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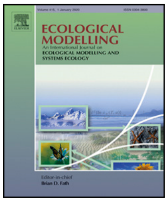

The role of squid for food web structure and community-level metabolism[☆]

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ABSTRACT

Squid differ from fish by their high growth rate, short life span, and feeding behavior. Their fast life strategy is thought to impose a high predation pressure on zooplankton, fish, and other squid preys, and a rapid transfer of energy to upper trophic levels of marine food webs. However, there is a lack of understanding of how squid's fast life cycle affects the food-web structure, which is needed to project squid biomass across marine regions under shifting climatic conditions. Here, we examine the role of squid on community metabolism and biomass by collecting data on squid somatic growth and incorporating squid in a size- and trait-based fish community model. We show that squid have a 5 times higher average somatic growth rate than fish. Due to their high food demands, squid are constrained to regions of high pelagic secondary production. The presence of squid in these systems is associated with a reduction in total consumer biomass. This decline is caused by an increase in community-level respiration losses associated with squid. Our results indicate that squid might have a large impact on ecosystem structure even at relatively low standing stock biomass. Consequently, the recent proliferation of squid in ecosystems around the world is likely to have significant ecological and socio-economic impacts.

1. Introduction

Squid populations have recently increased (from 1953 to 2013) (Doubleday et al., 2016). This increase is thought to be due to the loss of top predators from fishing and rising temperatures (Pecl and Jackson, 2008). Squid is an important fisheries resource representing about 4% of the global marine landings (Hunsicker et al., 2010; Arkhipkin et al., 2015; Rodhouse, 2005). Locally, squid can be very important for fisheries, for instance, they contribute up to 55% of the landings in the Patagonian Shelf and 30% in the Gulf of California. Squid also contribute indirectly to fisheries as a food resource for large predatory fish (Hunsicker et al., 2010) and are a major food resource for some whales (Garibaldi and Podestà, 2014).

Squid reach body mass comparable to large teleost fish (hereafter termed fish) but differ from fish by their rapid growth, short lifespan, and semelparous reproduction strategy. For example, the jumbo flying squid (*Dosidicus gigas*) can reach 140 cm in mantle length in less than two years (Goicochea-Vigo et al., 2019). These characteristics of squid imply that they must feed voraciously (Rodhouse et al., 1998, Chap. 13), which must be associated with high metabolic demand. These high feeding rates will lead to high predation pressure, potential top-down control of their prey, and rapid transfer of mass towards higher trophic levels (Rodhouse and Nigmatullin, 1996; Smale, 1996). The high metabolic demands and short life span make squid highly sensitive to inter-annual fluctuations in population biomass, potentially due to variations in prey availability and temperature (Boyle and Boletzky, 1996).

Besides the physiological differences between fish and squid, there are also differences in the feeding niche. Both squid and fish increase their trophic niche as they grow in size. Squid have a diverse diet that shifts from small crustaceans to fish and other squid during ontogeny (Vovk, 1985; Phillips et al., 2003; Macy III, 1982). Squid inhabiting open oceans show a clear preference for mesopelagic fish (Hoving and Robison, 2016; Phillips et al., 2001). Predator:prey size ratios for squid are difficult to measure and estimates are not consistent among studies. For instance Vovk (1985) show that *Loligo palei* prefers prey of 4 to 24% of their length, whereas Hoving and Robison (2016) show that species of the genus *Gonatus* have a preference for prey of their own size. Nevertheless, squid differ from fish in their

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feeding mechanics. Fish swallow their prey whole, whereas squid use their long prehensile arms and beak to remove pieces of flesh from a prey. In this manner, squid can consume larger prey than fish. It is therefore likely that squid have a smaller predator:prey size ratio and, possibly, feed on a wider range of prey sizes than most fish.

Squid also serve as prey for large predatory fish in marine ecosystems, suggesting potential bottom-up control of these predators (Coll et al., 2013; Smale, 1996). Moreover, the recent increase in squid abundance is partially ascribed to a top-down pressure release from large predatory fish (Doubleday et al., 2016), implying that predatory fish top-down control or compete with squid populations.

The difference in life history and feeding niche between squid and fish implies that squid must play a different role than fish in structuring the ecosystem. More specifically, they exert potential top-down regulations on small fish and zooplankton and serve as food to large predatory fish, i.e., top-down regulation from large predatory fish. Previous work on squid in food web models suggested the importance of squid in the marine food web (Coll et al., 2013). However, most models did not incorporate individual-based processes of energy allocation with size (de la Chesnais et al., 2019; Morato et al., 2016), and therefore ignore linkages between the individual-, population-, and community-level dynamics (Persson et al., 2014; Arkhipkin, 2013). These models are often *Ecopath* type of model, assuming constant flux of energy between groups such as squid. Resolving the size-structure of squid within the ecosystems allows us to understand the presence of squid and their role in structuring the ecosystem, i.e., top-down vs bottom-up regulations with fish and zooplankton.

In this study, we investigate how the distinct life history and feeding niche of squid, i.e., growth rate, semelparity, and predator:prey size ratio, in comparison to fish, may impact population and community-level dynamics. To this end, we collected trait data on somatic growth rate A and adult:offspring mass ratio M_∞/M_0 from several squid species, focusing on commercially important squid. We used this data to estimate two population metrics: the maximum population growth rate r_{max} and minimum sustainable resource level R^*, i.e., the resource needed to sustain a population. We compared both metrics to those previously derived for fish. To explore the community-level effects of squid on fish dynamics, we integrated squid in a size- and trait-based fish community model (FEISTY) (Petrik et al., 2019; van Denderen et al., 2021). This exploration was done for a range of simulated systems that varied in depth and ocean productivity. The structure and parameterization of the trait-based model reflected our aim of testing the community consequences resulting from the generic differences between squid and fish. The model and parameter values employed in this study do not aim to capture the entire ecological complexity and diversity of fish and squid species in natural systems. Rather, we represent the part of the community with the strongest impact on the community structure.

2. Materials & methods

The methods description contains 5 sections: 2.1 The squid physiological model of food-dependent growth and reproduction. The physiological model is similar to the one developed for fish in Denéchère et al. (2022) and van Denderen et al. (2020) but squid differs from fish in three main traits: growth rate, semelparity, and predator:prey ratio. 2.2 We use squid mass-at-age data to estimate the somatic growth rate and the maximum consumption rate used in our physiological model. 2.3 Assuming a constant level of food and predation in the squid physiological model, we next derive the maximum population growth rate r_{max} and the minimum sustainable resource level R^* using the methodology from Denéchère et al. (2022). 2.4 We briefly describe the data collected to estimate the somatic growth, and adult:offspring size ratio. 2.5 Finally, we embed the squid physiological model developed in part (1) into the full size- and trait-based fish community model FEISTY and explore the impact of squid on the fish community dynamics.

2.1. Squid physiological model

The squid physiological model involves encounter and consumption of food, losses from assimilation and standard metabolism, and allocation between growth and reproduction (Fig. 1A). The model will be used for calculating population metrics, i.e., maximum population growth rate r_{max} and minimum resource requirements R^*, and forms the basis for the dynamical FEISTY model. The physiological model is essentially based on the size- and trait-based models developed for fish (Andersen, 2019; Andersen and Beyer, 2006; van Denderen et al., 2020; Denéchère et al., 2022) but we assume that squid differ from fish in three traits: their maximum growth rate, and consequently consumption, semelparous reproductive behavior, and predator:prey mass ratio. All other life-history parameters are similar to fish. All physiological rates are described at the level of an individual squid as a function of its body mass m in units of gram wet weight.

The encounter with food (mass per time) is the product of the search area (area per time) and the resource concentration R (mass per area). We assume that the search area (area per time) scales with body mass as γm^q, with $\gamma = 70\ \text{m}^2\ \text{g}^q\ \text{yr}^{-1}$ the factor for search area and $q = 0.8$ the exponent for search area (Andersen and Beyer, 2006). This assumption leads to squid searching for food in larger areas through ontogeny.

Feeding is limited by the maximum consumption rate hm^n (mass per time). Here we assume a standard metabolic scaling of $n = 3/4$. We then describe the feeding level – the consumption relative to maximum consumption – with a functional response type II:

$$f = \frac{\gamma m^q R}{\gamma m^q R + hm^n}. \tag{1}$$

The consumed food fhm^n is assimilated with an efficiency $\epsilon_{\text{a}} = 0.7$ (van Denderen et al., 2020) and subjected to respiration losses. Respiration losses scales with the same exponent as the maximum consumption rate and are expressed as a fraction f_{c} of the maximum consumption rate (Hartvig et al., 2011). The available energy for growth and reproduction is then:

$$\nu(m) = \epsilon_{\text{a}} h(f - f_{\text{c}}) m^n, \tag{2}$$

where $f_{\text{c}} = 0.2$ is termed the "critical feeding levels" and is estimated from fish (Denéchère et al., 2022). The available energy (2) is used for growth and reproduction. As squid are predominantly semelparous, juveniles use all available energy for somatic growth (see (4)) and adults invest all energy in reproduction. The reproductive rate of an adult at maximum mass is (no. offspring per time):

$$b = \epsilon_{\text{r}} \nu(M_\infty)/M_0 \quad \text{for} \quad m < M_\infty, \tag{3}$$

where M_∞ is the maximum mass and the M_0 the mass at hatching. The reproductive efficiency ϵ_{r} encompasses the additional costs of creating and storing eggs, egg mortality, and other costs of reproduction such as migration or forgone feeding. In the absence of information regarding ϵ_{r} for squid (Boyle and Rodhouse, 2008), notably the survival from egg release to hatching, we considered the reproduction efficiency equal for fish and squid, i.e., $\epsilon_{\text{r}} = 0.01$ (Andersen, 2019).

Overall, the individual growth rate and the short life cycle are the major differences between the life history parameters of fish and squid. Differences in the metabolic level and consumed food drive differences in growth and reproduction output.

2.2. Estimating growth potential of squid

The coefficient for maximum consumption rate h represents the potential for somatic growth in our physiological model. We collected mass-at-age data to calculate h for squid. This estimation requires us to assume an average constant feeding level. We assume that natural individuals are not at the optimum condition of food and that f =

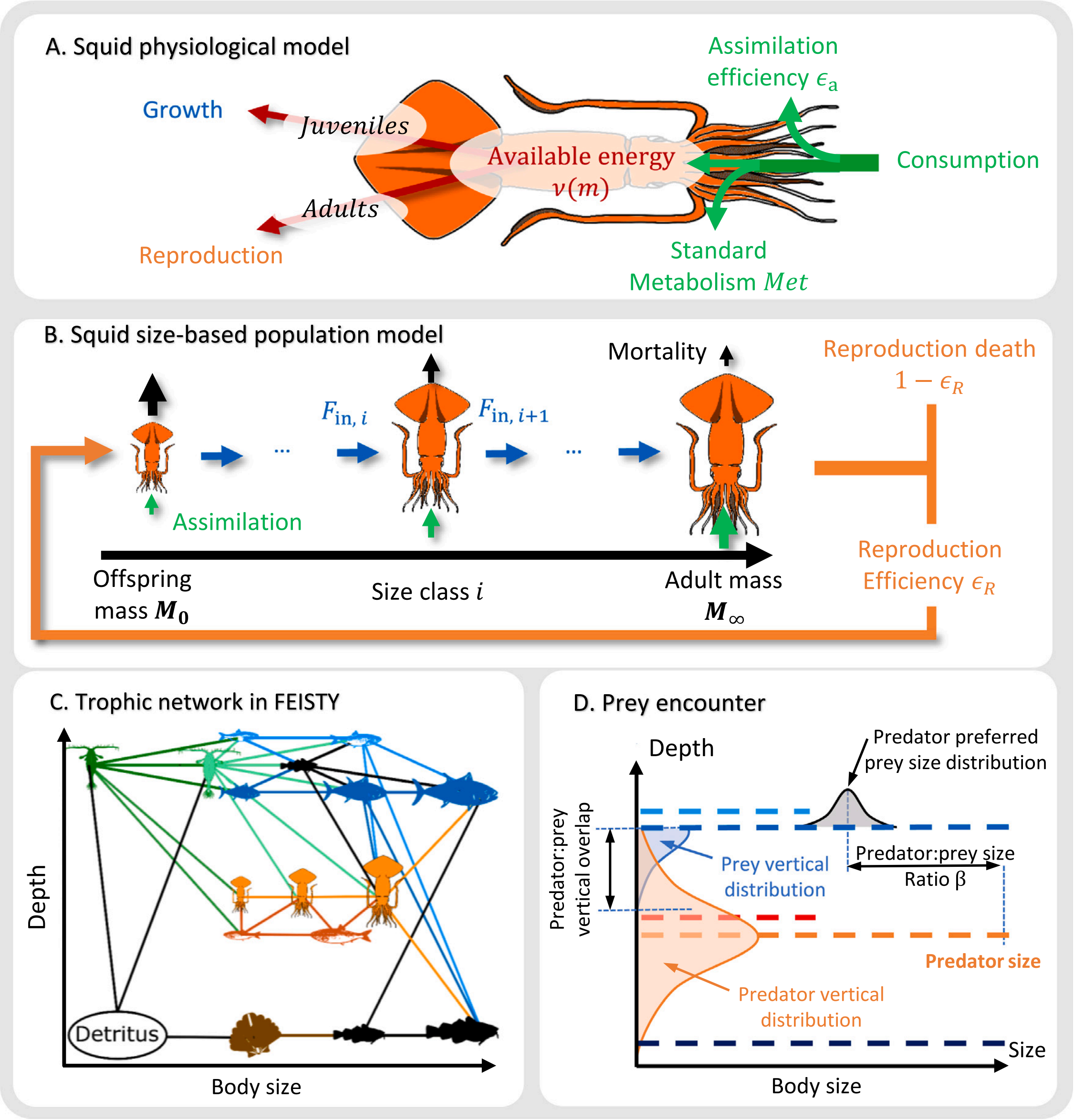

Fig. 1. Representation of squid in the FEISTY model. (A) Individual physiological model of squid. (B) Population processes of squid. (C) Schematic representation of the size, depth and interaction of the functional groups in FEISTY. The model has three resources: small and large zooplankton (dark and light green respectively) and a benthic resource (brown); and five functional groups: small and large pelagic fish (light and dark blue respectively), demersal fish (black), mesopelagic fish (red) and squid (orange). (D) An example of vertical and size interaction in the FEISTY model.

$f_0 = 0.6$ (Armstrong and Schindler, 2011; Andersen, 2019). With this assumption, somatic growth in juveniles can be rewritten from (2) as:

$$v = Am^n, \quad \text{where} \quad A = \epsilon_a h(f_0 - f_c) \quad \text{for} \quad m < M_\infty, \tag{4}$$

with A being the somatic growth rate constant (units of mass^{1-n} per time). The unit of A (mass^{1-n} per time) results from the equality with the somatic growth expressed in units of mass per time (i.e., v in (4)). Classically, A is the growth coefficient in the von Bertalanffy growth type of model (see more detail for the link between A and our physiological model in Denéchère et al. (2022, Supplement D) or Andersen (2019, chap. 10)). Solving (4), we find the mass as a function of age t (see Supplement A):

$$m(t) \approx [(1-n)At]^{1/(1-n)}, \tag{5}$$

which we used to estimate the somatic growth rate A and then the maximum consumption coefficient h using Eq. (4).

2.3. *Scaling from individuals to maximum population growth rate*

We calculated two population-level metrics to compare squid and fish: the maximum population growth rate r_{max} and the minimum sustainable resource level R^*. r_{max} describes the population growth rate in the absence of intra-population density dependence and can be interpreted as the invasive potential of a population. R^* is the average resource level needed to sustain a population. To evaluate R^* we assumed that intra-specific density dependence appears as a reduction in the level of resources available for an individual. We calculated R^* as the resource level at which $r_{\text{max}} = 0$, i.e., when the intra-population density dependence limits the population growth rate to 0. R^* represents the level of resource dependency or the level of intra-population density dependence of the population.

Scaling from individual-to population-level metrics – r_{max} and R^* – for squid followed the methodology from Denéchère et al. (2022). They derived r_{max} and R^* for any size-structured population from individual-level metabolism and life history traits, i.e., physiological level of mortality and growth coefficient. In the following, we detail the main assumptions and equations from Denéchère et al. (2022). We implemented $r_{\max}$ and R^* with physiological parameters specific to both taxa (see parameters in Supplement A; Table. SA1).

$r_{\max}$ is estimated for a semelparous population assuming that the feeding level is constant $f = f_0$ and that mortality is (units of per time) (Andersen and Beyer, 2006):

$$\mu(m) = aAm^{n-1}. \tag{6}$$

In this equation, mortality declines with body size and is proportional to the somatic growth coefficient A, assuming a linear trade-off between growth and mortality risk. This assumption accounts for faster-growing species enhancing their foraging activities to fuel their growth and consequently increasing their own risk of predation, as is observed, e.g., among *Menidia menidia* (Lankford et al., 2001). The physiological level of mortality a is a non-dimensional constant representing the ratio between mortality and mass-specific assimilated available energy A. We use $a = 0.42$ (Andersen, 2019). This formulation of predation mortality follows from considering mass balance in a community in equilibrium (Andersen and Beyer, 2006). Denéchère et al. (2022) derived from size-based mortality (6) and growth (2) the maximum population growth rate for a size-structured population growing exponentially (see their Appendix A):

$$r_{\max} \approx A(1-n)M_\infty^{n-1}[(1-a)\ln(M_\infty/M_0) + \ln(\epsilon_a)]. \tag{7}$$

The approximation shows that the maximum population growth rate (per time) increases proportionally to the growth rate coefficient A and declines with increasing mass at hatching M_0.

We can use the approximation of $r_{\max}$ to find the resource level R^* at which $r_{\max} = 0$. This quantity is a central part of modern competition theory (Tilman, 1982) as it shows the minimum resource level required for the population to survive. R^* is found by combining Eqs. (7), (4), and (1) and solving for the resource level where $r_{\max} = 0$:

$$R^* \approx \frac{f_c h}{\gamma(1-f_c)} M_\infty^{n-q}, \tag{8}$$

where γ and q are the parameters for search area from Eq. (1).

2.4. Trait data collection

We collected data on three life history traits: somatic growth rate A and the offspring and maximum masses M_0 and M_∞. We estimated the somatic growth rate by fitting mass-at-age curves for 11 species of squid with a somatic growth model (see Eq. (5) and references in Supplement A Table. SA1 and Table. SA2). The estimation of the somatic growth coefficient A did not show any significant relation with M_∞ (Fig. 3A), thus, a constant A is employed in our computation of $r_{\max}$, R^*, and for the FEISTY simulations. We obtained the offspring and maximum masses from 27 squid species from Neuheimer et al. (2015) and Villanueva et al. (2016). The maximum mass M_∞ was defined as the maximum recorded mass for a species.

2.5. Scaling to food-web structure

We used the squid physiological parameters to implement squid in the dynamic FEISTY framework (van Denderen et al., 2021). FEISTY then provides a dynamical food environment (feeding level f) and dynamic predation mortality. FEISTY describes how the food-web structure of a fish community changes across water depths and variations in secondary production (see Supplement B). FEISTY resolves several functional groups that differ in their maximum mass M_∞ and mass at hatchings M_0, and vertical position in the water column. Feeding is defined by the size of individuals following Eq. (1) and by the vertical habitat which determines the available resources R for each size class (Fig. 1D). Mortality is mainly due to predation emanating from the feeding of larger individuals from other functional groups or cannibalism. To represent the semelparity of squid, we assumed that squid die after reproduction (see Section 2.5.1).

We included small and large pelagic fish, demersal fish, mesopelagic fish, and squid in the model. We describe below how squid were embedded (Fig. 1C). Further details about the fish functional groups can be found in van Denderen et al. (2021). Equation and parameters for fish are in Supplement B.

2.5.1. Squid size-based population model

Both fish and squid populations are described by the biomass B_i (biomass per area g m^{-2}) in different size classes, each characterized by the geometric mean body mass within the size class m_i. Small fish species – small pelagic and mesopelagic – have 4 size classes and a maximum mass of 250 g. Large species – large pelagic, demersal, and squid – have 6 size classes. Large pelagic and demersal fish have a maximum mass of 125 kg. As squid are generally smaller than large pelagic fish, we assume that squid have an intermediate maximum mass of 5.6×10^3 g.

Changes in biomass B_i within a size class i are due to somatic growth in and out of the class, biomass accumulation within the class, and predation:

$$\frac{\mathrm{d}B_i}{\mathrm{d}t} = F_i - F_{i+1} + (\nu_i - \mu_i)B_i, \tag{9}$$

where F_i is the flux of biomass (biomass per time) from the lower size-class $i-1$, and F_{i+1} is the flux of individuals growing into $i+1$; $\nu_i B_i$ is the accumulation of mass from feeding (Eq. (2)), and $\mu_i B_i$ is the loss to predation.

The flux of mass between size classes is approximated by De Roos et al. (2008) as:

$$F_i = \frac{\kappa\nu_{i-1} - \mu_{i-1}}{1 - \alpha_i^{(1-\mu_{i-1})/(\kappa\nu_{i-1})}}, \tag{10}$$

where κ describes the fraction of available energy invested in growth, and α_i is the ratio between individual weight at the lower and upper boundary of a size class i. As juvenile squid invests all energy in growth $\kappa = 1$. Adults invest all their available energy in reproduction. We modeled the reproductive flux as a flux out of the last size class similar to growth, i.e., F_x, and discounted by the reproductive efficiency ϵ_r in (3). The reproductive flux is routed into the first size class: $F_1 = \epsilon_r F_x$, and assumes that adult squid die after reproduction (see Fig. 1B).

2.5.2. Respiration cost

We assumed a trade-off between respiration loss (or metabolic cost) Q and consumption h, where $Q = \epsilon_a f_c h m^q$ (2). As fish and squid have different somatic growth rates, and therefore different respiration losses, we examined the effect of squid vs. fish abundance on community-level respiration. The respiration from a group Q_{tot} is calculated as

$$Q_{\text{tot}} = \sum_j Q_j B_j, \tag{11}$$

with j the size classes of a functional group

2.5.3. Prey encounter

The squid population model is embedded in the food web (Fig. 1) via the resource R_i and predation mortality μ_i of each squid size class i. The resource is determined by the available food from other groups (zooplankton, fish, and the squid population itself), and predation mortality is determined by the food consumption by all groups (fish through predation and squid through cannibalism).

Each group's resource encounter is described as $R_i = \sum_j \theta_{i,j} B_{i,j}$, with $\theta_{i,j}$ the interaction matrix between squid of size i and a prey j, where j represent all size groups of all functional groups (including zooplankton and squid). The interaction matrix $\theta_{i,j}$ consists of two parts: the predator:prey size preference $\theta_{\text{size},i,j}$ and the vertical overlap

Table 1
Squid parameters used for $r_{\max}$ and FEISTY implementation.

Symbol	Name	Value	Unit	Note
M_∞	Maximum mass	5.6×10^3	g	[a,b]
M_0	Offspring mass	0.01	g	[a,b]
n	Exponent for max. consumption	3/4	–	(see Supplement A)
h	Coefficient for max. consumption rate	83	g^n yr^{-1}	Estimated from Eq. (2)
γ	Factor for search area	70	m^2 g^{-q} yr^{-1}	[c]
q	Exponent for search area	0.8	–	[c]
f_c	Critical feeding level	0.2	–	[d]
β	Predator:prey size ratio	50	–	Smaller than fish
σ	Width of size preference	1.3	–	[c]
ϵ_a	Assimilation efficiency	0.7	–	[c]
ϵ_r	Reproduction efficiency	0.01	–	[c]
a	Physiological level of mortality	0.42	–	For $r_{\max}$
		var.	–	For FEISTY

Note:
[a] Neuheimer et al. (2015).
[b] Villanueva et al. (2016).
[c] van Denderen et al. (2021).
[d] Andersen and Beyer (2006).

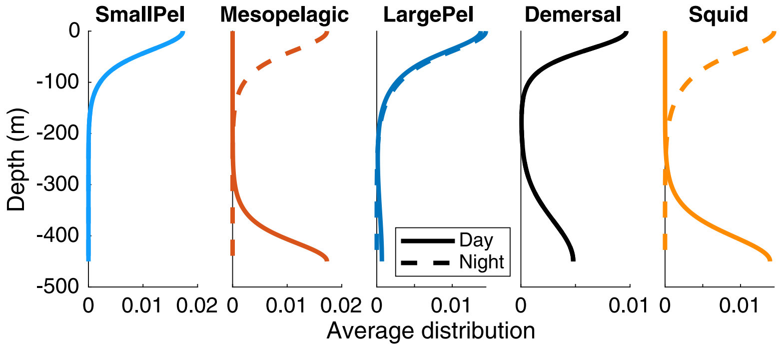

Fig. 2. Day and night vertical distribution of fish and squid in the FEISTY framework. The vertical distribution is the average of all the life stages.

of each stage $\theta_{v,i,j}$, such that: $\theta_{i,j} = \theta_{\text{size},i,j} \times \theta_{v,i,j}$. The size preference is described by the optimal predator:prey size ratio β and the width of the size preference σ (Fig. 1C; Supplement B). Estimations of the size preference, i.e., the predator:prey size ratio β and width of the preference σ, are rarely conclusive for squid, though their preferred prey size is larger than that of fish (Vovk, 1985; Hoving and Robison, 2016). We chose a $\beta = 50$ resulting in a preferred prey size 8 times larger than those of equivalent sized fish predators.

Note that the vertical distribution is only used for the calculation of the predation interaction and that the vertical dynamic movement is not explicitly resolved. The vertical distribution follows a bi-modal vertical distribution that represents diel vertical migration patterns of squid (see Fig. 2; Supplement B; Table. SB1). Oceanic squid dive into the twilight zone during the day and migrate to the surface at night (Roper and Young, 1975). For example, the jumbo squid (*Doscidicus gigas*) dives below 200 m depth during the day (William et al., 2006). The dive depth varies considerably between species and also, probably, depends on the resource availability. We therefore assumed that squid follow the day/night vertical movement of the migrating zooplankton and mesopelagic fish with a maximum concentration at similar depths. The vertical behavior of coastal squid has received less attention, we assumed that squid in shelf waters also realize diel vertical migrations from the surface waters to the seafloor. All functional groups in FEISTY feed days and nights.

2.5.4. Co-existence of squid in the FEISTY framework

Competitive exclusion between squid and fish groups is largely avoided by the differences in size and feeding niche between squid and fish. To avoid competitive exclusion between demersal fish and squid in shelf systems, we assumed that squid do not feed on benthic resources. This restriction was a necessary simplification of the empirical observations (see further discussion section).

2.6. Food web analysis

We examined the equilibrium conditions of fish and squid for varying zooplankton productivity (g m^{-2} yr^{-1}) and across sea floor depths (m). These variables also affect benthic resource productivity, which was changed accordingly (van Denderen et al., 2021) (Supplement B; Table. SB1 & SB2). Simulations have been made with and without squid to emphasize the effect of squid on the food-web structure. We chose two depths, 50 and 2000 m (hereafter termed shelf and open ocean, respectively) to illustrate our results but the main results were robust when other depths were used. We chose ten zooplankton productivities for both small and large zooplankton varying linearly from 10 to 150 g wet weight per m^2 per year, i.e., every 16 gww m^{-2} y^{-1}. For comparison, the North Sea has estimated productivity of 90 gww m^{-2} y^{-1} for each zooplankton group that is available as prey for fish (Stock et al., 2017). For each depth and productivity combination, we ran the model for 150 years and averaged over the last 40 years (by which time the model had converged). We ran the model using the `ode45` function from Matlab with variable time step size. Initial conditions of fish and squid biomass were 0.01 g ww m^{-2} for each size class and zooplankton and benthic biomass were 10% of the productivity of the system simulated. We verified that there were no alternative stable states by comparing simulations with increasing and decreasing zooplankton productivity.

The main squid traits used for $r_{\max}$ and R^* calculations and the FEISTY-squid simulations are summarized in Table 1.

3. Results

3.1. Individual and population growth rate

Our analysis of growth data reveals that squid are fast-growing species with an average somatic growth rate $A = 23.4$, compared

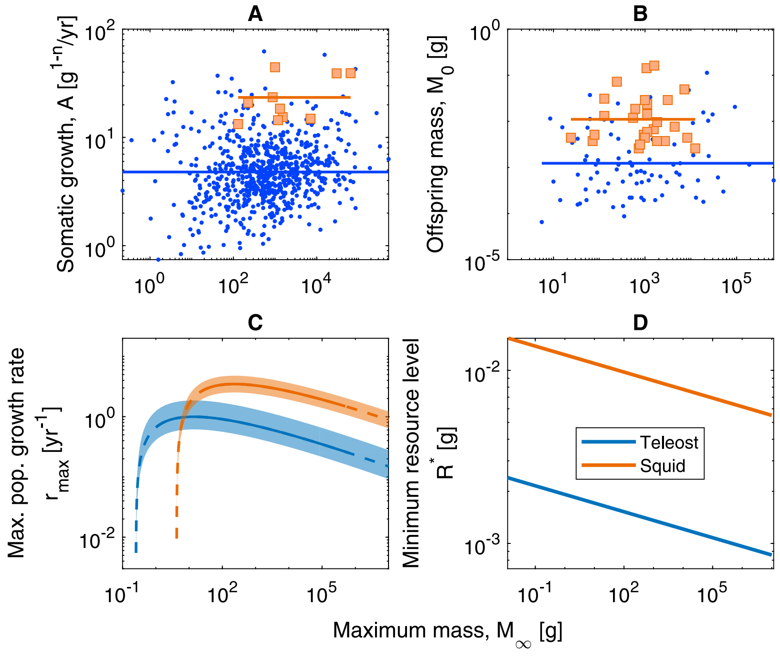

Fig. 3. (A) Somatic growth rate A, (B) offspring mass M_0, (C) maximum population growth rate $r_{\max}$, and (D) minimum resource level R^* for squid and fish (orange and blue respectively) as a function of maximum mass M_∞.

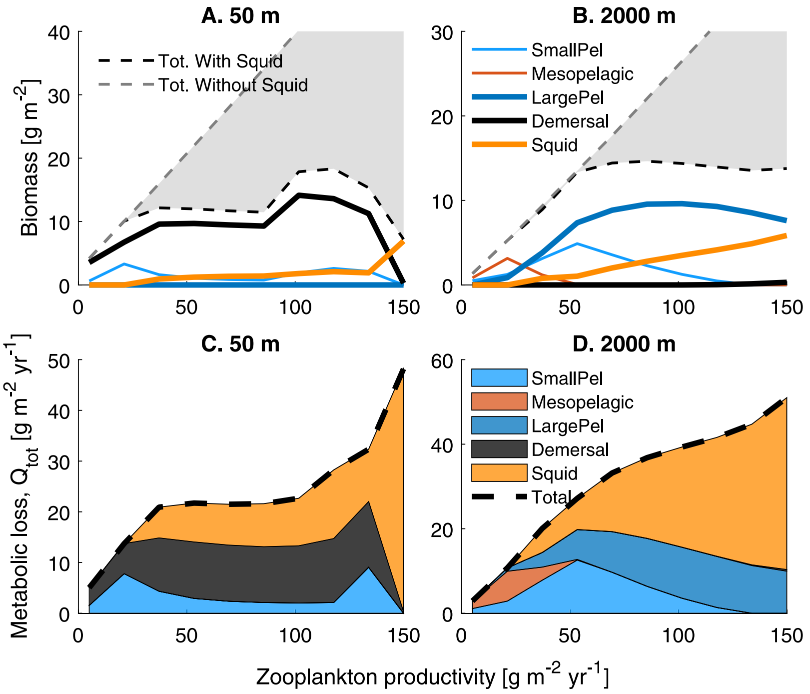

Fig. 4. Biomass (top panels) and rate of metabolic loss (lower panels) of each functional group with increasing zooplankton productivity in the FEISTY framework for a shelf region (50 m depth) and an open ocean (2000 m depth) system. The thickness of the lines refers to the asymptotic size of the functional group. “Pel” in the legend refers to “pelagic”. Total metabolic cost per group is estimated as the sum of the metabolic cost per size. The total biomass has been calculated with (black dashed line) and without (gray dashed line) squids to show biomass decline with squids.

to 4.7 g^{1-n} yr^{-1} for teleost fish (Fig. 3A and Supplement A). The linear regression between A and M_∞ reveals no significant relationship between these parameters (P-value of 0.17) and that A would vary from 17 to 32 g^{1-n} yr^{-1} with a 95% confidence bounds. The egg mass of squid is independent of maximum mass, just as it is for fish, but the average offspring mass is an order of magnitude higher, i.e., 0.01 and 0.001 g for squid and fish respectively (Fig. 3B). Their faster somatic growth rate A results in squid exhibiting a higher maximum population growth rate than fish (Fig. 3C). The minimum sustainable resource R^* is higher for squid than for fish suggesting that squid require higher food density to sustain their population size (Fig. 3D).

3.2. Food-web structure

The biomass of squid is primarily driven by the productivity of zooplankton (Fig. 4 top panels). Squid biomass is neglectable in both

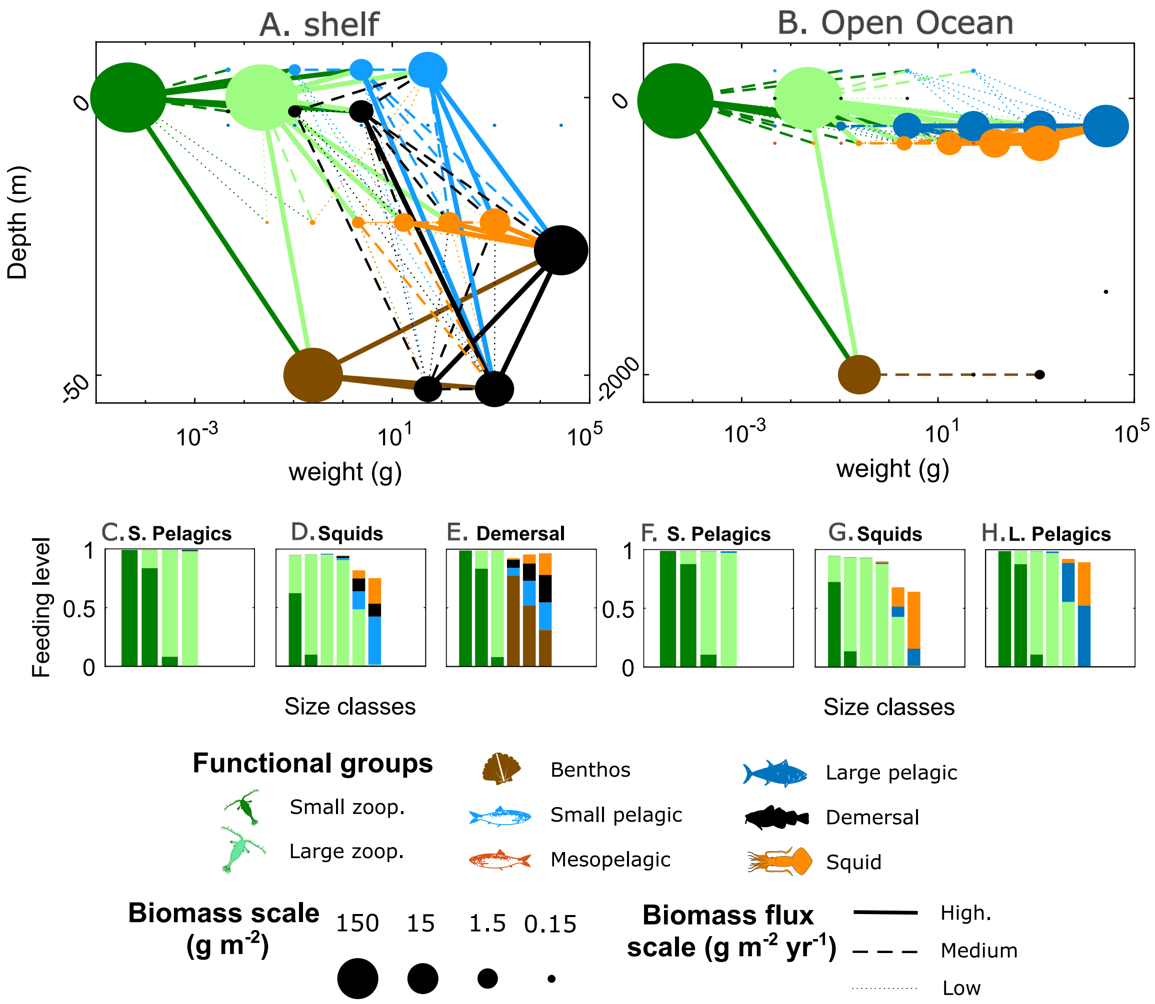

Fig. 5. Comparison of the food-web structure (top panels) and feeding levels (bottom panels) for a shelf (50 m depth) and an open ocean (2000 m depth) system. Dots width in the food-web panel A & B represents the biomass of each functional group: small and large zooplanktons (light and dark green, respectively), benthos (brown), small and large pelagics (light and dark blue, respectively), demersal (black) and squid (orange). Lines represent the biomass flux of prey consumed by a predator. The colors of the biomass fluxes represent the color of the functional type preyed. Feeding levels f (Eq. (1)) of small pelagic (light blue), demersal (black), and squid (orange) are presented for the shelf system, and small pelagic, large pelagic, and squid for an open ocean system. Feeding levels in panels C, D, and E refer to the shelf system in panel A, and feeding levels F, G, and H refer to the open ocean in panel B. All the simulations are made for a zooplankton production of 130 g m^{-2} yr^{-1}. For the sake of simplicity, we only represent the 75 highest fluxes in each food web plot, and scale from low (dotted lines), to medium (dashed lines) to high (plain lines). The biomass of each functional group is plotted over a logarithmic scale to enhance visualization.

shelf and open ocean when zooplankton productivity subceeds 25 g m^{-2} yr^{-1}. Moreover, the presence of squid in productive regions leads to a decline in total community biomass when contrasted to a system without squid (gray areas in Fig. 4A & B).

Both fish and squid switch trophic niches as they grow larger (Fig. 5). Squid and large pelagic fish shift from a diet of zooplankton to fish and squid (Fig. 5D, G, & E), while small pelagic fish shift from small to large zooplankton (Fig. 5C & F). Demersal fish switch from zooplankton to benthic prey and subsequently to fish and squid (Fig. 5E). As expected, demersal fish are dominant in shelf waters where they feed on both pelagic and benthic prey resources. In open ocean systems, mesopelagic fish are most dominant at relatively low zooplankton productivity, and large pelagic fish at higher productivity (Fig. 4B).

Squid biomass is relatively low in both shelf and open ocean up to the highest zooplankton productivity (respectively 10% and 24% of squid biomass in the system at 100 g m^2 yr^{-1}). Squid primarily feed on zooplankton and small pelagic fish in shelf areas (Fig. 5A & B) and on large pelagic in the open ocean areas. Their presence in the deep ocean results in a reduction of mesopelagic biomass compared to a system without squid (Fig. SE1).

Squid have low feeding levels, particularly at the adult stage, i.e., last size-class in Fig. 5D & G. Lower feeding levels imply that a larger fraction of their consumed prey is used to energetically cover the high respiration costs. All fish groups have higher feeding levels. This difference between squid and fish in feeding level shows that squid abundance is more resource-limited (Fig. 5A & B; Squids) and fish abundance is more controlled by predators (see Supplement D).

Squid account for a large proportion of the total metabolic losses considering their relatively low abundance in both shelf and open ocean systems (Fig. 4C and D). For instance, in a productive shelf system (50 m depth and 100 g m^{-2} yr^{-1} zooplankton productivity) squid account for 42% of the total metabolic cost but only represent 10% of the total biomass. For comparison, demersals account for 49% of the total metabolic losses and 79% of the biomass in the same system (Fig. 4A and C). Similarly, in a productive open ocean (2000 m depth and 100 g m^{-2} yr^{-1} zooplankton productivity) squid account for 60% of the total metabolic cost and 24% of the total biomass (Fig. 4B and D). We can further notice that the proportion of community metabolic losses increases with zooplankton productivity. Squid mass-specific metabolic costs are higher than for fish due to their higher growth rate and the proportionality between standard metabolism Q and individual growth rate A (2).

4. Discussion

The squid species examined grow on average 5 times faster than fish (average somatic growth rates of 23.4 vs. 4.7 g^{1-n}). Their faster growth leads to higher maximum population growth rate than fish, but also higher resource demand which constrains them to relatively productive systems. The presence of squid in our trait-based community model is associated with a reduction in total biomass in shelf and open ocean systems. The reduction of fish biomass is not related to a drop in the feeding level of fish, suggesting that the effect of squid on fish is predominantly the result of predation by squid on fish and less due to competition for a shared resource Supplement D. The model results further suggest that high respiration losses of squid could decrease the upper total community biomass in systems where squid are present. These results indicate that, within the scope of squid species and feeding strategies examined in this study, squid plays a significant role in shaping the ecosystem towards a state characterized by relatively low community biomass but high turnover of biomass.

4.1. Differences in ecological success between fish and squid

The most conspicuous difference between fish and squid is in the somatic growth rate. Average squid growth is about 5 times faster than average fish growth and only the fastest growing fish mahi mahi (*Coryphaena hippurus*), have similar growth rates. What makes it possible for squid to grow so fast? It seems that their very active metabolism associated with high respiration from both cutaneous and gill respiration can sustain rapid growth (O'dor and Webber, 1986). Squid's fast growth leads to high maximum population growth rates, which should allow them to out-compete slower-growing fish populations. Yet, fish are more dominant than squid (Morato et al., 2016; Hunsicker et al., 2010). Fast-growing species also experience a high risk of predation due to a more active lifestyle and risky behavior resulting from their high food demand, which is thought to result in a dominance of species with "submaximal" population growth rate (Schramski et al., 2015). However, the trade-off between growth and predation risk is already accounted for in our calculation of maximum population growth rate so the higher predation risk is insufficient to explain the proliferation of fish over squid. We highlight that the fast living strategy of squid leads to a higher minimal resource requirement R^* to maintain the population size (Fig. 3D). Consequently, squid populations are subjected to higher intra-specific competition and hence lower carrying capacity. We hypothesize that the reason for the lower success of squid compared to fish rests on their high resource requirements (high R^*).

4.2. Dependency on zooplankton productivity

Our results predict that fast-growing squid should mainly inhabit productive regions as a result of their high demand for resources. This result is in agreement with some observations. For example, Boyle and Rodhouse (2008) argued that the most abundant Ommastrephidae squid inhabits productive regions, e.g., up-welling systems. To further validate these results, we reviewed EcoPath models that include cephalopod biomass estimates in different regions varying in zooplankton productivity and depth (Supplement C; Fig. SC1). Conversely to our results, EcoPath models show no increase in the proportion of cephalopod biomass (relative to fish biomass) with increasing zooplankton productivity and the existence of squid in low-productive regions. These findings are in agreement with another study that found no relationship between cephalopod landings and primary production (Hunsicker et al., 2010). We have so far no definite explanation for why there is such a difference between our theoretical expectations and these observations and predictions. It is, however, worth noticing that these studies examined total cephalopod biomass or landings and cephalopods may exhibit a wide range of life history strategies that differ from the fast-growing squid examined here. The presence of cephalopods with lower than squid metabolic rates could explain the constant proportion of cephalopods and their presence in low-productive regions in the Ecopath results analyzed here (Seibel, 2007). Moreover, our FEISTY model uses yearly average productivity, but natural systems fluctuate from favorable to non-favorable conditions for squid. Incorporating time series could enhance the presence of squid in systems with lower yearly average productivity than predicted in our study.

4.3. Low standing stock biomass of fast living organisms

Following our results, the review of EcoPath models shows that cephalopods have relatively low biomass compared with pelagic fish (ranging between 5 to 10% in most regions Supplement C; Fig. SC1). The low biomass of squid populations is the result of their high growth rate which imposes a low carrying capacity. Similarly, their semelparous strategy implies a lower accumulation of biomass than for large fish. However, despite the low standing stock biomass, the productivity (production of biomass per standing stock biomass) can still be high because of their high somatic growth rate.

One EcoPath model of the Azores region showed a much higher ratio of cephalopod to fish biomass (see Supplement C; Fig. SC1B and Morato et al. (2016)). Seibel (2007) suggests that cephalopods living in deeper layers exhibit lower metabolic rates than pelagic ones. We expect that the cephalopods in this deep sea ecosystem, with seafloor depths up to 5000 m, exhibit slower growth and lower metabolism than the squid studied here and could result in higher standing stock biomass. Alternatively, this high ratio of cephalopods to fish can be explained by the presence of other than fish groups in the system that our FEISTY framework does not represent (e.g., marine mammals and elasmobranchs).

4.4. Somatic growth as a key trait

We showed that somatic growth is a key trait to make predictions at the population and the ecosystem level, changing the relative abundance of fast- and slow-growing strategies. Unfortunately, few works address the importance of somatic growth rate for population dynamic. Stawitz and Essington (2019) shows the important contribution of somatic growth to the biomass of fish populations. Since the somatic growth rate employed by Stawitz and Essington (2019) is a realized somatic growth, i.e., not corrected for food consumption, it is difficult to differentiate the growth strategy from the environmental condition in resources. One could expect ecosystems with a high secondary production to exhibit a higher abundance of fast-growing species, with less standing stock biomass but higher productivity. At the macro-ecological level, there is some evidence that fish grow, on average, faster in productive regions (van Denderen et al., 2020; Morais and Bellwood, 2018). Yet, the signal is not very strong. For cephalopods it has been shown that landings are not correlated to primary productivity (Hunsicker et al., 2010), suggesting that the abundance of fast-growing strategies is not related to the system's productivity. However, trophic transfer from the bottom to the top of ecosystems is complex and varies between regions. It is further known that fisheries catch (i.e. fish productivity) do not match with primary production (Ryther, 1969) similar to squid. Stock et al. (2017) showed that this mismatch between primary productivity could be solved by considering benthopelagic coupling and variation in transfer efficiency from primary to secondary producers between regions. This finding shows that a high primary production might not reflect the high productivity of squid resources that rely on secondary producers and small fish.

4.5. Model uncertainty

The prediction of squid biomass and productivity in our dynamic model of ecosystem food-web (FEISTY-squid) is strongly dependent on the individual growth rate A evaluated for squid. Our estimation for this parameter rests upon a low number of species (11 species). The species in the analysis are dominated by commercially important squid, which is probably biased towards highly productive fast-growing species. The results of our study will differ in systems where the dominant squid species grow equally fast or slower than the dominant fish species. Thus, examining variation in individual growth rate A of squid and fish species across a range of marine systems may help to better parameterize the model.

The vertical migration strategy of squid is well described for many open ocean species, which make diel vertical migrations and preferentially target mesopelagic fish (Roper and Young, 1975). Squid vertical behavior in species living in shelf waters is less well described. Feeding data show that some squid species feed on benthic organisms at intermediate sizes, suggesting that some shelf squid could occupy the niche of demersal fish. Juveniles live closer to the sea bed and transition to a more pelagic niche when reaching their adult size (Vovk, 1985). In our model analysis, we decided to ignore squid feeding on benthic organisms to allow for niche differentiation between demersal fish and squid. Allowing squid to feed on benthos in shelf systems in the model would result in competitive exclusion of demersal fish at high resource productivity (not shown). This indicates that there are differences in the feeding niche between squid and demersal fish that we do not describe adequately, such as a higher feeding efficiency or time spent feeding on benthic resources.

In our model analysis, we assumed that squid are strictly semelparous. However, several studies have shown that some squid species may exhibit several spawning events during their lifespan (Pecl, 2000; Hernández-Muñoz et al., 2016; Pérez-Palafox et al., 2019). These studies are controversial since they are unable to show truly iteroparous strategies in squid with gonad regeneration. The squid species are instead releasing already formed eggs several times during the season (Laptikhovsky et al., 2019). Since model predictions are primarily driven by the observed growth differences between fish and squid, implementing an iteroparous strategy for squid would not affect the qualitative results of the model.

Our study employs fundamental life history parameters of squid, namely A, M_∞, and β, which are challenging to quantify accurately or remain unestimated. We conducted FEISTY-squid simulations across varying levels of zooplankton productivity by manipulating these key traits (similar to our Fig. 4A & B). Our sensitivity analysis indicates that the squid predator:prey ratio β and the maximum mass M_∞ are key parameters defining the trophic and competitive niche of squid. As we mentioned, squid has a strong effect in regulating fish, and changes in M_∞ and β result in strong differences in system composition (Fig. SF1 and Fig. SF2A, B, E and F). This indicates that our model projections should be analyzed with caution considering the poor estimation of predator:prey ratios β for squid and that further analysis is needed to better evaluate this parameter. Additionally, we observed that variations in squid somatic growth rates did not exert significant impacts on our outcomes (Fig. SF1 and Fig. SF2C and D). However, lower somatic growth rates corresponded to enhanced squid biomass, imputed to reduced metabolic losses. This indicates that our results seem robust given the low number of species used to estimate A.

5. Conclusion and future direction

We show that squid have a potentially large impact on ecosystem structure and function even at relatively low biomass. We show that their fast growth and semelparous reproduction strategy drive this impact on ecosystem structure. We anticipate that the recent proliferation of squid in ecosystems around the world has likely caused significant ecological and socio-economic impacts on fisheries resources. This work could provide a framework for understanding the expanding presence of squid across various ecosystems in relation to climate change and fishing activities.

CRediT authorship contribution statement

Rémy Denéchère: Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **P. Daniël van Denderen:** Writing – review & editing, Supervision, Methodology. **Ken H. Andersen:** Writing – review & editing, Methodology, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data and code are available on GitHub: https://github.com/RemyDenechere/The-role-of-squid-for-food-web-structure-and-community-level-metabolism/releases/tag/Publication.

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Appendix A. Supplementary data

Supplementary material related to this article can be found online at https://doi.org/10.1016/j.ecolmodel.2024.110729.

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