ORIGINAL PAPER

Diet and prey preferences of larval and pelagic juvenile Faroe Plateau cod (*Gadus morhua*)

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Abstract

The availability of suitable prey during the early life of fish may determine recruitment to the adult population. Since larval and juvenile feeding can be highly selective, their preferences for certain prey species and sizes should be considered when estimating the availability of prey. In this study, diet composition (and prey preferences) of 4984 (1366) Faroe Plateau cod (*Gadus morhua*) larvae and juveniles between 3 and 63 mm sampled on the central Faroe shelf (62°N, 6.8°W) over an 8-year period was investigated. Cod preyed on successively larger food items as they grew. Yolk-sac larvae consumed phytoplankton, copepod eggs and nauplii before the yolk sac was exhausted. Copepod eggs followed by calanoid nauplii were the predominant and preferred food items in the early larval stage. In the late larval stage these were replaced by small to medium sized (0.6–1.2 mm) copepod species mainly *Pseudocalanus* sp., *Acartia* sp. and early stage *Calanus finmarchicus*, of which the two former species appeared most preferred. *Temora longicornis* was highly abundant in juvenile cod, but the preference for this species was neutral. Positive selection and high abundance of late stage (≥ 1.5 mm) *C. finmarchicus* was observed in early juveniles, but *C. finmarchicus* was replaced by decapod larvae in late juveniles. Other abundant prey species such as *Oithona* sp. and barnacle larvae occurred in varying numbers in the guts, but were generally not positively selected at any stage. Late larval and early juvenile cod appeared to suffer from unfavourable feeding conditions as they fed on smaller prey than what they prefer potentially indicating bottle necks in the feeding at these development stages.

Introduction

Changes in fish populations are largely driven by variability in recruitment, and fluctuations in recruitment are widely believed to be determined during the early life stages. Although recruitment may be affected by many factors during the early life stages, food availability is often considered to be a key factor affecting growth and survival of fish larvae (Hjort 1914; Anderson 1988; Cushing 1990; Leggett and Deblois 1994). Hence, much research on the feeding

ecology of the early life stages of fish has been initiated in a pursuit to identify potential relationships and causes for the variability in recruitment. In cod (*Gadus morhua*), early studies focused on the prey abundance and timing of prey production in order to explain the variability, but more recent studies have highlighted the importance of prey quality e.g. species and size composition (e.g. Beaugrand et al. 2003; Robert et al. 2011; Swalethorp et al. 2014).

The early life stages of cod are very opportunistic and adaptive in relation to variability in prey abundance, species composition and size distribution (Heath and Lough 2007), although gape size is a major constraint (Munk 1997). Moreover, larvae reared on only one size class of prey eventually grow to a point where the metabolic cost of search and capture exceeds the calorific value of individual prey items, and growth and survival are hence compromised (Folkvord et al. 1994). Therefore, to optimize energy input cod larvae and juveniles undergo a gradual shift in selecting progressively larger prey during ontogeny. The general feeding pattern of pelagic cod through ontogenetic development is: copepod eggs→calanoid nauplii→copepods→malacostraca (Heath

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and Lough 2007) (Fig. 1). However, some prey items are clearly preferred over others both with respect to species and size (e.g. Beaugrand et al. 2003; Buckley and Durbin 2006). Munk (1997) found larval and pelagic cod juveniles to prefer prey about 5% their own size. Yet, large prey often have better predator avoidance capabilities than small prey, and thus at some point metabolic cost can supersede the energy return from pursuing increasingly larger prey. Consequently, especially at low prey abundances cod may predate on less preferred prey that are more easily attainable (Seljeset et al. 2010). A lack of specific prey sizes and prey types may compromise growth and survival at any point during the early development of a cohort of cod. For North Sea juvenile cod a significant decrease in the mean size of prey together with changed seasonal timing and abundance of key prey has likely contributed to a reduction in growth, survival and recruitment to the adult population (Beaugrand et al. 2003). As prey abundances vary in time and space, an assessment of the general diet and prey selectivity is essential for improved understanding of the early life history of cod.
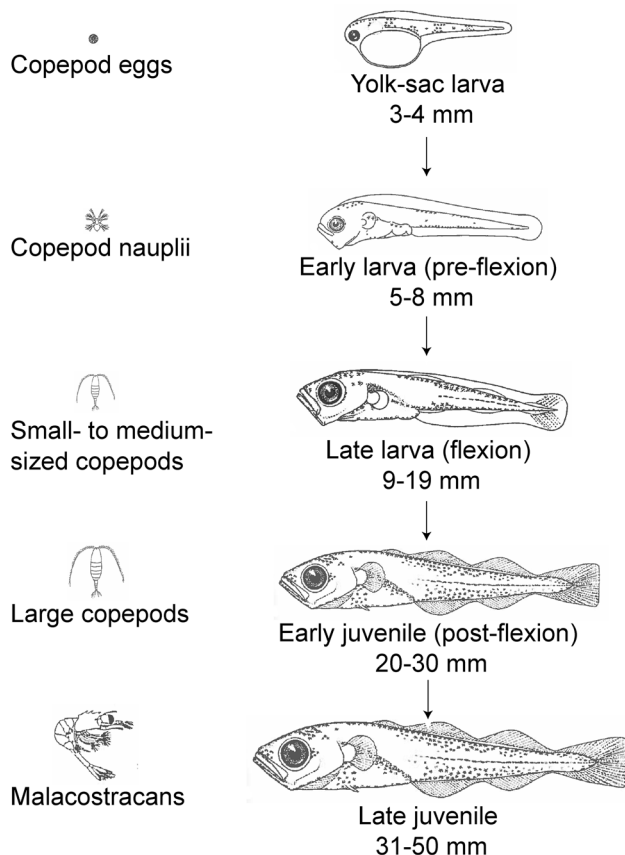

Fig. 1 Simplified schematic representation of prey for pelagic cod during ontogenetic development. Illustrations of zooplankton and cod are from Castellani and Edwards (2017) and Munk and Nielsen (2005), respectively

Faroe Plateau cod is historically the most important commercial fish species on the Faroe shelf. Assessments based on annual surveys have revealed large inter-annual variations in the recruitment of age 2 cod (Steingrund et al. 2010), which partly appears to be determined at the pelagic larval stage (Jákupsstovu and Reinert 1994; Steingrund et al. 2010). A few studies have examined the feeding of larval and pelagic cod on the Faroe shelf (Gaard and Steingrund 2001; Gaard and Reinert 2002); however, main questions such as prey species and prey size preferences of the Faroe Plateau cod remain largely unresolved.

In the present study, detailed information is presented from a comprehensive dataset on the diet composition and prey selection at different length-classes of cod larvae and juveniles on the Faroe shelf. The study is based on material sampled during the years 1998–2005 on two recurrent cruises covering the shelf: one placed in the last week of April and the other placed in the second half of June. The aim of the study was to explore the general feeding ecology of larval and pelagic juvenile cod on the Faroe shelf including prey size and prey species preferences and to identify main prey items in terms of mass and abundance. We hypothesize that the diet composition and prey preferences change with ontogeny in the larvae and pelagic juveniles and that specific prey species and sizes are preferred and hence are more important than others. Finally, we discuss whether feeding conditions during the larval and pelagic juvenile stage potentially influence the annual variability in Faroe Plateau cod 0-group abundance indices.

Materials and methods

Data collection

The samples were collected with R/V Magnus Heinason on annual standard cruises during the last week of April (hereafter termed April) 1998–2005 (except 2002) and the second half of June (hereafter termed June) 2000–2005 on the Faroe shelf (Fig. 2, Table 1). Sampling was carried out between 6:30 and 18:30. The sampling area covered the whole central shelf inside the 130 m bottom depth contour i.e. inside the shelf front (Larsen et al. 2009) (Table 1). As the sampling area is very well mixed (Larsen et al. 2008), the distribution of plankton is expected to be quite homogenous horizontally and vertically (Eliasen et al. 2017) and not markedly influenced by diel vertical migration.

In April, zooplankton, including ichthyoplankton, samples were collected with a Bongo net (diameter 0.6 m) with a mesh size of 100 μm. The net was lowered slowly down to 50 m depth and up again, while the ship was towing at a forward speed of about 1.3 m s^{-1}. Thus, the samples were collected as double oblique net hauls in the upper
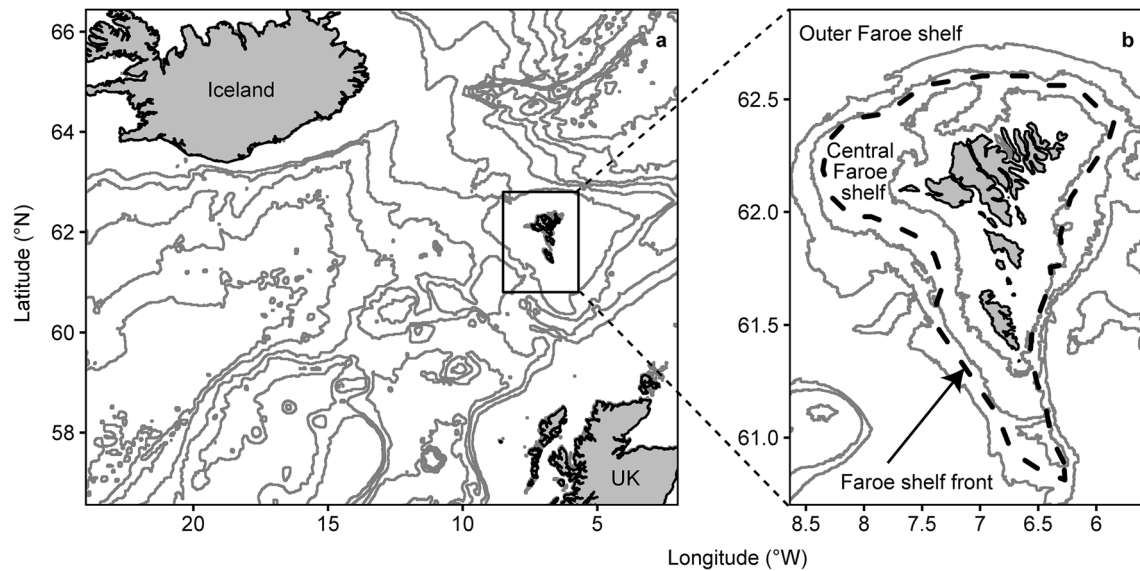
Fig. 2 **a** Map of the research area with bathymetry (from Pante and Simon-Bouhet 2013) and **b** the Faroe shelf with bathymetry (100, 150 and 200 m) and the average position of the shelf front (dashed line) (Larsen et al. 2009). All samples discussed in the text were collected inside the dashed line i.e. in the central Faroe shelf

Table 1 Sampling dates and data collection summary

Sampling dates	No. of fish	No. of trawl stations	No. of zooplankton stations	Average depth (m)	Min. depth (m)	Max. depth (m)
April 17–24, 1998	1035	22	7	92	49	117
April 23–27, 1999	481	15	6	100	84	118
April 28–30, 2000	185	7	6	97	76	115
June 23–30, 2000	248	18	11	91	68	124
April 20–22, 2001	520	13	5	94	60	116
June 22–28, 2001	171	11	7	85	73	120
June 21–29, 2002	265	18	9	93	63	125
April 25–28, 2003	321	8	6	99	80	122
June 21–26, 2003	213	14	12	88	63	125
April 20–26, 2004	372	19	6	95	58	122
June 18–25, 2004	217	11	13	90	71	116
April 15–25, 2005	720	24	20	96	62	128
June 24–July 2, 2005	236	20	12	92	63	125

50 m. The volume of the filtered water was measured with a Hydro-Bios flow meter mounted on the nets openings. The samples were preserved in 4% formaldehyde.

In June, zooplankton was collected with vertical hauls from 50 m depth to the surface. A WP-2 ring net with a mesh size of 200 μm was used and the towing speed was 0.3–0.5 m s^{-1}. Fish larvae/juveniles were collected with a pelagic trawl with 5 mm mesh size and a mouth opening of about 8 m (horizontally) times 4–5 m (vertically). The trawling depth was approximately 30–40 m; the exact depth chosen was based on the recordings on the echo-sounder. The towing speed was 1.5 m s^{-1} and the duration of each haul was 30 min.

Sample handling

Zooplankton samples were rinsed of formaldehyde and split with a Motoda splitter until a subsample of at least 200 individuals were left for identification, enumeration and length measurement. For copepodites, prosome length was measured, while for decapod larvae, barnacle larvae (mainly nauplii) and calanoid nauplii carapace length was

measured. Dry weight of the zooplankton was estimated based on length–weight relationships derived from the literature (Table 2).

A random subset of cod larvae and juveniles were standard length measured to the nearest mm. No correction for shrinkage due to fixation and preservation was made. Guts of the larvae were dissected with surgical needles and content was identified to the lowest taxonomic level possible and measured to the nearest 0.05 mm. As for the zooplankton, the dry weight of prey items from the gut content was calculated from length–weight keys (Table 2). Thus, the prey weights are calculated weights when they were ingested rather than the weights of the actual gut or stomach content. In total, 4984 guts were analysed (Table 1).

Data processing

For comparison of diet, cod were divided into 2 mm right-hand closed length classes (Fig. 3). Zooplankton and gut content data was reduced to 11 of the most common prey

groups (Table 2), which both in terms of abundance and dry weight occupied > 90% of the total gut content.

To evaluate the importance of the food items we applied the index of relative importance (IRI) (Pinkas et al. 1971):

$$IRI = (\%N + \%V)\%F$$

where N = numeric frequency of prey, V = weight frequency of prey and F = percentage occurrence in the gut.

Selectivity analysis on prey species selection was done for 10 of the most common prey groups (everything in Table 2 aside from fish larvae), while selectivity analysis on prey lengths included the same 10 prey groups sorted into 13 right-hand closed length classes as follows: lengths 0.1–0.6 mm: 0.1 mm intervals, 0.6–1.2 mm: 0.2 mm intervals, 1.2–2 mm: 0.4 mm intervals, 2–3 mm: 0.5 mm intervals and 4–5 mm: 1 mm interval.

Chesson's selectivity index (Chesson 1978) was employed to analyse selectivity:

$$\alpha_i = (r_i/p_i)/\Sigma(r_i/p_i), \quad i = [1, 2, \dots, m]$$

Table 2 Length to dry weight conversion table for the 10 most common zooplankton species/groups found in the study

| Group/species	Equation	Unit weight	Unit length	References
Copepod eggs	DW = 0.460 μg ind^{-1}	μg		Hirche et al. (2001)
Calanoid nauplii	DW = 0.0173L^2.27	mg	mm	Hay et al. (1991)
Barnacle larvae	log DW = 3.773(log L) − 9.455	μg	μm	Uye (1982)
Oithona sp.	DW = 2.034 μg ind^{-1}	μg		Hay et al. (1991)
Acartia sp.	DW = 0.0152L^2.97	mg	mm	Hay et al. (1991)
Pseudocalanus sp.	DW = 0.0190L^2.73	mg	mm	Hay et al. (1991)
Temora longicornis	DW = 0.0313L^3.06	mg	mm	Hay et al. (1991)
Calanus finmarchicus	DW = 0.0154L^2.71	mg	mm	Hay et al. (1991)
Decapod larvae	Log DW = − 0.963 + 2.59 × log(CL)	mg	mm	Lindley (1988)
Fish larvae	DW = 0.0013L^2.9856	mg	mm	Gaard, pers meas
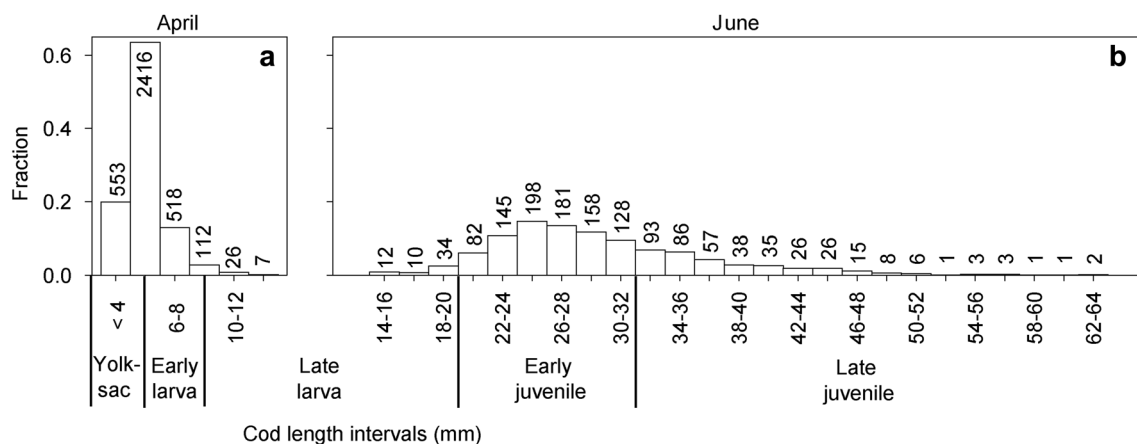
Fig. 3 Length histogram of larvae and juvenile cod selected for gut analysis in **a** April and **b** June during the years 1998–2005 together with number of observations. Vertical black lines indicate shifts in cod larvae development stages (Munk and Nielsen 2005)

with r_i = the proportion of food type i in the diet and p_i = the proportion of food type i in the environment and m = the number of food types in the environment. Selectivity values were then converted to electivity values according to Chesson (1983):

$$e_i = (m\alpha_i - 1)/[(m-2)\alpha_i + 1], \quad i = [1, 2, \ldots, m].$$

The electivity index ranges from -1 to $+1$ with a value of 0 representing neutral preference. -1 indicates complete avoidance while $+1$ indicates total preference. Only prey items within the size range accessible to the cod larvae (< gape size) were included in the analysis. Gape size was calculated from length-gape size relationships found in Rowlands et al. (2006).

The selectivity analysis was only done on cod sampled at stations where corresponding zooplankton data was available (Table 1). Fish with empty guts were not included in the analysis. In total, the selectivity analysis was based on gut data from 1366 cod larvae and juveniles (Table 3).

Table 3 Number of cod larvae and juveniles used in the selectivity analysis sorted by length in April and June, respectively

Fish length (mm)	No. of larvae in the preference analysis	
	April	June
<4	57	–
4–6	665	–
6–8	181	–
8–10	44	–
10–12	10	–
12–14	–	–
14–16	–	–
16–18	–	–
18–20	1	5
20–22	–	14
22–24	–	41
24–26	–	78
26–28	–	76
28–30	–	67
30–32	–	49
32–34	–	35
34–36	–	17
36–38	–	17
38–40	–	5
40–42	–	1
42–44	–	2
44–46	–	0
46–48	–	1
Total	958	408

Statistical tests were performed using R (R Core Team 2018). When comparing preference values with mean values, the Welch two sample t test was used. Variations in preference values were fitted using a general linear model calling the function lm using R, with cod length as covariate, to test effects of prey length, prey species and the interaction of these two factors. P-values of 0.05 or lower were considered statistically significant.

Results

Cod length

The majority of larvae caught in April were < 10 mm (Fig. 3). Cod eggs were also observed on a regular basis, but these were not counted. The length distribution of cod in April was skewed to the left, with most fish in the length range 4–6 mm. The largest larva caught in April was 19 mm. In June the length ranged from 13 to 63 mm, although large inter-annual differences in mean length occurred (refer to Jacobsen et al. 2019).

Prey environment

The small plankton (< 0.2 mm) was dominated by copepod eggs (∼ 140 μm in diameter and thus presumably mainly *C. finmarchicus* eggs). Calanoid and barnacle nauplii dominated in the length range 0.2–0.4 mm, while larger plankton was mainly composed of copepodites of different species. The most abundant copepods in the length range 0.4–1 mm were *Acartia* sp. followed by *Oithona* sp., *Pseudocalanus* sp. and *T. longicornis*. *C. finmarchicus* was numerous in the length range 1–3 mm and generally dominated the prey biomass together with decapod larvae (Fig. 4).

Diet composition

Overall, 4190 of the 4984 analyzed cod had food in their stomach.

Of the 3634 larvae caught in April 519 (∼ 14%) had yolk sac or yolk sac remnants. The amount of larvae with yolk sac decreased from 100% at a length of 3.2 mm to 0% at 4.7 mm (Fig. 5a). The number of empty guts in yolk-sac larvae decreased with increasing length (Fig. 5b). Cod larvae started feeding at a length of 3.3 mm (Fig. 5b). Small unidentified particles of phytoplankton origin, approximately 30 μm in diameter, occurred quite frequently in the guts of small larvae, but due to their small size and fragile structure their occurrence was only noted as present or non-present (Fig. 5b). Phytoplankton was almost completely absent in larvae > 6 mm. Occurrence of copepod eggs and calanoid nauplii increased with increasing length of the larvae with
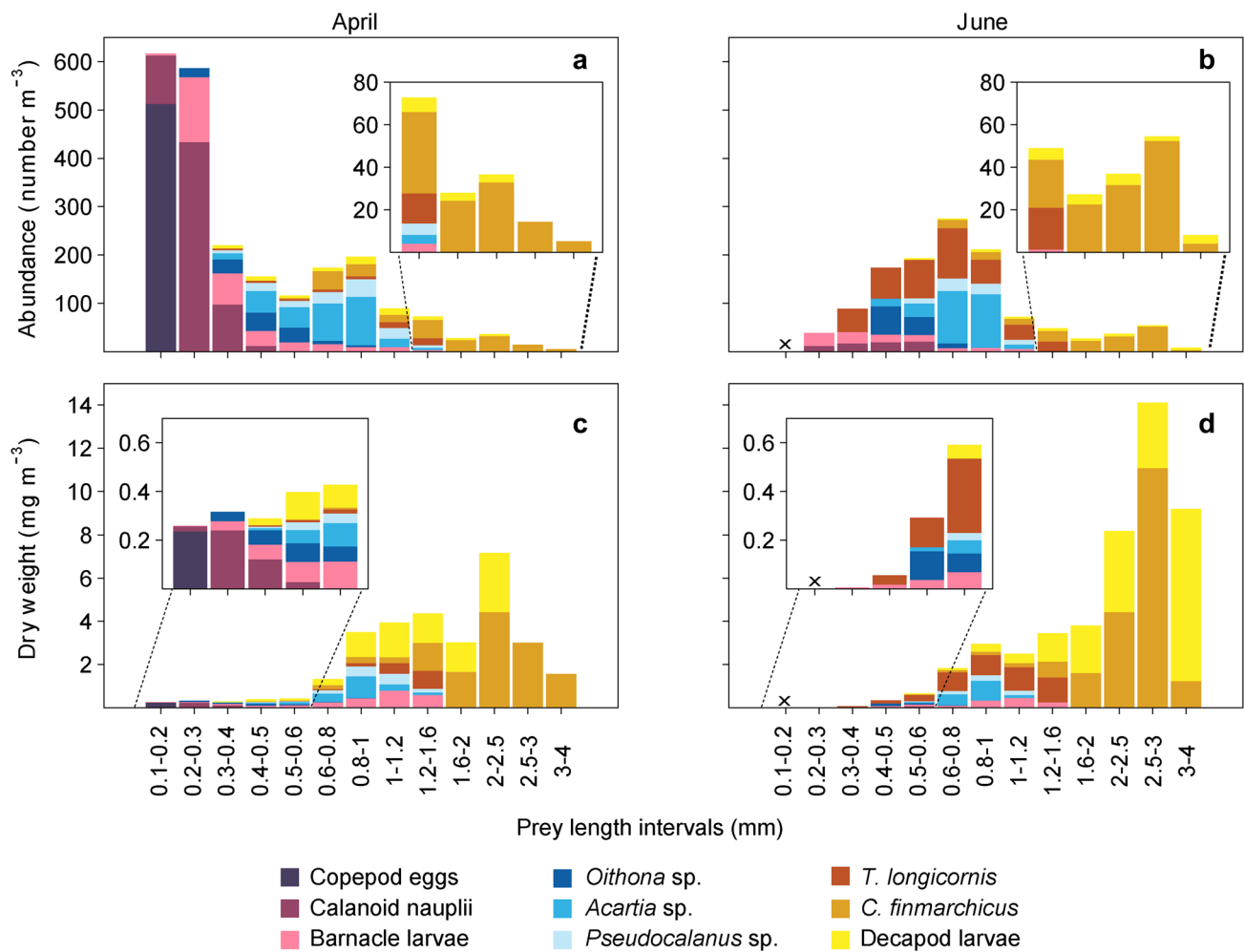
Fig. 4 Mean prey in situ abundance (**a**, **b**) and dry weight (**c**, **d**) in length intervals (see Materials and methods) on the Faroe shelf in April (100-μm Bongo net) and June (200-μm WP-2 net), respectively
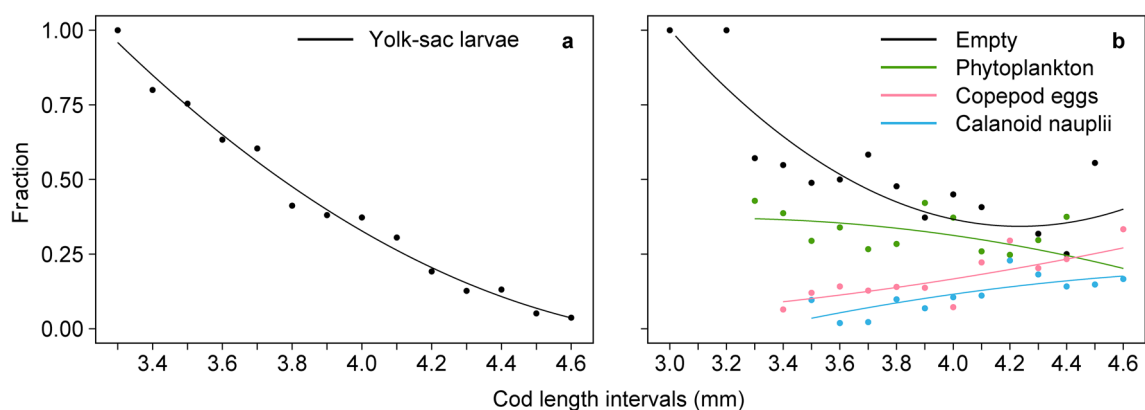

Fig. 5 **a** Fraction of yolk-sac larvae in relation to cod larval length and **b** occurrence of empty guts, phytoplankton, copepod eggs and calanoid nauplii in the diet of yolk-sac larvae in late April. The points show mean values at 0.1 mm intervals and the lines are best fit lines. $n = 519$
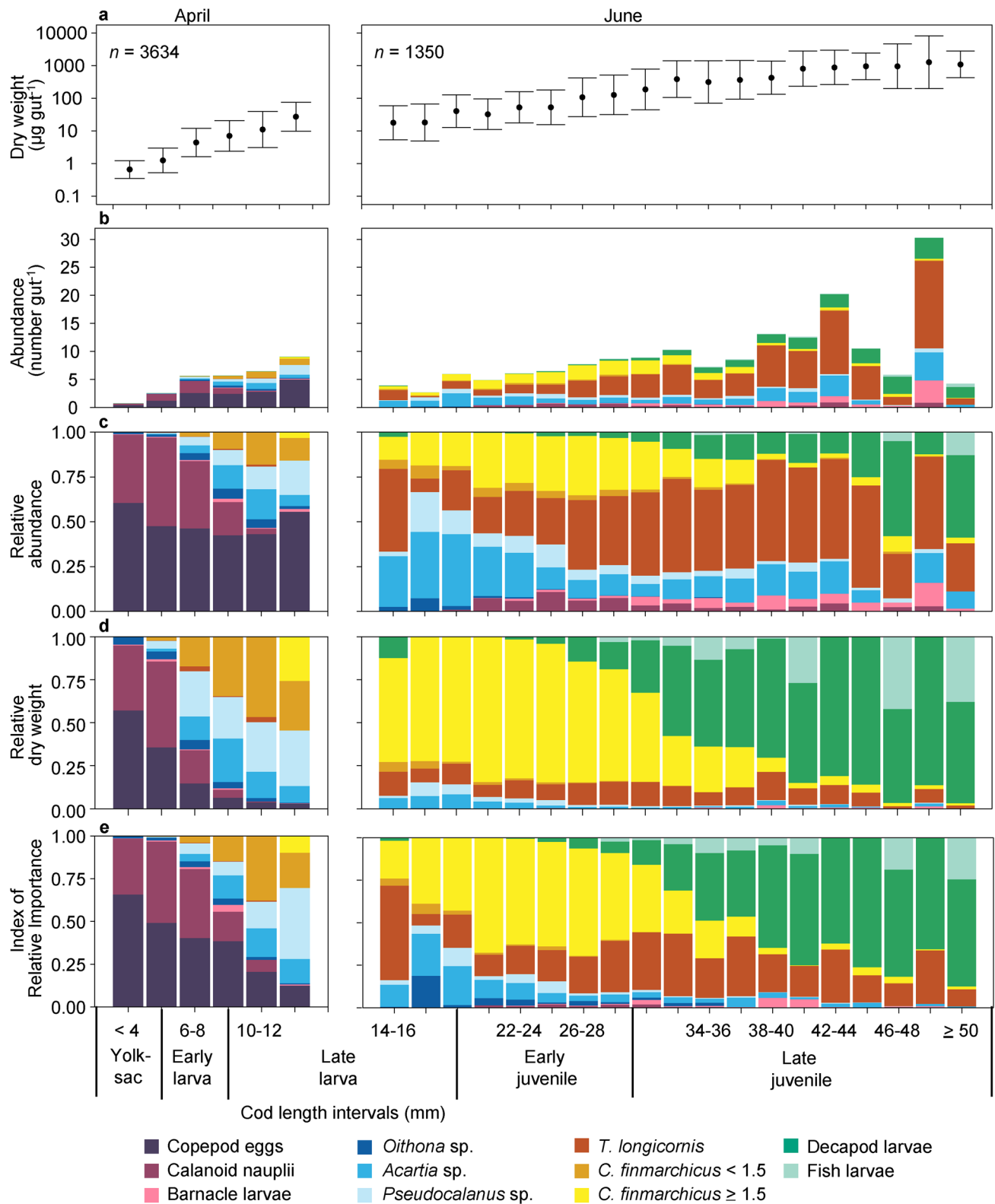
Fig. 6 Overall mean of **a** prey dry weight with standard deviation (note that the *y*-axis is log scaled) and **b** prey abundance and relative diet composition by **c** abundance **d** dry weight and **e** index of relative importance. Vertical black lines indicate shifts in cod larvae development stages (refer to Fig. 3)
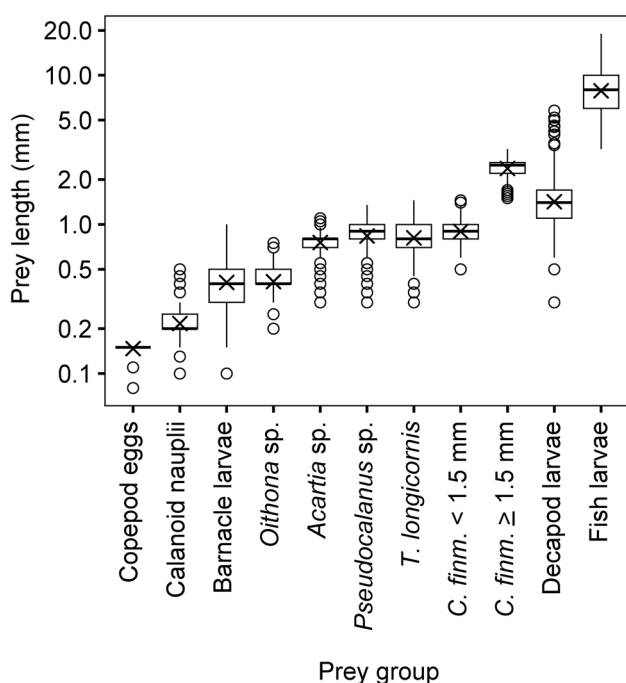
Fig. 7 Box plot of prey sizes in the guts of cod larvae and juveniles sorted by prey group. The line in the middle of the boxes represents the median, and the left and right ends of the box are the 25 and 75% quartiles respectively. The left and right whiskers are constructed according to R's default box plot code (R Core Team 2018). Open circles (o) are outliers and the crosses (x) indicate mean lengths. Note that the *y*-axis is log scaled

yolk sac remnants (Fig. 5b). Other small prey objects found less frequently in the guts of the first feeding cod larvae were small diatoms, protozoans (e.g. ciliates), foraminifers and eggs from other invertebrates.

The mean weight of prey per gut increased with increasing cod length (Fig. 6a). The mean number of prey per gut showed the same tendency, but stagnation and even drops in mean number of prey per gut were observed at lengths of about 8, 20 and 32 mm (Fig. 6b) paralleling ontogenetic shifts in cod stage development (Fig. 1) and corresponding to major changes in prey species consumption i.e. shifts from copepod eggs and calanoid nauplii to small and medium-sized copepods (i.e. < 1.5 mm) to late stage (i.e. ≥ 1.5 mm) *C. finmarchicus* copepodites and finally decapod larvae (Fig. 6c–e).

The size of the different prey groups is shown in Fig. 7. The abundance of copepod eggs ~ 0.15 mm in diameter, and thus presumably mainly *C. finmarchicus* eggs, increased with increasing larval length in all larvae observed in April (Fig. 6b). However, the relative contribution of copepod egg mass to the diet decreased from > 50 to < 10% from the yolk-sac stage to the end of the early larval stage (Fig. 6d). The relative importance of copepod eggs was > 50% in yolk-sac larvae and > 30% in early stage larvae (Fig. 6e). The

presence of calanoid nauplii with a mean carapace length of ~ 0.2 mm was high in the guts of yolk-sac and early stage larvae, and dominated the prey mass in larvae 4–6 mm (Fig. 6c, d). Overall, the relative importance of calanoid nauplii in yolk-sac and early stage larvae was slightly lower than the relative importance of eggs (Fig. 6e). Barnacle larvae ~ 0.3 mm and *Oithona* sp. ~ 0.4 mm were present, but not very abundant and/or important in the guts of yolk-sac and early stage larvae. A shift towards larger prey items, mainly *Acartia* sp., early stage (i.e. < 1.5 mm) *C. finmarchicus* and *Pseudocalanus* sp. copepodites with a prosome length of approximately 0.6–1.2 mm, was observed during the transition from early larvae to the late larvae stage. *Acartia* sp. and *Pseudocalanus* sp. were present in relatively high numbers throughout the late larvae, early and late pelagic juvenile stages (Fig. 6c). The mean prey mass of *Acartia* sp. and *Pseudocalanus* sp. was particularly high (i.e. 40–50%) in late stage larvae collected in April (Fig. 6d). Their relative importance was highest i.e. > 50% in late larvae 12–14 mm (Fig. 6e), while their importance was ~ 30% in late larvae collected in June. *T. longicornis* ~ 0.8 mm in length was highly abundant in all cod collected in June, but was rarely observed in April (Fig. 6c). The mean relative importance of *T. longicornis* was approximately 20% in all cod collected in June. *C. finmarchicus* copepodites were observed in larvae as small as 5 mm. The mean abundance of *C. finmarchicus* increased in the fish up to the late juvenile stage and then decreased again (Fig. 6b). While the larvae caught in April almost exclusively consumed early stage (i.e. < 1.5 mm) *C. finmarchicus* copepodites, ~ 85% of the *C. finmarchicus* observed in cod juveniles in June were late stage copepodites (i.e. ≥ 1.5 mm) with a mean length of 2.5 mm. The relative abundance of *C. finmarchicus* was highest during the early juvenile stage (~ 30%) (Fig. 6c), while the relative mean dry weight increased steadily from ~ 15% in early stage cod larvae to > 80% in early juveniles before declining again (Fig. 6d). Late stage *C. finmarchicus* were the most important prey item for early juvenile cod (Fig. 6e). Decapod larvae with a mean carapace length of 1.5 mm (mainly zoeae in the infraorders Anomura, Brachyura and Caridea) started appearing in the guts during the early juvenile period and dominated the prey biomass in late juveniles (Fig. 6d). Decapod larvae were the most important prey item for late juvenile cod (Fig. 6e). In addition, fish larvae (mainly gadoid) around 9 mm in length were observed on occasion in late juveniles (Fig. 6b–e).

Prey size preference

There was a clear tendency for prey preference towards larger sizes as the fish grew larger (Fig. 8a). Overall, the prey lengths of maximal preference was slightly higher
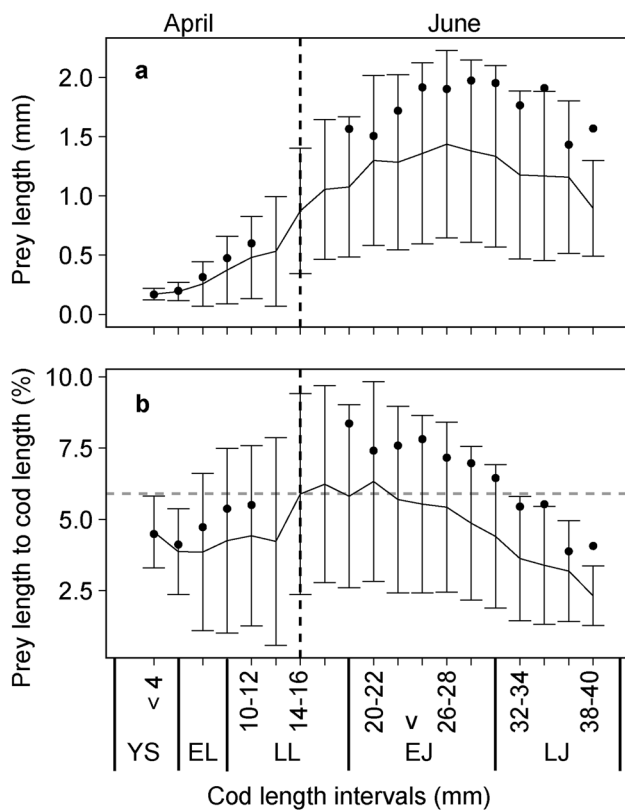
Fig. 8 Mean prey lengths with standard deviation ingested in relation to predator length and prey lengths of maximal preference (black dots (●)) (Chesson 1978). **a** Absolute values of prey lengths and **b** prey to predator length ratio (the horizontal grey dashed line indicates the overall preferred prey length relative to cod length). The vertical black dashed line separates samples collected in April ($n = 958$) from samples collected in June ($n = 408$). Vertical black lines indicate shifts in cod larvae development stages (*YS* yolk-sac, *EL* early larva, *LL* late larva, *EJ* early juvenile, *LJ* late juvenile) (refer to Fig. 3)

than the mean lengths of prey ingested (Fig. 8a) (Welch two sample *t* test, $t16 = 1.77$, $P = 0.09$). The variation in prey lengths ingested by larval and juvenile cod relative to cod length was highest in late larval and juvenile cod (Fig. 8b). The average preferred prey length relative to cod length generally increased throughout the larval phase before declining again during the juvenile phase (Fig. 8b). Overall, the preferred prey length relative to cod length was 5.9% (range 3.8–8.4%) (Fig. 8b). The overall mean prey length ingested relative to cod length was significantly smaller than the preferred prey length (Welch two sample *t* test, $t16 = 3.18$, $P < 0.01$).

Prey species preference

Yolk-sac and early larval cod had a positive preference for copepod eggs (Fig. 9a). Calanoid nauplii were also marginally positively selected in early larval cod (Fig. 9b), but to a lesser degree than copepod eggs. Barnacle larvae

and *Oithona* sp. were generally selected against during the whole larval and juvenile period (Fig. 9c, d). *Acartia* sp. and *Pseudocalanus* sp. were increasingly preferred starting at the early larval stage and seemingly throughout the late larval stage, but appeared less important for juvenile cod (Fig. 9e-f). Unfortunately no preference data was available for cod 12–18 mm. *T. longicornis* and early stage (i.e. < 1.5 mm) *C. finmarchicus* were not positively selected for at any cod length (Fig. 9g, h). However, early juvenile cod showed a clear positive preference for late stage (i.e. ≥ 1.5 mm) *C. finmarchicus* (Fig. 9i), while decapod larvae appeared highly preferred in late juvenile cod (Fig. 9j). Since the concentration of fish larvae was low in the net samples, no preference analysis was done for this prey group.

Preference for prey size and species

Some prey species were preferred over others, even when the prey were of the same length (e.g. *Pseudocalanus* sp. vs. *C. finmarchicus* in the length range 1–1.2 mm) (Fig. 10). In addition, for most copepod groups large individuals (i.e. late stage copepodites) were generally preferred over small individuals (i.e. early stage copepodites). Overall, preference values were significantly affected by prey species and by the interaction between prey length and prey species (Linear regression, $r^2 = 0.2$, $F20, 18,257 = 225.9$, $P < 0.001$) (Table 4).

Discussion

In this paper, feeding ecology of cod during the pelagic period on the Faroe shelf along with prey size and prey species preferences during ontogenetic development was investigated. Overall, the study showed that during the pelagic period cod larvae and juveniles successively feed on copepod eggs → calanoid nauplii → copepods → malacostraca (Fig. 6), and that the shifts in diet roughly correspond to major shifts in cod development (Fig. 1). Cod larvae and juveniles preferred prey about 4–8% of their own length (Fig. 8b). Thus, this study largely agrees with similar studies on the feeding ecology of cod larvae and pelagic juveniles in other areas of the North Atlantic (Kane 1984; Thorisson 1989; Fossum and Ellertsen 1994; Munk 1997; Rowlands et al. 2008; Robert et al. 2011; Swalethorp et al. 2014). The main results from the current study demonstrate that cod prefer increasingly larger prey as they grow (Fig. 8a), but that certain prey species are preferred over others (Fig. 9), even when the prey are of the same length (Fig. 10, Table 4). This suggests that other characteristics, such as prey body composition, behaviour or visibility affect their importance as prey. Furthermore, prey abundance appears to affect the
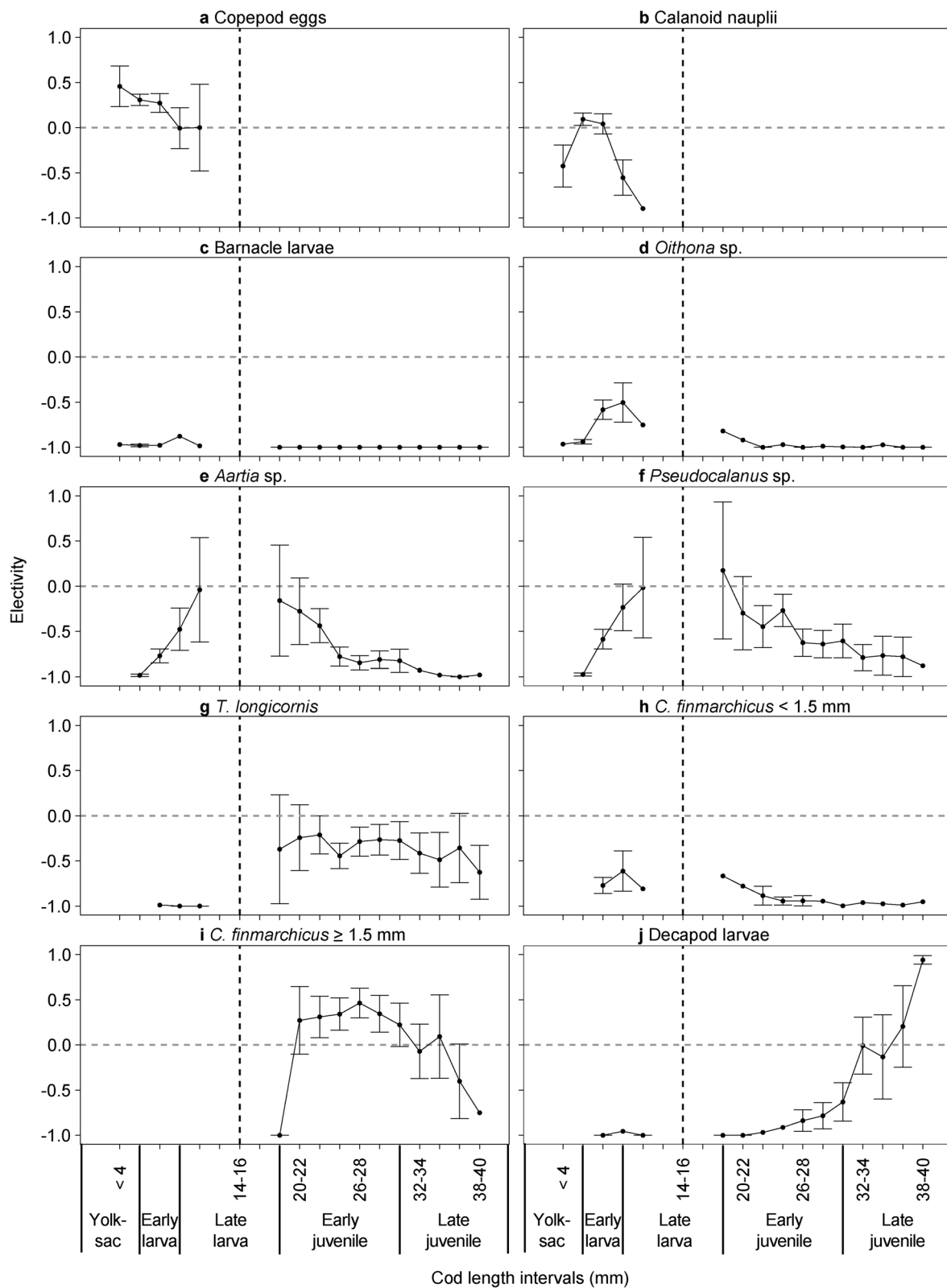
Fig. 9 Mean preference (Chesson 1983) expressed by electivity in comparison of 10 groups of prey during ontogenetic development of pelagic cod on the Faroe shelf. Error bars indicate 95% confidence intervals around the mean. The vertical black dashed line separates samples collected in April ($n = 958$) from samples collected in June ($n = 408$). Vertical black lines indicate shifts in cod larvae development stages (refer to Fig. 3)

feeding behaviour, but overall the preference of prey species changes with size and development of the predator. This is discussed below.

Yolk-sac and early larvae

In agreement with other studies, yolk-sac larvae captured prey before the yolk sac was exhausted and phytoplankton was quite abundant in the guts at the onset of first feeding, but was not present in larvae >6 mm (Fig. 5) (Kane 1984; Thompson and Harrop 1991; Fossum and Ellertsen 1994; Gaard and Steingrund 2001). While phytoplankton may provide a nutritional boost to the smallest larvae and improve first feeding capabilities (van der Meeren and Næss 1993; Overton et al. 2010), it remains unclear to which extent phytoplankton is important in the diet of cod larvae on the Faroe shelf. However, the increased occurrence of copepod eggs and calanoid nauplii among the yolk-sac larvae indicates that phytoplankton is not an adequate food source for larvae >4 mm (Fig. 5b).

Copepod eggs represented an essential part of the diet during the yolk-sac and early larval phase (Fig. 6). This is in agreement with another study on the first-feeding of Faroe Plateau cod (Gaard and Steingrund 2001), but stands in contrast with most studies from other areas who observe that copepod eggs are replaced by calanoid nauplii when the larvae are ~6 mm in length (Heath and Lough 2007 and references there in). The present observations indicate that there is a lack of other suitable prey (i.e. copepod nauplii) in the environment in April. Indeed, the comparison between prey length and cod length (Fig. 8a) suggests that this may be the case as early stage larvae on average consumed smaller prey than what they normally prefer. However, the prey species preference analysis suggests that copepod eggs are a highly preferred prey in all yolk-sac and early stage larvae (Fig. 9a). But note, that the preference analysis on copepod eggs might be biased towards positive selection as a proportion of eggs may pass through the 100 µm sampling net (Nichols and Thompson 1991). Calanoid nauplii, on the other hand, were only preferred in larvae 4–8 mm (Fig. 9b), and it appeared that nauplii in the length range 0.2–0.4 mm were more preferred than their smaller and larger kin, which may be due to nutritional and behavioural differences (Jung-Madsen et al. 2013; Swalethorp et al. 2014). Any which way, the high abundance of copepod eggs in yolk-sac and early stage cod larvae very likely make them an essential part of the Faroe Plateau cod larvae's diet.

The fecundity and abundance of the most common copepod species on the Faroe shelf are highly dependent on food availability (Debes et al. 2008a) i.e. the timing and intensity of the spring bloom, which rarely occurs prior to May (Debes et al. 2008b; Eliasen et al. 2017; Jacobsen et al. 2018). Hence, there is presumably a limited concentration of small prey available to cod larvae in late April. However, the copepod *C. finmarchicus* has a significant egg production fuelled by winter lipid reserves prior to the spring bloom in the Faroe shelf area (Gaard 2000; Debes et al. 2008a; Madsen et al. 2008). In fact, large-scale studies on the egg production of *C. finmarchicus* suggest that both the spring production and the spring abundance of spawning *C. finmarchicus* females is higher on the Faroe shelf than in several other adjacent areas (Richardson et al. 1999; Stenevik et al. 2007; Jónasdóttir et al. 2008). This indicates a higher abundance of copepod eggs in the Faroe area during spring compared with neighbouring areas, and may explain the relatively high proportion of copepod eggs in the guts of Faroe Plateau cod larvae in April. Furthermore, *Calanus* eggs are likely more nutritious than starved nauplii (Jung-Madsen et al. 2013). The high abundance and immobility of copepod eggs could make them more favourable as prey than calanoid nauplii.

Small nauplii of barnacles are within the suitable size for early stage larvae (Figs. 4a, 7a) and are often highly abundant on the Faroe shelf during spring (Gaard 1999; Jacobsen et al. 2018), but the current study showed that they are generally not selected by the cod larvae (Figs. 6, 9c) presumably because their frontal horns make them unsuitable as food (Fossum and Ellertsen 1994). Also *Oithona* sp. copepodites are small enough to be eaten by early stage cod larvae, but similar to other studies they are rarely observed among the stomach content (Fig. 6) and are not a highly preferred food item (Fig. 9d) (Kane 1984; Fossum and Ellertsen 1994; Pepin and Penney 1997; Robert et al. 2011; Swalethorp et al. 2014). These findings stress the importance of focusing on abundance of preferred prey species when assessing the actual prey availability to larval cod.

The late larval period

Late larval Faroe Plateau cod are most abundant in May, and since the present study is based on samples collected in April and June, respectively, there were relatively few larvae caught in the late larval length range (i.e. cod 9–19 mm) (Table 3). What's more, the prey field on the Faroe shelf is very likely different in May compared with April and June (Gaard 1999; Debes and Eliasen 2006). Hence, it is difficult to estimate the real prey preferences of late larval cod and future investigations are necessary to validate the conclusions that can be drawn from this study regarding cod in their late larval period. Having said that, the present results show that the medium-sized copepods *Acartia* sp. and *Pseudocalanus* sp. in the size range 0.6–1.2 mm were highly important for late larvae (Fig. 6) and appeared to be the most preferred species in the intermediate range of prey sizes in late larval cod (Figs. 9, 10). Early stage (<1.5 mm) *C. finmarchicus* copepodites were also highly represented in the
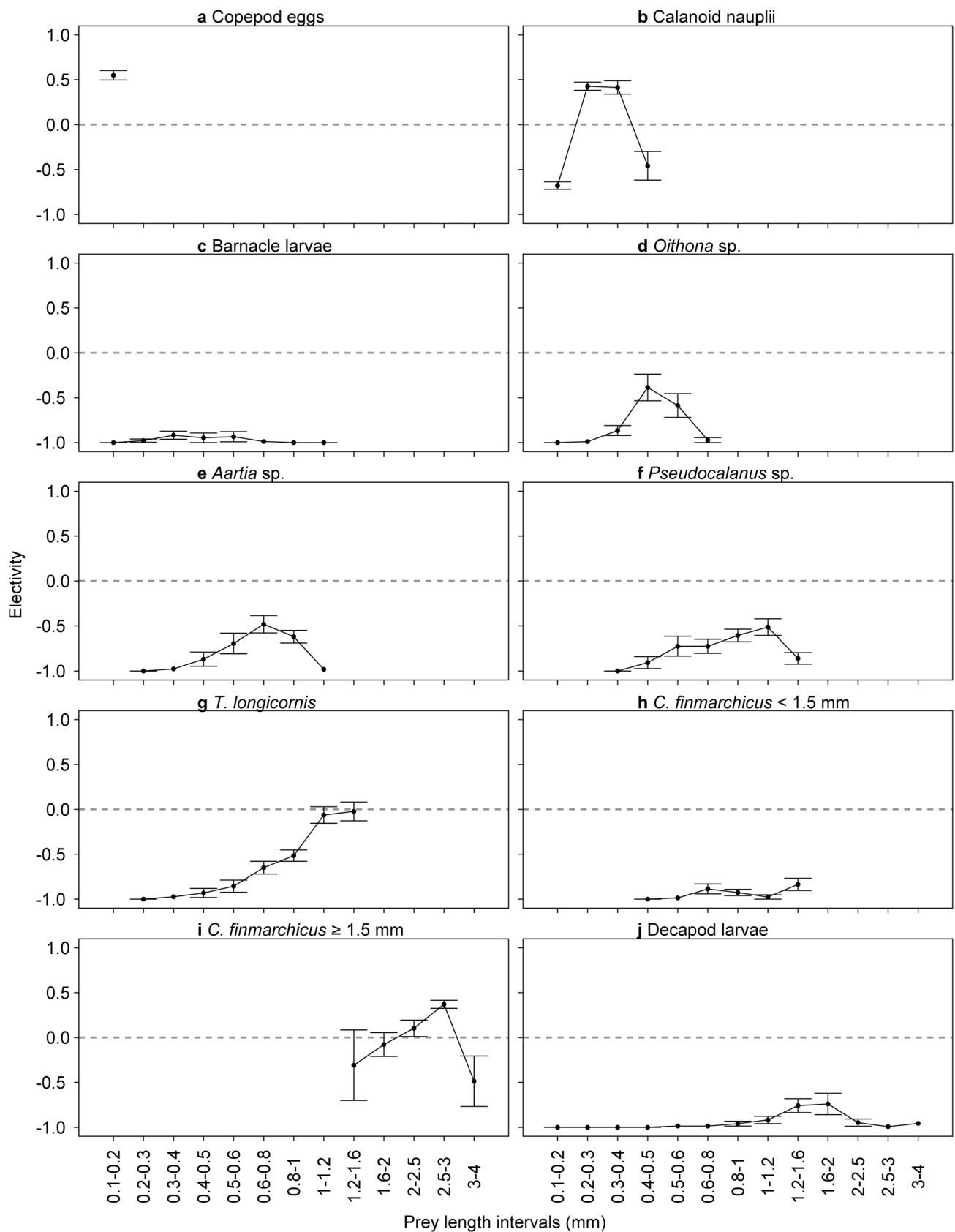
Fig. 10 Mean preference (Chesson 1983) expressed by electivity in comparison of 10 groups of prey along an axis of prey length intervals. The figure includes all cod larvae development stages. Error bars indicate 95% confidence intervals around the mean

Table 4 Linear model test results for effects of prey length and prey species on the preference (square root of α) of prey consumed by cod, accounting for cod length

	Sum Sq	Df	F	P
Prey length	0.21	1	3.06	0.080
Prey species	6.12	9	9.69	< 0.001
Cod length	95.73	1	1365.13	< 0.001
Prey length × prey species	23.47	9	37.18	< 0.001
Residuals	1280.24	18257		

guts of late larvae (Fig. 6), but their presence appeared more related to high abundance in the environment than to active selection by the cod (Fig. 8h). Lipid content in copepods is highest in copepodite stages IV and V (Kattner and Krause 1987; Hygum et al. 2000; Svetlichny et al. 2006), which probably explains why late larval cod prefer *Pseudocalanus* sp. and *Acartia* sp. more than early stage *C. finmarchicus* copepodites. The remaining abundant copepod in the intermediate size range in the zooplankton assemblage, *T. longicornis*, generally seemed not to be positively selected by cod in their late larval period (Fig. 9g), maybe because it has a broader body shape and thus is too large for late larval cod compared with e.g. *Acartia* sp. and *Pseudocalanus* sp., but maybe also because it was not very abundant in April (Fig. 4a) when most late larval cod were sampled. Late larvae generally ingest prey with a body width of $13 \pm 5\%$ the mouth gape (Swalethorp et al. 2015). For a 15 mm larvae that is copepods with a prosome width of 0.15–0.35 mm which encompass all *Acartia* and *Pseudocalanus* copepodite development stages, but only *Temora* copepodite stages I–III (Conway 2006). The findings of the current study are generally in accordance with observations from other areas of prey selection in late larval cod. A high preference for *Pseudocalanus* sp. at the late larval stage is described in many cod populations across the North Atlantic (Kane 1984; Munk 1997; Rowlands et al. 2008; McLaren and Avendaño 2011; Robert et al. 2011; Swalethorp et al. 2014). Furthermore, a study on larval and pelagic juvenile Irish Sea fish shows positive selection for *Acartia clausii* and negative selection for *T. longicornis* in cod in their late larval stage (Rowlands et al. 2008).

Cod in their late larval period undergo extensive physiological and morphological changes and consequently have relatively high energy requirements, and it is at this stage that competition for food is expected to commence (Thompson and Harrop 1991). This is in line with our study which shows that it was at the late larval development stage that the change in mean prey size consumption was the largest (Fig. 8a). What's more, the variation in relative prey length to cod length was particularly high in the late larval period (Fig. 8b) possibly indicating unfavourable feeding conditions at this stage (Seljeset et al. 2010). Interestingly, the mean prey dry weight and mean prey abundance per gut in late larvae was low compared to other studies (Kane 1984; McLaren et al. 1997) indicating a rather low mean abundance of prey items suitable for late stage larvae in the environment on the Faroe shelf. The spring/early summer abundance of intermediate sized copepods, i.e. copepods 0.8–1.2 mm, is highly dependent on the local primary production (i.e. chlorophyll concentration) (Jacobsen et al. 2018). In addition, cod 0-group indices, which are based on the June survey, closely resemble the local primary production index (Jacobsen et al. 2019). Together, these observations suggest that sub optimal feeding conditions during the late larval period may be a main critical phase for survival to the end of the pelagic stage in Faroe Plateau cod.

The early juvenile period

In terms of relative importance, late stage *C. finmarchicus* dominated the diet of early juvenile cod (Fig. 6e). Late stage *C. finmarchicus* were also the most preferred prey during the early juvenile period (Fig. 9i) supporting the hypothesis that *C. finmarchicus* is a key prey item for early pelagic juvenile cod in most areas in the North Atlantic (Heath and Lough 2007 and references there in).

There was, however, a discrepancy between the mean size of prey ingested compared with the preferred size of prey ingested by early juvenile cod (Fig. 8a). Early juvenile cod generally ingested smaller prey than what they prefer indicating once again that there may be a low abundance of preferred sized prey for early pelagic juveniles. The Faroe shelf summer zooplankton community generally shifts between being dominated by *C. finmarchicus* and dominated by smaller, neritic copepods i.e. *T. longicornis* and *Acartia* sp. (Gaard 1999, 2003). The neritic copepods are more abundant in years with high primary production (Jacobsen et al. 2018), while the summer abundance of *C. finmarchicus* is related to inter-annual differences in predation pressure from 0-group fish e.g. cod (Jacobsen et al. 2019), the variable exchange rate between on- and offshelf waters (Gaard and Hansen 2000) as well as the general production in the open ocean and on the shelf (Gaard 2000). Thus the difference in the mean size of prey ingested compared with the preferred size of prey ingested by early juvenile cod is most likely caused by a combination of high abundance of small prey together with a low abundance of preferred sized prey depending on the contemporary environmental conditions. This complies with a parallel study by Jacobsen (in preparation) investigating inter-annual differences in the feeding of pelagic Faroe Plateau cod. The study shows that the abundance of late stage *C. finmarchicus* in early juvenile cod is lower in years with high primary production than in years with low primary production. While late stage *C. finmarchicus* was the

most preferred species in early juveniles, the neritic copepod *T. longicornis* was the most abundant prey species at this particular development stage (Fig. 6b, c). In addition, *T. longicornis* appeared relatively important for cod juveniles (Fig. 6e), and thus this species is likely a good supplement to the cod diet when food is sparse.

The late juvenile period

Decapod larvae were the most important food item for late juvenile cod (Fig. 6e). Most other studies report euphausiids/mysids as the main prey for the largest pelagic juvenile cod (Heath and Lough 2007). However, in this study, only a total of 33 euphausiids were found in all of the stomachs (i.e. 1.4% of the total dry weight in the group malacostraca), most likely because euphausiids are not abundant on the shelf. Instead, meroplanktonic decapod zoeae appear to be very important in the feeding ecology of cod juveniles on the Faroe shelf (Fig. 7j). In addition, fish, primarily gadoids, were present in the guts of late juvenile cod. Thus, cannibalism in cod may start already at this early life stage potentially regulating the recruitment. Cannibalism is likely more severe when other prey species are limited.

Conclusion

Larval and pelagic juvenile Faroe Plateau cod (*Gadus morhua*) generally show the same feeding patterns as other North Atlantic cod stocks with high selectivity towards some prey species while avoiding others. Copepod (most likely *C. finmarchicus*) eggs are particularly important for early stage larvae followed by calanoid nauplii. At the late larval stage copepods of the genera *Acartia* and *Pseudocalanus* appear to be of particular importance and the feeding conditions at this stage may be the most critical for successful cod larval development and endurance. In the early juvenile period late stage *C. finmarchicus* copepodites are clearly the most favoured prey, while decapod larvae are the most preferred prey for late juveniles. However, since the gut content at any point in time most likely is affected by the contemporary prey availability and since the Faroe shelf prey availability is highly variable between years, a study investigating inter-annual differences in feeding is warranted. Furthermore, the possibility that it is a lack of suitable prey during the late larval period of cod that is most critical for survival to the end of the pelagic stage also calls for further exploration, and we recommend that future studies focus more on the period when late larvae are most abundant i.e. mid May.

Compliance with ethical standards

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