

**Ontogenetic diet shifts of rough scad *Trachurus lathami* in the North Patagonian shelf (South West Atlantic Ocean)**

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## ABSTRACT

Rough scad *Trachurus lathami* is a key pelagic fish in the Argentinean Continental Shelf (ACS, South West Atlantic Ocean), with recent increases in abundance. It is a main prey of fishes and marine mammals, and shares the environment with commercially relevant pelagic species (*Engraulis anchoita* and *Scomber colias*), playing an important role linking lower and upper trophic levels in the ecosystem. This study aims to determine the ontogenetic changes in the diet composition, feeding strategy, trophic niche breadth, and trophic level of *T. lathami* in the North Patagonian Shelf (43°–45°30'S). The stomach contents of adult fish (n = 238) were analyzed. Results suggested a clear ontogenetic shift in the diet at a size of ~190 mm. Smaller individuals (160-190 mm) were specialized on misidaceans, and showed the highest trophic level, while larger *T. lathami* (221-230 mm) consumed decapods (*Peisos petrunkevitchi*) and teleosts (eggs and larvae). Trophic niche breadth was higher at the medium-size class (191-220 mm), which mainly preyed upon copepods (*Calanoides carinatus*) and chaetognaths (*Sagitta* spp.), evidencing a more diverse diet and a rather generalist strategy. Updated information on the trophic ecology of *T. lathami* evidences its extremely plastic feeding behaviour, being able to adapt its trophic niche to the most readily available food items from the mesopelagic community.

## Keywords

Argentinean Continental Shelf, small pelagic fish, Carangidae, stomach contents, trophic niche breadth, trophic level

## INTRODUCTION

From the Rio de la Plata south to Tierra del Fuego, the Argentinean Continental Shelf (ACS) in the South West Atlantic is among the richest and most diverse ocean regions (Piola *et al.*, 2018). It is a habitat for populations of fishes and squids of high economic and ecological value (Sánchez & Bezzi, 2004), and it also includes the migration corridors and breeding grounds of many charismatic marine mammals and birds (Falabella *et al.*, 2009). Within the ACS, the North Patagonian shelf (NPS, 43°-45°30'S) is a highly productive area, with high phytoplankton (Carreto *et al.*, 2007) and zooplankton (Temperoni *et al.*, 2014) abundances reported, in association with a marked tidal front system that extends southwards from Península Valdés (42°30'S) along the Patagonian coast to 45°S (Sabatini & Martos, 2002). It starts to develop during spring as the seasonal thermocline originates offshore, and persists until autumn when stratification weakens. This scenario creates a diversity of spawning habitats for adult fishes and different breeding conditions for eggs and larvae (Sánchez & Ciechomski, 1995).

The rough scad *Trachurus lathami* Nichols, 1920 is the only species of the genus known in the South West Atlantic (Saccardo, 1980; Pacheco Tack, 1988), with a broad distribution from the Gulf of Maine (USA) (43°N) to Central Patagonia (47°S) in Argentina (Bovcon *et al.*, 2011; Cousseau & Perrotta, 2013). In the ACS, this benthopelagic species has a large biomass and is captured as by-catch with the Argentine anchovy *Engraulis anchoita* Hubbs & Marini 1935 and the Atlantic chub mackerel *Scomber colias* Gmelin 1789 (Orlando *et al.*, 2018), but it is not a target for pelagic fisheries. Since mid 90's, an increasing number of *T. lathami* individuals has been captured in the ACS between 35°-41°S for research purposes (Orlando *et al.*, 2018). It has been mentioned as a key prey in the diet of many bony fishes of commercial interest (i.e. striped weakfish *Cynoscion guatucupa*, García & Marí, 2008; Brazilian flathead *Percophis brasiliensis*, Milessi & Marí, 2012; Argentine hake *Merluccius hubbsi*, Cousseau, 1967), elasmobranch fishes (i.e. skates, Barbini & Lucifora, 2011a, 2011 b, 2016a, 2016b), and marine mammals (i.e. franciscana dolphin *Pontoporia blainvillei*, Paso-Viola *et al.*, 2014; South American sea lion *Otaria flavescens*, Jarma *et al.*, 2019).

Hence, both as prey and/or as a potential competitor for food items with co-occurrent *E. anchoita* and *S. colias*, the species can be considered an important component of the ACS marine ecosystem. Small pelagic fishes are key components of the food web due to their large biomasses and intermediate positions that connect the lower (zooplankton) and upper (fishes, birds, and mammals) trophic levels (Cury *et al.*, 2000; Palomera *et al.*, 2007). Therefore, studies focused on their trophic ecology are crucial to gain further understanding on their feeding preferences through ontogenesis, and how these habits might impact the flow of matter and energy as well as predatory-prey interactions in the whole ecosystem. In this context, the analysis of stomach content may provide relevant scientific advice for fisheries management with an ecosystem approach (Hyslop, 1980; da Silveira *et al.*, 2020). However, the ecology of *T. lathami*, including its feeding habits, is still poorly known and outdated for the region.

Body size has major implications upon aspects of an organism's ecology (Brown *et al.*, 2004), such as niche breadth (Costa, 2009) and trophic level (Layman *et al.*, 2005). When the use of food sources shifts during development, small and large individuals of any given species may play different roles within a community, and may hence be considered functionally different species in terms of trophic dynamics (Ross, 1986). Therefore, it is critical to identify ecological traits related to intrinsic factors such as body size. Although ontogenetic diet and feeding strategy shifts have been reported for different *Trachurus* species (e.g. *T. mediterraneus*, Bayhan *et al.*, 2013; *T. Trachurus*, Šantić *et al.*, 2005; *T. picturatus*, Battaglia *et al.*, 2020), a previous study on the feeding habits of *T. lathami* (66-255 mm total length) from the ACS is limited to a mere description of dietary composition (Cousseau, 1967). In this context, the purpose of this study was to provide updated information on the feeding habits of *T. lathami* from coastal Patagonian waters in the ACS. The specific objectives were to: (1) describe the diet composition by means of stomach content analyses, (2) identify changes in the diet with increasing body size, (3) assess the feeding strategy, and (4) determine if body size influences the trophic niche breadth and the trophic level. On the basis of current knowledge, we hypothesize that *T. lathami* diet composition becomes less diverse

as body size (total length) increases, with a concurrent decrease in the niche breadth and an increase in the trophic level.

## MATERIALS AND METHODS

### Sample collection

*Trachurus lathami* were collected by Rawson's (Chubut province, Argentina) coastal trawl fleet (16-21 m ice-chilling boats) targeting Argentine red shrimp *Pleoticus muelleri* in the NPS, in January-February 2016 (Figure 1; Table 1). This fleet operates within 12 nautical miles of the shore targeting shrimp at depths less than 40 m. Specimens were immediately frozen at -20°C to ensure that the digestion of the stomach contents was halted. Once in the laboratory, the total length of fish ( $L$ , in mm) was measured. Stomachs were extracted and preserved in a 5% formalin solution. One damaged stomach during dissection was discarded from the analysis. Stomach contents were analyzed individually, sorted, and identified under stereoscopic microscope (maximum magnification 50X) to the lowest possible taxonomic level. The number of each prey was counted.

### Data analysis

Feeding incidence was calculated as the percentage of individuals with at least one prey item in the gut content (Arthur, 1976). To determine the contribution of each prey, the composition of diet was presented as percentage frequency of occurrence (% $O_i$ , percentage of stomachs which contained a particular prey  $i$ ) and percentage in number (% $N_i$ , number of a particular prey  $i$  expressed as percentage of total number of consumed prey) (Hyslop, 1980). The relative importance (RI) of each prey item in the diet was calculated by multiplying the % $O_i$  and the % $N_i$  of such prey (Laroche, 1982), and expressed as a percentage.

To determine whether a sufficient number of individuals was sampled, the stomachs were randomised 100 times and the mean cumulative Shannon diversity index ( $H' = \sum P_i * \ln P_i$ , where  $P_i$  is the proportion of each different prey item contributing to the whole diet) was plotted as a function

of sample size (Magurran, 2004) for three size groups: 160 – 190 mm *L*, 191 – 220 mm *L*, and 221 – 230 mm *L*. Sample size was considered sufficient to describe feeding habits if the cumulative prey curve reached an asymptote.

To identify changes in the diet of *T. lathami* with body size, six prey categories in the stomach contents were considered due to their relative importance: copepods (Family Calanidae), misidaceans, the decapod *Peisos petrunkevitchi*, other non-identified decapods, chaetognaths *Sagitta* spp., and teleost fishes (eggs and larvae). For each prey category, zero-inflated count data regression models were fitted (Zeileis *et al.*, 2008), considering the number of prey consumed as the response variable and *L* as the explanatory variable. To detect possible curvilinear relationships between both variables, quadratic functions (i.e.  $L + L^2$ ) were included in the models. Models without the independent variable (i.e. null model) were fitted to evaluate the hypothesis that the variable tested did not have an effect on the consumption of a prey category. The Akaike information criterion (AIC) (Franklin *et al.*, 2001; Johnson & Omland, 2004) was applied for each model fitted within a prey category, selecting that with the lowest AIC as the best one explaining the observed data. To obtain the relative likelihood of each fitted model given the data, Akaike's weight ( $w$ ) was calculated.

The feeding strategy (from generalist to specialist) and phenotype contribution (variation in resource use within and among individuals) to niche width of *T. lathami* was assessed using the modified Costello (1990) graphical method (Amundsen *et al.*, 1996) for the three size groups. For each prey type, the specific abundance %P<sub>i</sub> (the percentage of a prey taxon out of all prey items in only those predators in whose stomachs it occurs) was plotted against the %O<sub>i</sub> on a two-dimensional graph (Figure 4a).

To determine if body size influences the dietary niche breadth, the Levins's standardized index of niche breadth (Krebs, 1989) was calculated for the same three size groups. This index provides a continuous measure of niche breadth on a scale from 0 to 1. Values closer to 0 indicate a narrower and more specialized diet than values closer to 1, which show a broader and more

generalist diet (Krebs, 1989). The relationship between size groups and the Levins's standardized index was analysed using generalized linear models (GLM). For that purpose, the observations were randomly sampled 100 times with replacement in order to obtain the frequency distribution of the Levins's standardized index. A GLM was then used to model the Levins's standardized index as a function of size groups. We fitted a null model to judge whether or not body size had an effect on dietary niche breadth.

To determine *T. lathami* position within the food web, the trophic level (TL) was calculated for the three size groups using the method proposed by Cortés (1999) as:  $TL = 1 + \sum (TL_j * P_j)$ , where  $TL_j$  is the trophic level of each prey category  $j$  and  $P_j$  is the proportion of each prey category  $j$  (using %RI) in the diet. Eight prey categories were used to calculate TL, for which trophic level information was available from the literature: copepods, misidaceans, *Peisos petrunkevitchi*, decapods, amphipods, euphausiids, chaetognaths, and teleostei. Trophic levels of prey were obtained from Ebert & Bizarro (2007), Horn *et al.* (2013), Grigor *et al.* (2015), and Chen *et al.* (2018). The observations were randomly sampled 100 times with replacement in order to obtain the frequency distribution of TL and to get mean and standard deviation values.

All statistical analyses were performed using the R statistical environment, version 3.6.3 (R Core Team, 2020).

### **Ethical statement**

Fishes were collected as part of commercial trawls carried out by Rawson's (Chubut province, Argentina) coastal fleet targeting Argentine red shrimp in the NPS, with agreement of the Argentinean government. Specimens were killed during capture from the sea with the fishing net. No experimental work was undertaken. No ethical permission was required.

## **RESULTS**

### **Overall diet**

A total of 238 stomach contents was analysed. The size of the individuals ranged from 161 to 228 mm *L* (mean = 204 mm, standard deviation SD = 114) (Figure 2). A high number of individuals had identifiable prey in their guts, evidencing a feeding incidence of 81% (n = 192). A total of 8976 prey items, which belonged to 11 taxa, was identified (Table 2). The cumulative curves of prey diversity reached an asymptote, indicating that sample size was sufficient to describe the diet in the three size ranges considered (Supporting Information Figure S1). In terms of relative importance, the calanoid copepod *Calanoides carinatus* was the main prey, followed by chaetognaths *Sagitta* spp. and the decapod *P. petrunkevitchi* (Table 2). Similarly, calanoid copepods were the most important prey in terms of percentage frequency of occurrence. Decapods, fish eggs and larvae, and chaetognaths also occurred frequently in the diet of *T. lathami*. The most important prey by number were chaetognaths and calanoid copepods, followed by *P. petrunkevitchi*. The consumption of amphipods, euphausiids, ostracods and cephalopods was considered occasional (RI < 0.5%).

### **Body size-related shift in diet**

Fitted models for the different prey categories evidenced a significant relationship between prey consumption and *L* of *T. lathami* (Table 3). Misidaceans were mostly consumed by the smallest individuals (160-190 mm *L*) (Figure 3). Contrarily, decapods (*P. petrunkevitchi* as well as non-identified species) and teleosts (eggs and larvae) were mostly present in the stomach contents of individuals ranging between 221-230 mm *L*. The number of Calanidae copepods and chaetognaths consumed had a significant humped relationship with *L* (Figure 3). According to these last models, large amounts of copepods and chaetognaths were consumed by *T. lathami* of medium sizes (191-220 mm *L*).

### **Feeding strategy**



While for smaller *T. lathami* (160-190 mm) a specialist feeding strategy might be suggested, i.e. targeting misidaceans and unidentified crustaceans (Figure 4b), the medium-sized group (191-220 mm) showed a trend to a wider niche, with certain specialization upon *Sagitta* spp., *P. petrunkevitchi*, and euphausiids. In larger fish (221-230 mm), a population feeding specialization upon *P. petrunkevitchi*, as well as an individual specialization upon non-identified decapods, ostracods and teleostei was observed.

### **Dietary niche breadth**

The dietary niche breadth was significantly different among size groups (AIC = - 1163.3;  $\Delta_i$  = 682.7;  $w$  = 0.99). Prediction of the model parameters for Levin's standardized index were: 160-190 mm = 0.074; 191-220 mm = 0.283; 221-230 mm = 0.029. The mean Levin's standardized index values (Figure 5) indicated that the diet of *T. lathami* at the extremes of the size distribution (i.e. 160-190 mm and 221-230 mm *L*) was dominated by few prey items (Shannon diversity index mean  $\pm$  SD: 160-190 mm =  $0.715 \pm 0.11$ ; 221-230 mm =  $0.346 \pm 0.10$ ), reflecting a narrow dietary niche breadth with a specialized diet. On the contrary, at medium sizes (191-220 mm *L*), mean values of the index were higher, evidencing a more diverse and rich diet (Shannon diversity index mean  $\pm$  SD =  $1.351 \pm <0.01$ ) and a wider niche breadth.

### **Trophic level**

Mean trophic level of *T. lathami* was 3.426 (SD = 0.019). Differences were observed in TL when considering the three size categories derived from fitted models and trophic niche breadth estimation. Values were slightly higher in the size class 160-190 mm *L* (TL = 3.570; SD = 0.297), compared to 191-220 mm *L* (TL = 3.446; SD = 0.033), and 221-230 mm *L* (TL = 3.414; SD = 0.021).

## **DISCUSSION**

This paper presents updated information on the feeding habits of *T. lathami* in the ACS during austral summer. The analysis of the stomach contents showed that this species is able to feed on a large number of prey, mainly planktonic and micronektonic that belong to the mesopelagic and lower epipelagic environments (Sabatini & Martos, 2002; Temperoni *et al.*, 2014; Viñas *et al.*, 2015). Dietary indices indicated that the Calanidae copepod *C. carinatus*, chaetognaths *Sagitta* spp., and the decapod *P. petrunkevitchi* were the most frequent and abundant prey items in the diet of *T. lathami*, whereas amphipods, misidaceans, cumaceans, cladocerans and fish eggs were less frequent. The importance of copepods in the diet was also reported by Cousseau (1967) in individuals (65-245 mm total length) collected in coastal waters (~38°S) of the ACS, and by de Carvalho & Soares (2006) in *T. lathami* (53-175 mm) collected in Brazilian waters during summer. These results are in agreement with our data and highlight the trophic preference of the species for mesopelagic zooplanktonic prey. It is worth noting, however, that the same *Trachurus* species from different sampling locations can exhibit diverse dietary compositions, as evidenced from a review of existing literature based on stomach content analysis of species worldwide (Supporting Information Table S1). Such differences might be linked to prey availability in the environment, depth distribution of the schools, competition for food with co-occurring fishes, and the dietary needs of the species (Georgieva *et al.*, 2019). Overall, the shift in the preferred prey among locations evidences *Trachurus* ability to modify the diet in response to the most readily available food items, thus being extremely plastic in their feeding behaviours.

In the NPS, results from zooplankton net tows indicate that copepods, and particularly *C. carinatus* (Viñas *et al.*, 2015), are dominant in the community during austral summer (Temperoni *et al.*, 2014), which would explain their importance (RI > 55%) in the diet of *T. lathami*. Chaetognaths *Sagitta* spp. are also frequent on the ACS (Daponte *et al.*, 2004), with *S. friderici* as the dominant species in Patagonian waters during the summer (Mazzoni, 1990). With respect to the epibenthic decapod *P. petrunkevitchi*, records of abundance are scarce for the NPS. However, it has been mentioned as the main food item of Argentine hake *Merluccius hubbsi* near Rawson's port (Ruiz &

Fondacaro, 1997), evidencing its predominance in coastal waters nearby our sampling location. The seasonal presence of a highly productive tidal front during austral spring and summer in the NPS (Sabatini & Martos, 2002; Carreto *et al.*, 2007) probably influences the structure of the zooplankton community (Temperoni *et al.*, 2014), producing high concentrations of these prey that are available for fish predators such as *T. lathami*. It is worth mentioning that abundances for some of the prey categories were either not available or underestimated due to sampling gears, which prevents further conclusions on this topic. In the same way, the stomach contents are a snapshot in time of the diet, and we could not determine where the prey were captured in the vertical range, or even the horizontal. This limits the value of the comparison with zooplankton samples at the same time of catch. However, *T. lathami* has been described as a benthopelagic species (Cousseau, 1967), which was reflected in the diverse types of prey consumed, both including individuals from the pelagic domain (e.g. copepods and chaetognaths) as well as other with epibenthic habits (e.g. *P. petrunkevitchi*).

Results show that *T. lathami* food habits were strongly associated with body size (i.e. *L*). Small (160-190 mm *L*) and medium-size (191-220 mm *L*) individuals were mostly zooplanktophagous, while larger specimens (221-230 mm *L*) were mainly consumers of fish eggs and larvae. The threshold size separating fish by diet composition was ~190 mm. Body-size related dietary shifts have been previously observed in most of *Trachurus* species; in *T. mediterraneus* (Bayhan *et al.*, 2013), *T. trachurus* (Kompowski, 1976; Cabral & Murta, 2002; Šantić *et al.*, 2005) and *T. picturatus* (Kompowski, 1976; Battaglia *et al.*, 2020), size at which the dietary shift occurs was similar (c. 180, 200, and 210 mm, respectively) to the value observed in this study. It is worth noting that *T. lathami* from the ACS is smaller than other *Trachurus* species present in different areas, with a maximum size of 250 mm *L* (Cousseau, 1967) which is nonetheless similar to that recorded for the species in Brazilian waters (Saccardo & Katsuragawa, 1995). Contrarily, larger sizes were observed in *T. capensis* from Benguela waters (Kadila *et al.*, 2020), *T. trecae* in waters of Mauritania (Guschin & Corten, 2017) and *T. murphyi* in Chilean waters (Medina & Arancibia,

2002; Alegre *et al.*, 2013; Orrego & Mendo, 2015). In this species, maximum *L* reached c. 400-500 mm. In spite of these differences in maximum body length, ontogenetic dietary changes have been recorded in all *Trachurus* species. In general, a gradual switch from mesopelagic crustaceans such as copepods and/or euphausiids to larger prey such as decapods or fish occurs at varying threshold sizes.

In the *T. lathami* analyzed in this study, the size-shift in diet was reflected into the dietary niche breadth, which was maximum at the medium-size class (191-220 mm), with a trend to a generalist feeding strategy. In many fishes, a positive relationship between body size and niche breadth has been observed, which derives from the incorporation of multiple prey as individuals grow (Scharf *et al.*, 2000). However, and confirming our initial hypothesis, dietary niche breadth was higher at medium-size *T. lathami*, but diminished in larger individuals with a clear specialist feeding strategy. This was reported in *T. picturatus* (Battaglia *et al.*, 2020), *T. mediterraneus* (Georgieva *et al.*, 2019), *T. trachurus*, and other pelagic species such as Atlantic mackerel *Scomber scombrus* (Bachiller & Irigoien, 2015). The decrease in consumed prey diversity along with grow, feeding on larger and less diverse target prey groups (e.g. decapods or fishes), could be explained considering that predators become larger in size and more effective in catching large prey. Changes in the feeding apparatus through ontogenesis would turn fish into more effective predators, owing to a variety of factors that include increased sustained swimming speeds, better visual acuity and improved handling of prey (Beamish, 1978; Blaxter, 1986; Folkvord & Hunter, 1986). However, medium-size individuals can also ingest the smallest prey, showing an increase in trophic-niche breadth and a more diverse diet. This suggests the ability of large competitors to eat a wider range of prey sizes than small ones, large fish being able to use essentially all of the prey size spectrum available to small ones, plus particles too large for the small ones (Pearre, 1986).

Prey size is generally found to increase with predator size for most fishes (Scharf *et al.*, 2000). *T. lathami* results show that, even with a shift towards the incorporation of larger prey in the diet of individuals of ~ 220 mm (such as decapods and fish eggs and larvae, size range > 10 mm

total length), small and medium-size prey such as Calanidae copepods (size range 1.5-3 mm total length) and chaetognaths (5-10 mm total length) remain as important items in medium-size individuals (191-220 mm), creating the observed dome-shaped curves. This kind of prey length/predator length relationship contrast with optimal foraging theory (MacArthur & Pianka, 1966; Costa *et al.*, 2008), and suggest that *T. lathami* keep including small-bodied prey in their diet even when growing to large sizes due to their high encounter rates, greater abundance and a high probability of capture. Copepod prey dominate the zooplankton community of the NPS (Temperoni *et al.*, 2014) and form dense patches that would favour a filter-feeding behaviour. Thus, their retention in the diets of medium-size *T. lathami* reflect profitable foraging decisions. Notwithstanding, active catching of larger and more nutritious prey (i.e. decapods such as *P. petrunkevitchi*; Temperoni & Derisio, 2018) also occurs in larger individuals, since *T. lathami* can shift between filter-feeding (through the gill rakers) and active predation, depending on the availability of different prey items (Meneghetti & Alves, 1971). This implies not only a greater efficiency in capturing larger prey with increasing size but also a size-selective feeding along with ontogenesis. However, it has been suggested that the largest relative prey sizes tend to be absent in the diets of the largest predators, because those sizes are relatively scarce in the environment (Juanes, 2016). In this sense, compared to smaller predator, larger predators are constrained in the range of relative prey sizes they consume, which translates into a narrower trophic niche, as observed here for the 221-230 mm size class.

Trophic relationships in most marine communities are strongly determined by body size, with the general rule being that predators are bigger than their prey (Brose *et al.*, 2006), from which derives the premise: the bigger an organism, the higher its trophic level. The trophic level of *T. lathami* indicates that it is a secondary consumer in the NPS, constituting the first TL estimation for the species in the ACS. This value can be useful for the development of ecosystem-based fishery management strategies. The obtained value is similar to that reported for the species (i.e. 3.45) by Froese & Pauly (2006). Similarly, values of 3.20-3.70 and 3.40-3.90 were reported for *T. trachurus*

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and *T. mediterraneus*, respectively (Stergiou & Karpouzi, 2002), while Romero *et al.* (2021) estimated a value of  $3.09 \pm 0.05$  for *T. picturatus* by means of stable isotopes analysis. Given that larger individuals have access to larger prey, like fish eggs and larvae, a higher TL in the larger *T. lathami* size class was expected. However, TL was slightly higher in the size range 160-190 mm *L*, matching the preference for misidaceans, prey that exhibits elevated TL values due to their feeding behaviours (Horn *et al.*, 2013). A recent review showed that for many species, the trophic level does not increase with body size, suggesting that size-independent feeding is not rare in marine fishes (Galván *et al.*, 2010; Ríos *et al.*, 2019). Predators may rapidly change their trophic niche, therefore changing the whole configuration of the web, to adapt for different prey abundance and availability. This shift challenges the use commonly made of the concept of trophic level (Garrido & Murta, 2011), and deserves further research in the NPS pelagic food web.

On the basis of current knowledge regarding the feeding habits of pelagic fish in the north Patagonian region of the ACS, such as *E. anchoita* and *S. colias*, a partial overlap of their diets with *T. lathami* could be inferred. This fact, which was already mentioned by Angelescu (1980), deserves attention since both species sustain fisheries of commercial interest (Secretaría de Agricultura, Ganadería y Pesca Argentina, 2020), and might suffer changes in population biomass when facing food constraints. Crustacean zooplankton, particularly copepods (>90% of relative importance in the diet), are the main prey item of *E. anchoita* (Angelescu, 1980; Pájaro, 2002) and *S. colias* (Padovani & Pájaro, 2014; Padovani & Leonarduzzi, 2017). Hence, a dietary overlap between the three species might occur upon this prey item, but could not necessarily mean competition if food availability is sufficient (Holbrook & Schmitt, 1989; Irigoien & De Roos, 2011; Bachiller & Irigoien, 2015). Future work should be carried out to gain further insight into this topic, which has implications on stock management of pelagic species in the ACS. This is particularly true if the amount of foods becomes limited, and one species could stand up from the others due to the higher ability to change between prey size ranges or groups. In addition, if food availability is scarce, then a high niche overlap could result in potential intraguild predation effects (i.e. fish

egg/larvae consumption of potential competitors) (Irigoién & De Roos, 2011; Bachiller & Irigoien, 2015). These aspects highlight the importance of multi-species approaches, which are critical for marine food web modelling, since investigations in this field are still mostly based on a single-species diet approach.

In conclusion, *T. lathami* occupies an intermediate trophic position in the pelagic food web of the NPS. The observed feeding habits reflect a high number of trophic interactions with different pelagic prey, particularly within the mesopelagic community. A clear size-related shift in feeding was observed, from smaller prey such as copepods to larger prey such as decapods and fish eggs and larvae, with a wider niche breadth at medium sizes. Predation on these intermediate-trophic position organisms assures material (organic matter) and energy transfer to upper trophic levels, and acts as an important regulating force on these lower trophic level species. Future work is needed to shed light on trophic interactions and/or potential diet overlap with co-occurrent pelagic fish of commercial interest. In this sense, results of this study could be corroborated using multi-proxy analyses, i.e. combining microscope visual analysis with other techniques, such as stable isotope and fatty acid analyses.

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#### **SUPPORTING INFORMATION**

Additional supporting information may be found online in the Supporting Information section at the end of this article.

## CONTRIBUTIONS

B. T. sampled *T. lathami* individuals, performed stomach content analysis and wrote the manuscript with significant contributions from all authors. S. B. performed stomach content analysis, made the statistical data analysis, and wrote the manuscript. P. O. and C. C. B. planned samplings, sampled *T. lathami* individuals, and critically revised the drafted paper. All authors helped for the interpretation of data and approved the manuscript.

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## FIGURE CAPTIONS

**Figure 1.** Map of the sampling area in the North Patagonian Shelf showing positions of the hauls where rough scad *Trachurus lathami* were collected. The rectangle in the inset shows the location of the study area in South America.

**Figure 2.** Length (*L*)-frequency distribution of *Trachurus lathami* in the North Patagonian Shelf. Vertical dashed lines indicate the three size groups considered in the analyses: 160 – 190 mm *L*, 191 – 220 mm *L*, and 221 – 230 mm *L*

**Figure 3.** Changes in ingestion (number of prey) of Calanidae, misidaceans, *Peisos petrunkevitchi*, non-identified decapods, chaetognaths *Sagitta* spp., and non-identified teleost (eggs and larvae) by *Trachurus lathami*, in relation with total length (mm).

**Figure 4.** (a) Explanatory diagram from Amundsen et al. (1996) and its interpretation on feeding strategy. BPC: between-phenotype component, WPC: within-phenotype component, (b) feeding strategy of *Trachurus lathami* of three size groups (mm) in the North Patagonian Shelf. Amph: amphipods, Cop: Calanidae copepods, Chaet: chaetognaths *Sagitta* spp., Crus: non-identified crustaceans, Cepha: cephalopoda, Deca: non-identified decapods, Euph: euphausiids, Mis: misidaceans, Ost: ostracods, *Pp*: *Peisos petrunkevitchi*, Tel: teleostei.

**Figure 5.** Boxplot of Levins' standardized index in three size groups (mm) of *Trachurus lathami*. Horizontal lines indicate medians, the boxes extend to the 25 and 75 percentiles respectively, and the whiskers extend to the 5% and 95% quantiles. Outliers are indicated with circles.

## SIGNIFICANCE STATEMENT

*Trachurus lathami* is a key pelagic fish species in the Argentinean Continental Shelf (ACS), as prey of bony and elasmobranch fishes, and marine mammals. It shares the food web with commercial small pelagic zooplanktivorous species (*Engraulis anchoita* and *Scomber colias*), linking lower and upper trophic levels. Updated trophic information of this species is relevant to understand its role within the bottom-up (zooplankton eater) and top-down (prey for top predators) control mechanisms in the ACS ecosystem.

**Table 1.** Details of the samplings performed in the North Patagonian shelf in January-February 2016 where rough scad *Trachurus lathami* were collected. *L*: total length, n: number of stomach contents analyzed per sampling station. Mean and standard deviation (SD) values for each *L*-range in every station are presented.

| Station | Ship           | Date     | n  | <i>L</i> -range (mm) |             |             |
|---------|----------------|----------|----|----------------------|-------------|-------------|
|         |                |          |    | 160-190              | 191-220     | 221-230     |
| 33      | Misal          | 03-03-16 | 40 | 185.0 ± 2.8          | 206.2 ± 9.9 | 226.7 ± 1.6 |
| 212     | Misal          | 02-21-16 | 13 |                      | 207.3 ± 8.6 | 223.5 ± 0.7 |
| -       | Non-identified | 02-10-16 | 21 | 188                  | 201.4 ± 5.6 |             |
| 6       | Don Oscar      | 02-23-16 | 18 |                      | 207.4 ± 6.9 |             |
| 4       | Don Oscar      | 02-21-16 | 20 |                      | 209.2 ± 4.6 |             |
| 3       | Don Oscar      | 02-17-16 | 10 | 180.5 ± 6.4          | 198.8 ± 2.2 |             |
| 3a      | Don Oscar      | 02-25-16 | 35 |                      | 206.6 ± 5.9 | 225         |
| 3b      | Don Oscar      | 03-06-16 | 10 |                      | 203.9 ± 7.9 |             |
| 3c      | Don Oscar      | 02-21-16 | 4  |                      | 217.5 ± 1.3 |             |
| 1       | Pachaca        | 02-08-16 | 36 | 176.3 ± 9.0          | 199.5 ± 4.7 |             |
| 1a      | Pachaca        | 02-09-16 | 31 | 185.0 ± 2.6          | 204.7 ± 6.2 | 222.0 ± 0.0 |

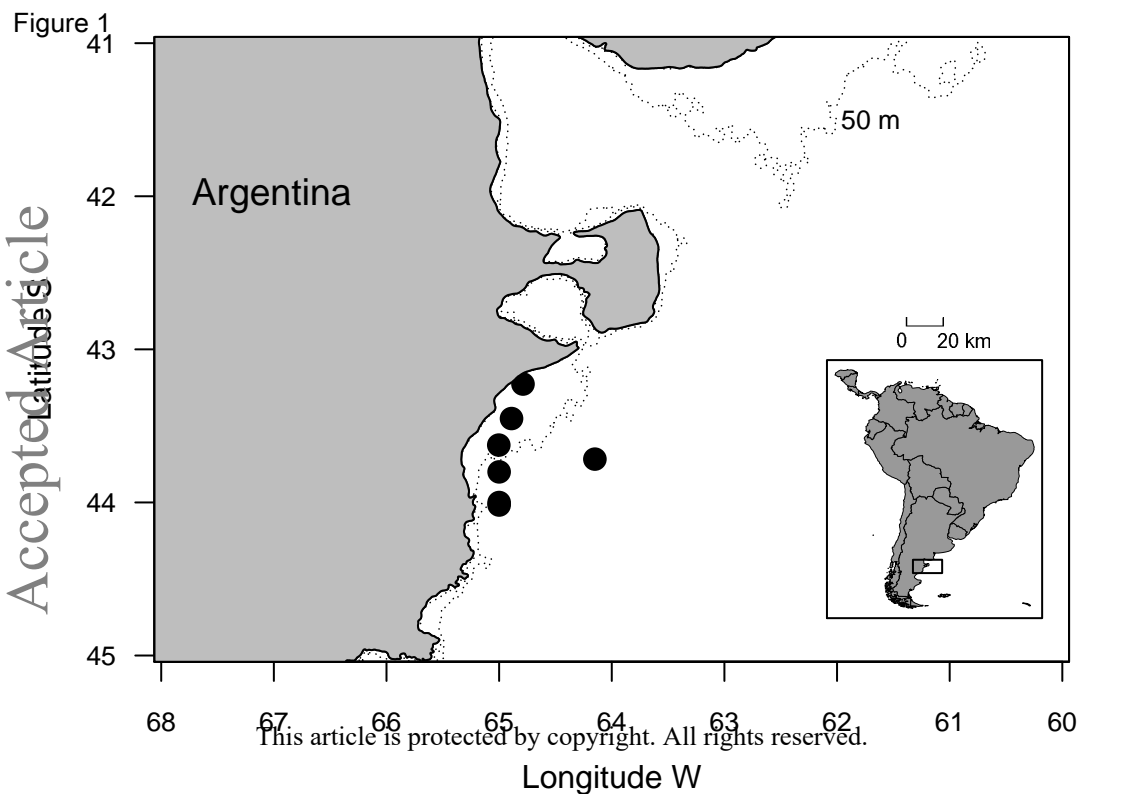
**Table 2.** Diet composition of rough scad *Trachurus lathami* in the North Patagonian shelf presented as frequency of occurrence (%O<sub>i</sub>), percentage in number (%N<sub>i</sub>), and relative importance expressed as a percentage (%RI).

| Prey item (i)                   | %O <sub>i</sub> | %N <sub>i</sub> | %RI    |
|---------------------------------|-----------------|-----------------|--------|
| CRUSTACEA                       |                 |                 |        |
| Copepods (Family Calanidae)     | 22.52           | 34.41           | 56.48  |
| Amphipods                       | 5.11            | 0.50            | 0.19   |
| Euphausiids                     | 4.20            | 1.33            | 0.41   |
| Misidaceans                     | 6.61            | 1.47            | 0.71   |
| Ostracods                       | 1.20            | 0.19            | 0.02   |
| <i>Peisos petrunkevitchi</i>    | 7.81            | 22.36           | 12.72  |
| Non-identified decapods         | 15.32           | 2.52            | 2.81   |
| Non-identified crustaceans      | 16.52           | 1.11            | 1.34   |
| CHAETOGNATHA                    |                 |                 |        |
| <i>Sagitta</i> spp.             | 9.61            | 35.42           | 24.80  |
| CEPHALOPODA                     |                 |                 |        |
| Non-identified larvae and beaks | 0.30            | 0.01            | < 0.01 |
| TELEOSTEI                       |                 |                 |        |
| Non-identified eggs and larvae  | 10.81           | 0.68            | 0.54   |

**Table 3.** Performance of zero-inflated models fitted between number of prey categories and the explanatory variables for rough scad *Trachurus lathami*. *L*: total length; AIC: Akaike information criterion;  $\Delta_i$ : difference in AIC; *w*: AIC weights; \*Null model. The bold denotes the best model for each prey.

| Prey item                    | Explanatory variables           | AIC           | $\Delta_i$ | <i>w</i>    |
|------------------------------|---------------------------------|---------------|------------|-------------|
| Copepods (Calanidae)         | <i>L</i>                        | 956.31        | 7.40       | 0.02        |
|                              | <b><i>L + L<sup>2</sup></i></b> | <b>948.91</b> | <b>0</b>   | <b>0.93</b> |
|                              | 1*                              | 954.65        | 5.74       | 0.05        |
| Misidaceans                  | <i>L</i>                        | 239.95        | 7.77       | 0.02        |
|                              | <b><i>L + L<sup>2</sup></i></b> | <b>232.18</b> | <b>0</b>   | <b>0.98</b> |
|                              | 1*                              | 255.90        | 23.72      | < 0.01      |
| <i>Peisos petrunkevitchi</i> | <i>L</i>                        | 414.46        | 2.52       | 0.22        |
|                              | <b><i>L + L<sup>2</sup></i></b> | <b>411.94</b> | <b>0</b>   | <b>0.78</b> |
|                              | 1*                              | 431.35        | 19.41      | < 0.01      |
| Non-identified decapods      | <b><i>L</i></b>                 | <b>423.24</b> | <b>0</b>   | <b>0.87</b> |
|                              | <i>L + L<sup>2</sup></i>        | 427.12        | 3.88       | 0.13        |
|                              | 1*                              | 438.61        | 15.37      | < 0.01      |
| <i>Sagitta</i> spp.          | <i>L</i>                        | 536.25        | 5.56       | 0.06        |
|                              | <b><i>L + L<sup>2</sup></i></b> | <b>530.69</b> | <b>0</b>   | <b>0.90</b> |
|                              | 1*                              | 536.85        | 6.16       | 0.04        |
| Non-identified teleostei     | <b><i>L</i></b>                 | <b>257.79</b> | <b>0</b>   | <b>0.70</b> |
|                              | <i>L + L<sup>2</sup></i>        | 259.69        | 1.90       | 0.27        |
|                              | 1*                              | 264.42        | 6.63       | 0.03        |





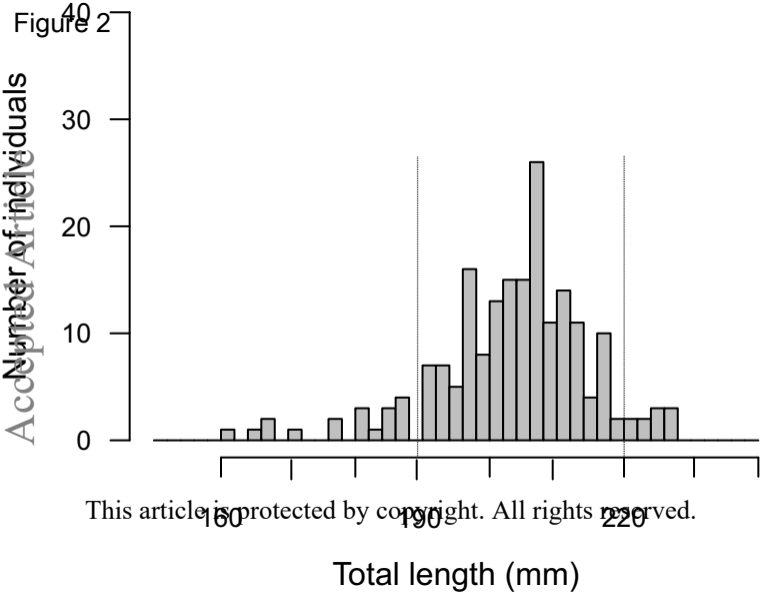
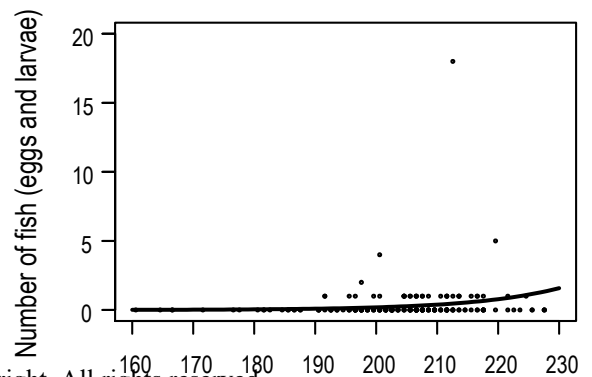
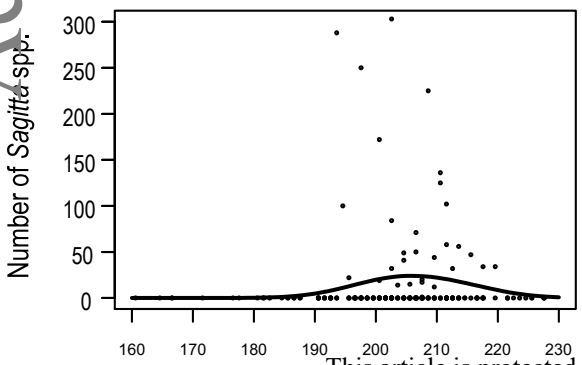
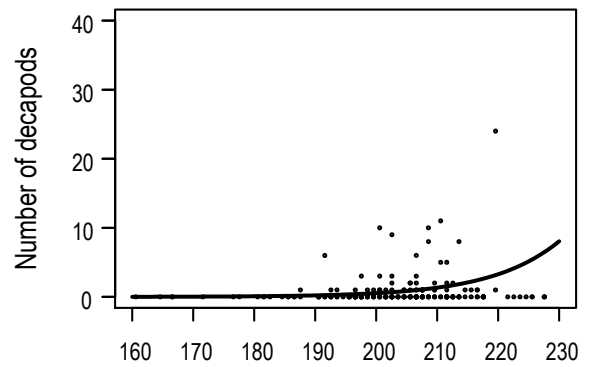
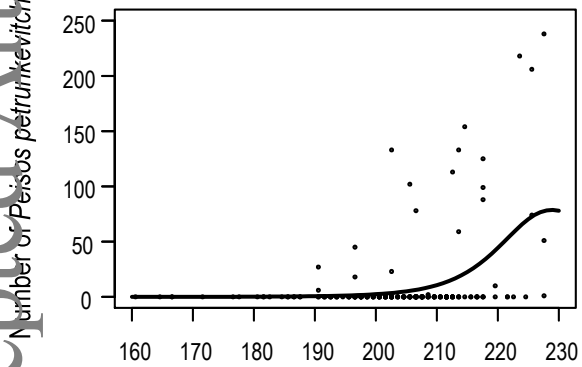
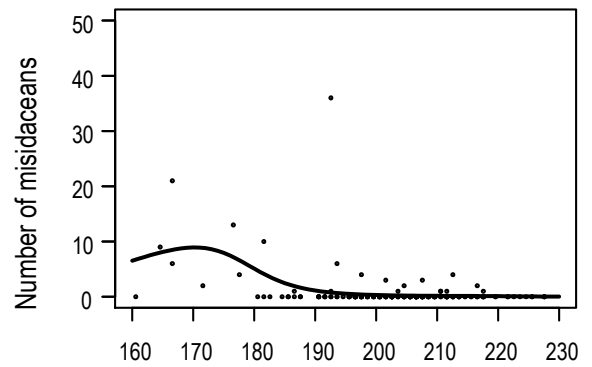
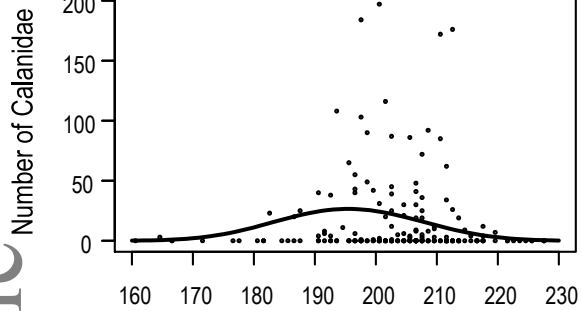


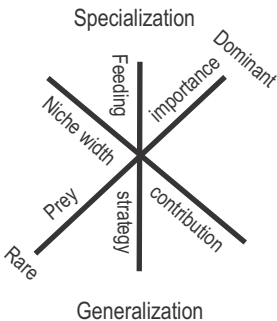
Figure 3



Total length (mm)

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Total length (mm)



&gt; WPC

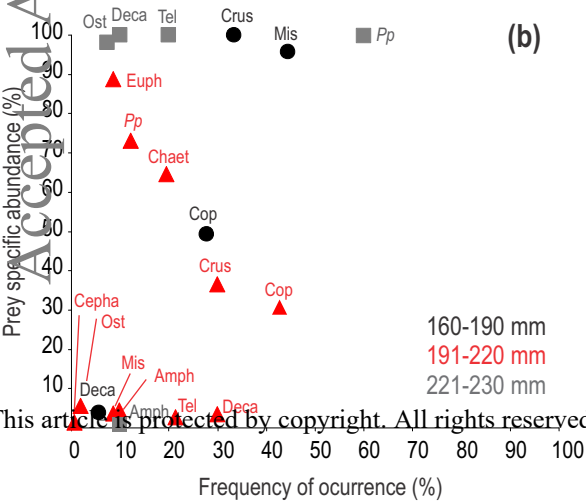
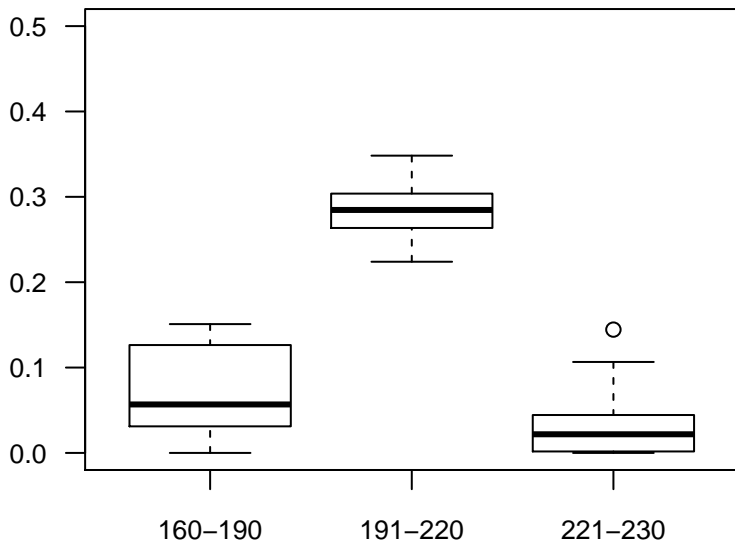


Figure 5



Size groups (mm)

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