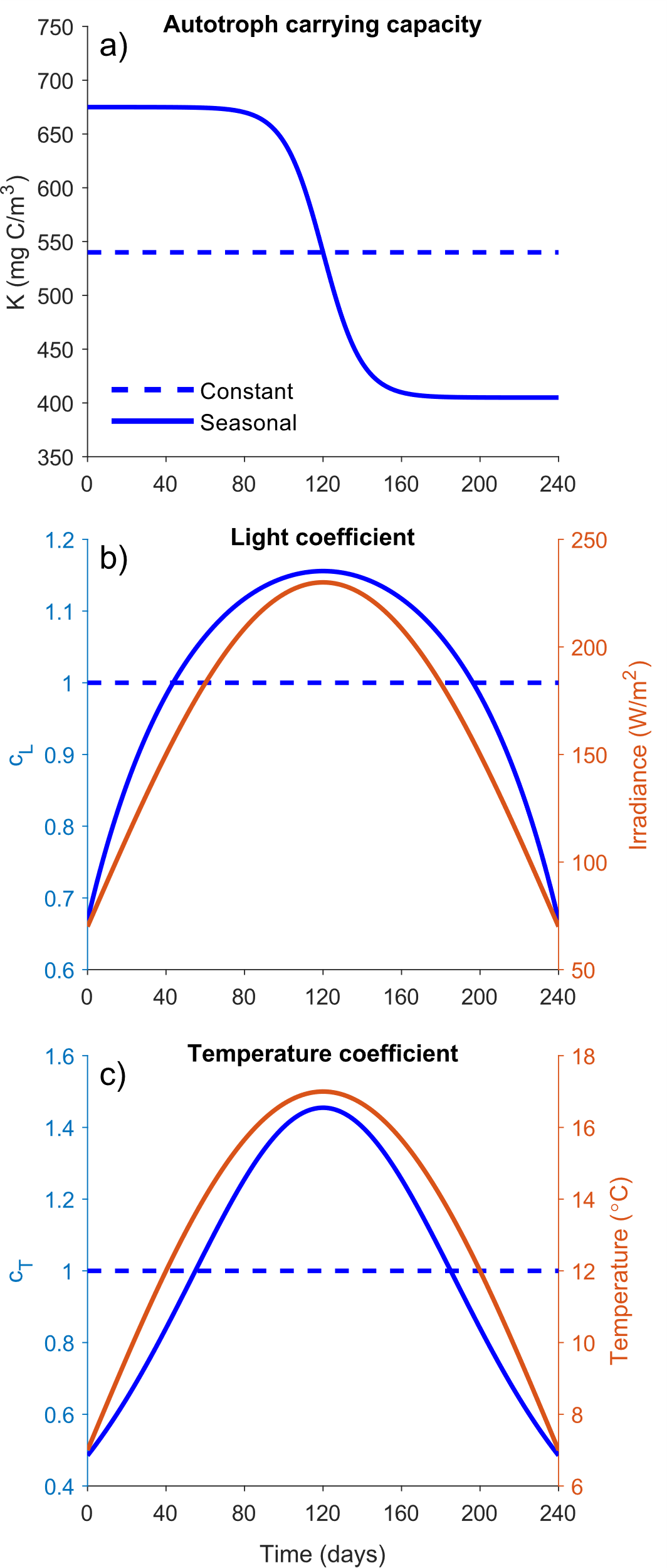
**Figure 4**. Relative (%) biomass distribution among producer (Phytoplankton) and consumer guild groups depending on the ATN model configuration. The results are based on ATN simulations where all or one of the following parameters are set either as a constant value or they follow a seasonal pattern (cf. Figure 1): = producer carrying capacity, = light-dependent growth rate of autotrophs, and = temperature-dependent mass-specific metabolic rate of consumers. Adjusted and refers to seasonal ATN model configuration where the irradiance level (eq. 8) is reduced by 50 W m–2 (to simulate reduced light availability) and temperature is increased by 2 °C (to simulate warming effect).

**Figure 5**. Relative (%) consumption gains (“productivity”) of consumer groups depending on the ATN model configuration. The results are based on ATN simulations where all or one of the following parameters are set either as a constant value or they follow a seasonal pattern (cf. Figure 1): = producer carrying capacity, = light-dependent growth rate of autotrophs, and = temperature-dependent mass-specific metabolic rate of consumers. Adjusted and refers to seasonal ATN model configuration where the irradiance level (eq. 8) is reduced by 50 W m–2 (to simulate reduced light availability) and temperature is increased by 2 °C (to simulate warming effect).

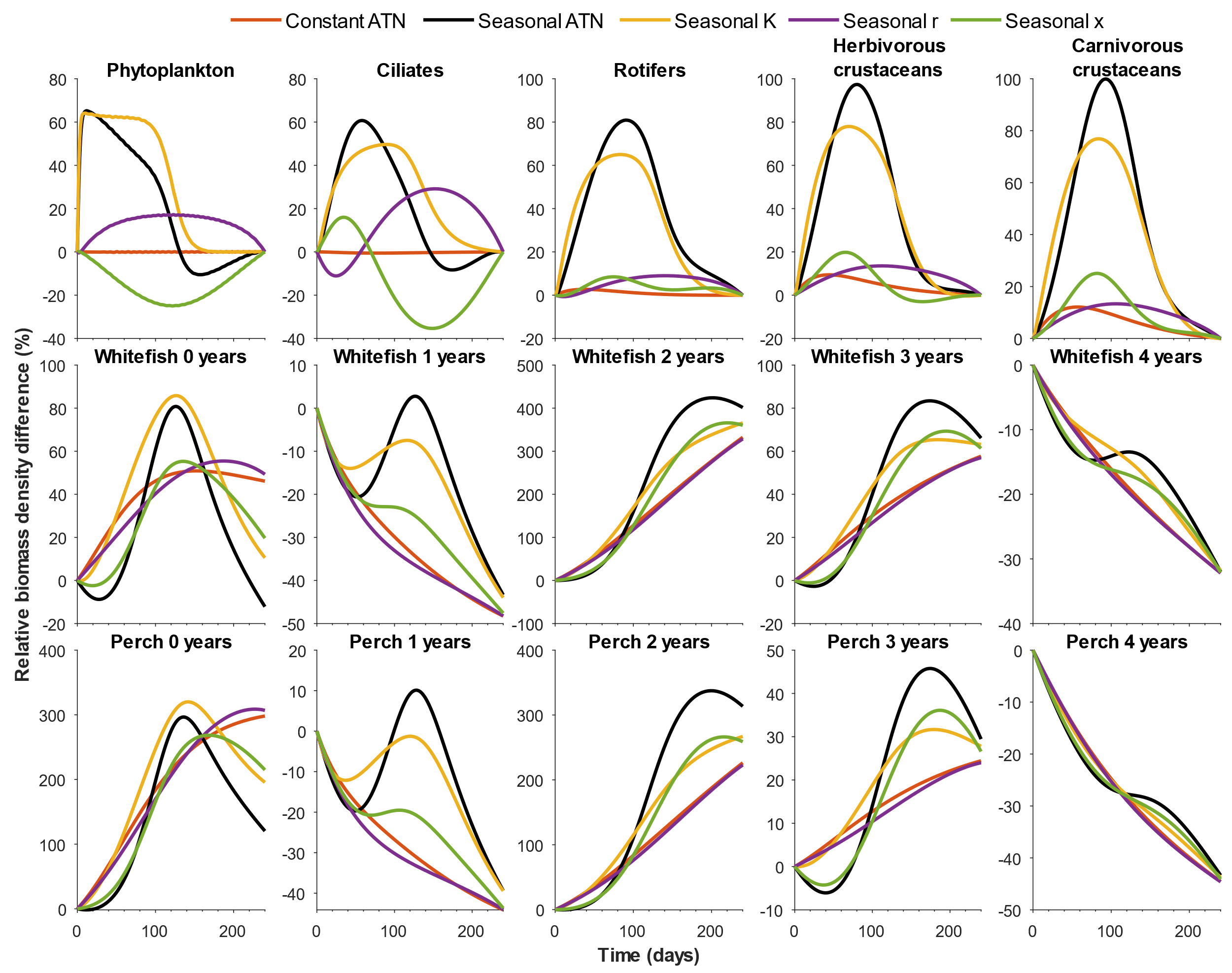
**Figure 6.** Relative changes in the productivity of primary producers (i.e., phytoplankton) and consumption gains of different consumer guilds along a simulated gradual temperature increase of 0.037 °C year–1 observed in Lake Constance (Adrian et al. 2009). The points indicate the times equalling to a simulated fixed temperature increase of 2 °C.

**Figures**

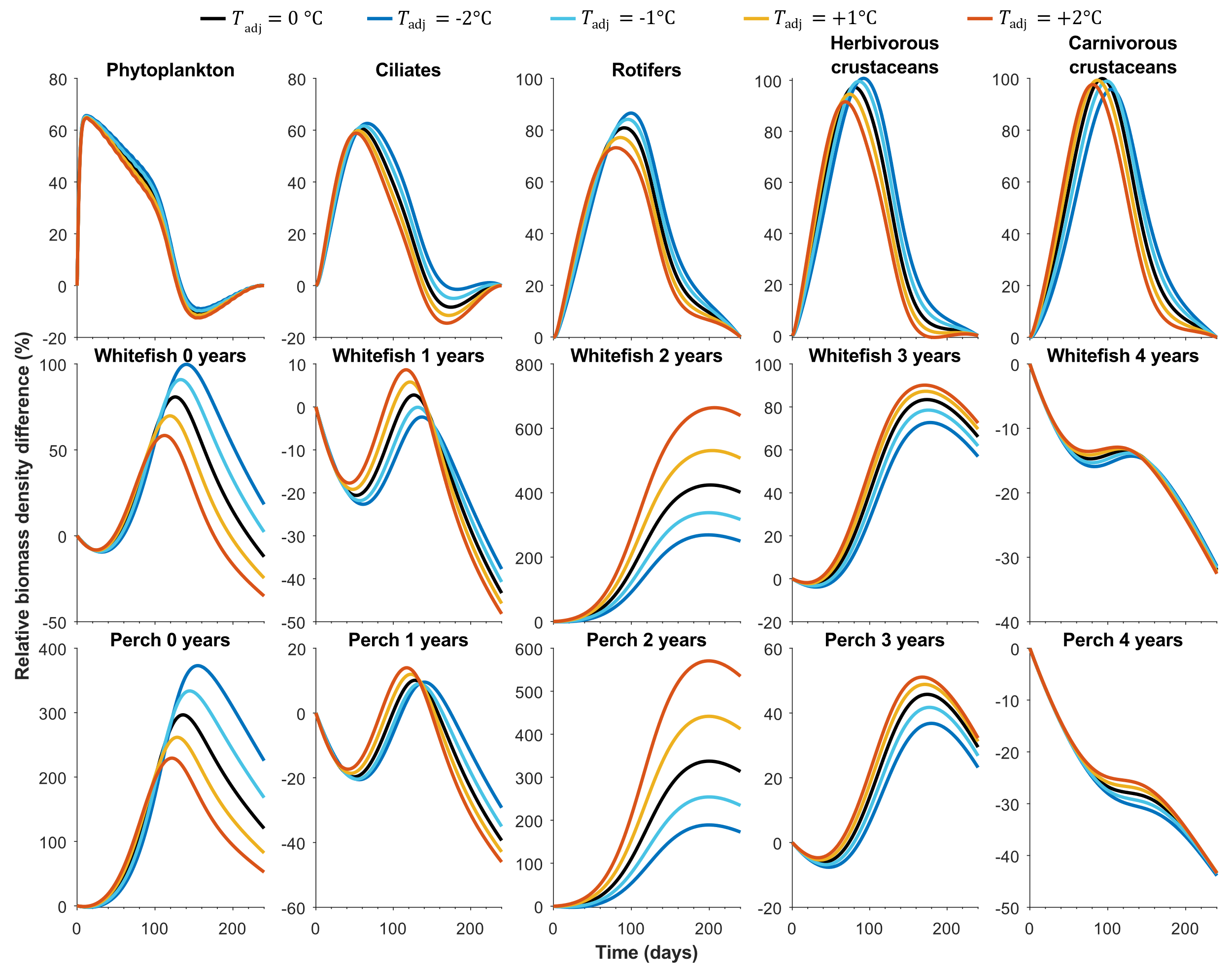
**Figure 1.**



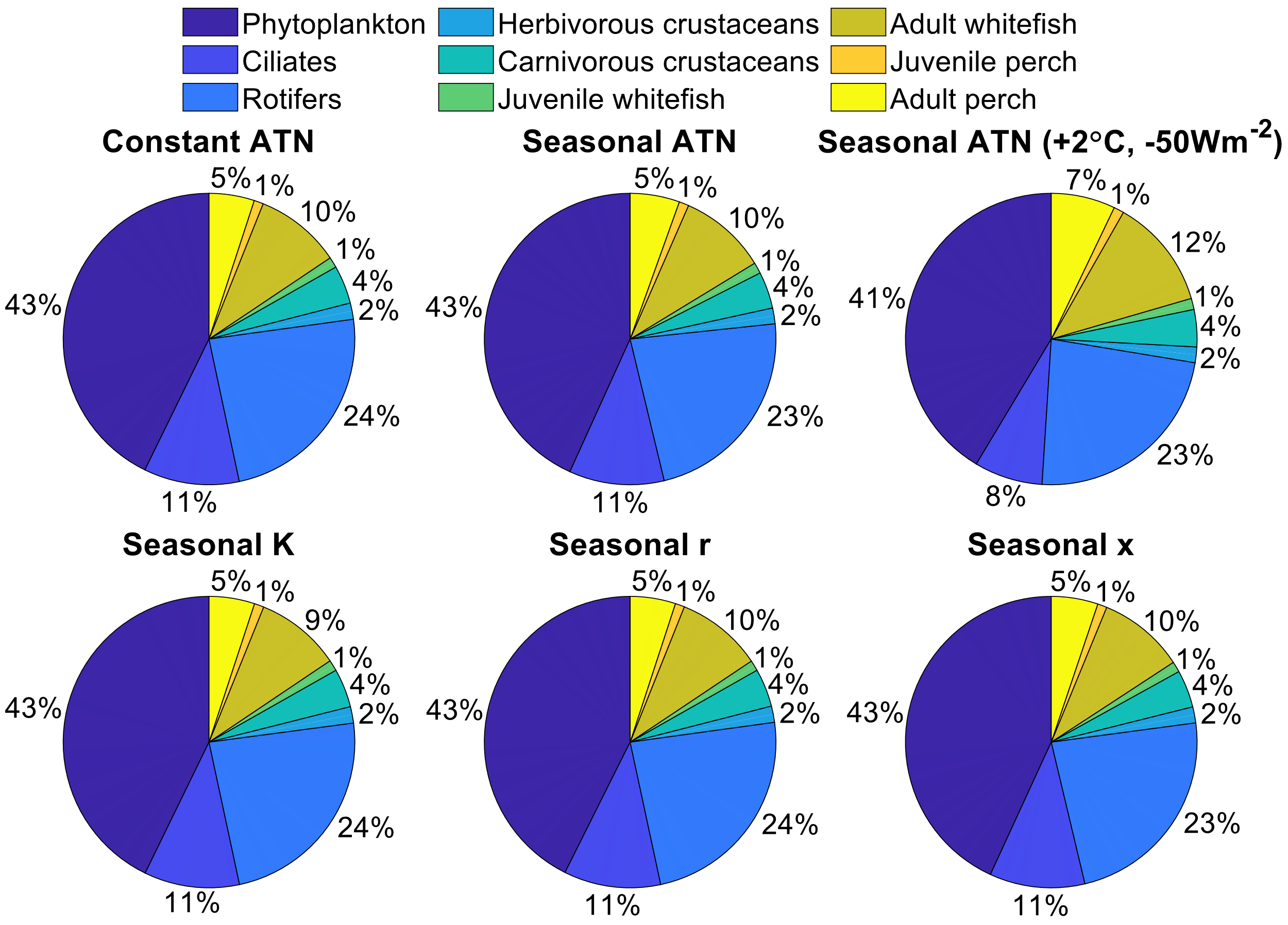
**Figure 2.**



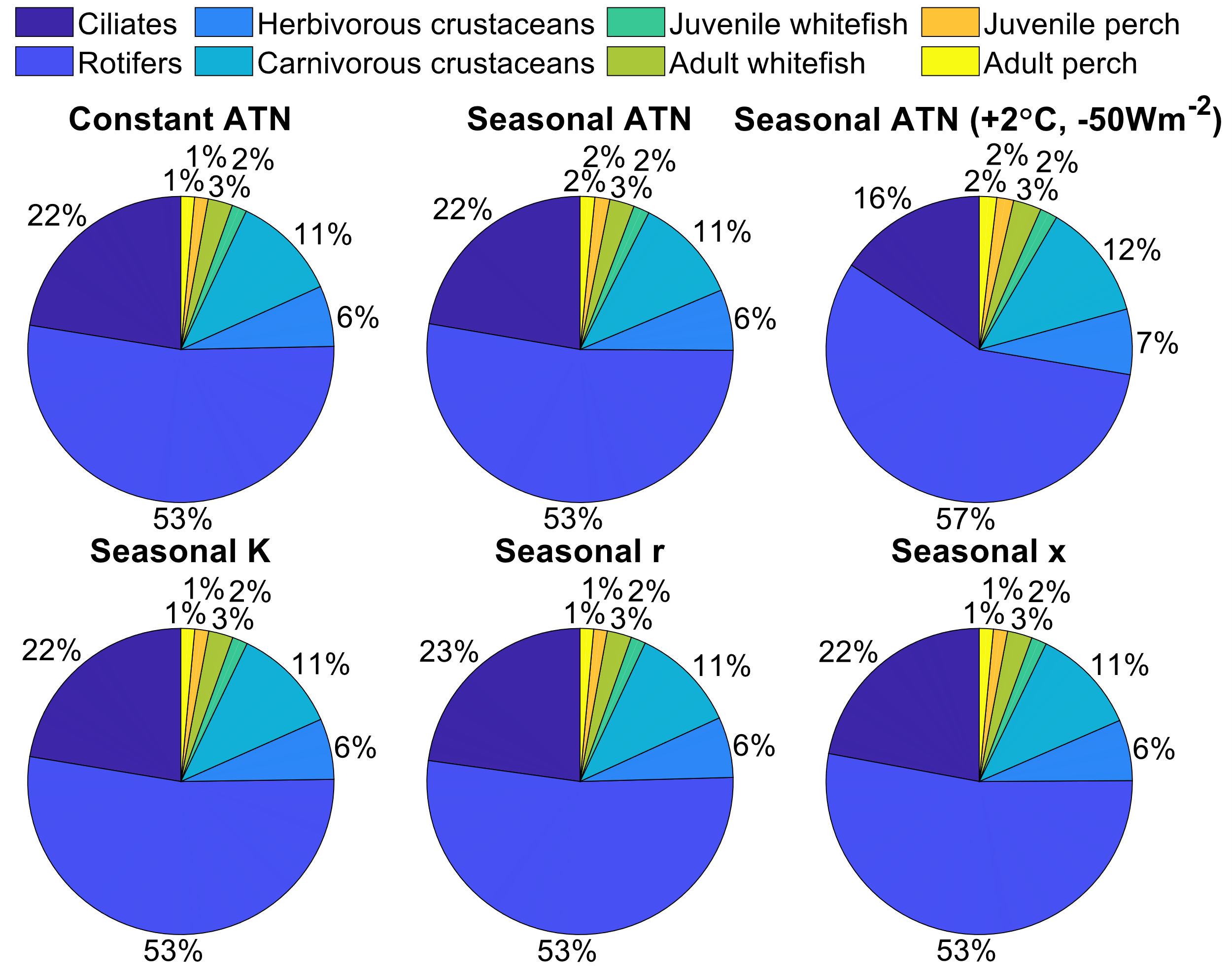
**Figure 3.**



**Figure 4.**



**Figure 5.**



**Figure 6.**

