

Feeding ecology and condition of larval and pelagic juvenile redfish *Sebastes* spp.

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ABSTRACT: Eggs and nauplii of *Calanus finmarchicus* were the preferred prey types of redfish larvae whereas *Oithona* spp. copepodites were not, even though they were within the preferred size range. Significant seasonal and annual differences in larval diet of redfish resulted from differences in the availability of preferred prey. Seasonally, feeding was related to the succession of the spring dominance of *C. finmarchicus* to summer dominance of *Oithona* spp. Interannually, feeding was related to differences in the timing of spring spawning and temperature-dependent development of *C. finmarchicus*. Earlier spawning and faster development of *C. finmarchicus*, dependent on warmer water temperatures, resulted in poorer feeding conditions for redfish larvae. Under these conditions redfish larvae: (1) ate predominantly nauplii and copepodites of *Oithona* spp.; (2) ate less food by weight; (3) had lower relative body condition; and (4) there was a delayed size at metamorphosis from larvae to pelagic juveniles. Total prey concentrations between years did not determine better feeding and condition of redfish larvae, whereas the availability of preferred prey types did. Specifically, a lower abundance of *C. finmarchicus* nauplii resulted in better feeding conditions than a higher abundance of *Oithona* spp. copepodites. These results emphasize that measuring total prey biomass within preferred prey sizes is not sufficient when evaluating larval redfish feeding conditions. There was a switch in diet for pelagic juveniles to include *Oithona* spp. copepodites as preferred prey, in addition to copepod eggs and nauplii. This switch in diet coincided with changing prey availability due to the seasonal succession of zooplankton on Flemish Cap, Canada. Metamorphosis from larvae to juveniles at smaller sizes and younger ages is hypothesized to be advantageous to annual survival of redfish due to an increased foraging ability.

KEY WORDS: Redfish · *Sebastes* spp. · Diet · Prey preferences · *Calanus finmarchicus* · *Oithona* spp. · Metamorphosis

INTRODUCTION

Since Hjort (1914), fisheries research into the causes of recruitment fluctuation has centered on the role of successful feeding by fish larvae. However, it has proven difficult to demonstrate a direct relationship between larval feeding and subsequent recruitment to the fishery (Leggett 1986, Wooster & Bailey 1989). Successful feeding might result from surviving the transition to exogenous feeding, starvation during any point of the larval period, or to different feeding rates throughout the larval period (Anderson 1988). While starvation mortality has been reported in nature during the larval period, there is no evidence that it significantly affects recruitment (O'Connell 1980, Fortier & Leggett 1985, Hewitt et al. 1985, McGurk 1985,

1989, Theilacker 1986, Buckley & Lough 1987). Peterman & Bradford (1987) tested Lasker's (1975, 1981) first feeding hypotheses for northern anchovy, based on 13 yr of data, and found no relationship with year-class strength. However, Fortier & Leggett (1985) demonstrated increased mortality in capelin at the time of first feeding, consistent with Hjort's critical period hypothesis.

Greater feeding rates should result in better condition and increased growth and development rates. Increased growth and development rates are expected to result in higher survival (Ware 1975, Shepherd & Cushing 1980, Houde 1987). Feeding is hypothesized to be directly related to the availability of preferred prey types and sizes. Availability of preferred prey will be dependent on seasonal production of zooplankton,

but also may be affected by physical processes (Rothschild & Osborne 1988, Sundby & Fossum 1990). Some studies have examined larval diet in relation to growth and survival, but comprehensive estimates of prey availability were lacking (Cohen & Lough 1983, Ware & Lambert 1985). Estimates of prey selectivity by fish larvae have been reported (Kane 1984, Peterson & Ausubel 1984, Monteleone & Peterson 1986), but these studies were restricted in time and the results were not related to variables such as larval condition, development, growth or survival. Almost 2 decades after the review of May (1974) the role of feeding by fish larvae and the ways in which feeding variations among years effect differences in fish populations is still unresolved.

The aim of this research was to determine the diet and prey preferences of redfish larvae (*Sebastes* spp.) and how these varied seasonally with the transition from larvae to pelagic juveniles and between years in relation to prey availability. Interannual differences in feeding are related to fish condition and size at metamorphosis, as well as to previously published estimates of growth rates. Subsequent work will examine the direct effects of prey concentrations and temperature on larval growth rates and, finally, the relationship of larval growth rate to survival.

STUDY AREA

Flemish Cap is an offshore fishing bank situated east of the Grand Bank of Newfoundland, Canada, with distinct redfish and cod populations and an identifiable oceanographic regime (Templeman 1976, Lilly 1987). During this study redfish accounted for $\geq 90\%$ of all ichthyoplankton sampled. Three species of redfish have been reported for Flemish Cap (Templeman 1976, Ni 1982). Comparative analyses of larval morphology demonstrated that no single criterion successfully discriminates among these 3 species (Penney 1985, 1987). Also, it appears that *Sebastes mentella* and *S. marinus* larvae are more similar to each other than either of them is to *S. fasciatus* (Penney 1987). *S. mentella* and *S. marinus* spawn primarily during April while peak spawning of *S. fasciatus* occurs during June (Barsukov & Zakharov 1972, Templeman 1976, Penney 1987). Of these 3 species, *S. mentella* is the most numerous while *S. marinus* is always reported in low numbers (Templeman 1976, Ni & McKone 1983, Penney et al. 1984). It was concluded that *S. mentella* was the predominant species sampled in this study because of its numerical dominance and peak spawning which occurs in April, as reported elsewhere. Any mixture of species which did occur in these samples should have a negligible effect on interpretation of results.

MATERIALS AND METHODS

Ichthyoplankton used for the feeding analyses were collected with bongo nets towed obliquely from 200 m, or from near the bottom when water depth was < 200 m. Samples were collected on a 24 h basis such that the samples for each cruise were collected at all times of the day. A detailed summary of collection methods is contained in Anderson (1984). While 0.333 mm mesh nets were used most often, in some cases 0.505 mm mesh nets were also used. To test the null hypothesis that there were no sampling differences in abundances or lengths of redfish, paired *t*-test comparisons were made for 4 cruises in which both 0.333 and 0.505 mm mesh nets were fished simultaneously: GAD011, GAD019, GAD020, GAD035 (Table 1). In each case there were no statistical differences in abundances for all 4 cruises ($0.4135 \leq p \leq 0.7706$). There were no statistical differences in lengths sampled for 3 cruises ($0.1572 \leq p \leq 0.6830$). However, in 1 cruise (GAD020) the paired comparison indicated a statistical difference ($p = 0.0417$) where redfish averaged 0.2 mm larger in the 0.333 mm mesh samples. Therefore, it was concluded that there was no systematic sampling bias in which 0.505 mm mesh nets captured larger redfish.

Redfish larvae were selected for feeding and morphometric analyses from preserved samples (3 to 5% formalin) collected during 12 research cruises on Flemish Cap (Table 1). Where available, redfish larvae were examined from each station sampled within a cruise. In each case a maximum of 3 fish were randomly selected for each mm size class, except in 1979 when more than 3 redfish per mm size group were selected (Table 1).

Prior to examination of stomach contents, each fish was measured for standard length (i.e. to the nearest 1.0 mm) and morphometric measurements (to the nearest 0.1 mm) were made of body height, head width, head height, and maxillary length using a binocular microscope and micrometer. Head width was measured dorsally or ventrally immediately posterior to the eyes, and head height was measured sagittally at the same point as head width. Body height was the maximum body depth measured sagittally at the insertion of the pectoral fin. Maxillary length was measured from the tip of the snout to the posterior end of the maxilla. For cruises near the end of the larval phase, a measure of metamorphosis from the larval to the pelagic juvenile stage was made based on the degree of notochord flexion. During metamorphosis, involving ossification of body parts, the occurrence of head spines and body pigmentation, the notochord changes from straight to being flexed upwards at its posterior end. Flexion of the notochord occurs due to the formation of the

Table 1. *Sebastes* spp. Summary of samples collected on each cruise and number of redfish analyzed for diet on Flemish Cap, 1978–82. Mean: mean no. of redfish examined for each mm size for each station sampled; range: minimum and maximum no. of redfish examined

Cruise	Sampling date	Samples (Stns)	Total no. of fish examined	Redfish size class		Empty (%)
				Mean	Range	
GAD011	16–23 Jul 1978	1	17	1.7	1–4	23.5
GAD019	20–24 Mar 1979	25	135	2.3	1–6	18.5
GAD020	23–27 Apr 1979	62	748	2.8	1–6	6.6
DAW079	10–14 Jul 1979	19	242	3.7	1–20	5.0
GAD035	6–13 Apr 1980	37	218	1.2	1–3	6.0
GAD037	20–26 May 1980	56	861	1.2	1–3	5.3
ZAG004	22–28 Jul 1980	30	204	1.1	1–3	8.3
GAD050	2–9 May 1981	39	279	1.1	1–3	7.9
GAD051	22–27 May 1981	34	248	1.1	1–2	4.4
HAWPAN	26–30 Jun 1981	38	213	1.0	1–2	2.8
HAW002	1–4 Aug 1981	10	33	1.1	1–2	6.1
ATC331	1–3 Aug 1982	8	27	1.0	1	3.7

hypural plates which begin to form early during ossification and are completely formed by the end of metamorphosis to a pelagic juvenile. As these plates begin to appear, the notochord is gradually pushed upwards. First appearance of the hypural plates in conjunction with the beginning of notochord flexion was taken as the onset of metamorphosis. Complete formation of the hypural plates with maximum flexion of the notochord was taken as the completion of metamorphosis to pelagic juveniles.

Two estimates of mouth width are available. Head width was measured immediately posterior to the eye, just behind the extension of the maxilla. Therefore, head width can be regarded as a direct measure of maximum mouth width. Mouth width was also estimated from maxillary length based on the empirical relationship of Shirota (1970). Comparison of the 2 measures of mouth width indicated they were not different: $y = -0.01 + 1.08x$, ($F = 16882$, $p < 0.0001$, $R^2 = 0.905$, $n = 1769$), where y = mouth gape estimated from Shirota (1970) and x = head width. The slope was not different from 1 and the intercept was not different from zero. Therefore, either measure of maximum mouth width is considered to be appropriate. For estimates of mouth width used here, head width was regressed against standard length for all available data (8 cruises) to derive the linear relationship: $HW = -0.724 + 0.226SL$, where HW = head width (mm) and SL = standard length (mm) ($F = 21,897$, $p < 0.0001$, $R^2 = 0.913$, $n = 2098$).

Stomach contents were identified to species where possible. Life history stage was assigned to 1 of 5 categories: egg, nauplii, copepodite, larva and juvenile. Parts of copepods and other food items were also identified and recorded as fragments. For each of these headings an effort was made to distinguish between cyclopoids and calanoids, nauplii stages NI to NVI,

copepodite stages CI to CVI, and larval forms such as gastropod veligers. In the case of copepod nauplii, classification to 1 of 6 stages was frequently impossible. Therefore, nauplii were categorized into 1 of 3 size classes: ≤ 0.2 , $0.21-0.40$, ≥ 0.41 mm. Similarly, for small cyclopoid copepodites when specific stage identification was not possible they were classified into 1 of 3 size classes: ≤ 0.4 , $0.41-0.80$, ≥ 0.81 mm. In the case of the shelled gastropod (*Limacina* sp.) the shell was measured along its longest axis. Estimates of stomach weights were based on published, measured or derived weights (mg wet wt) for each species/stage level of classification (Anderson 1992).

Redfish dry wt (μg) was determined for formalin-preserved fish with an electrobalance, after drying each specimen at 55°C for 24 h on a tared pan and then storing the specimen in a desiccator for at least 24 h prior to weighing.

To reduce the many prey types into a more manageable subset for analyses, stomach contents were aggregated into 15 prey categories. The rationale for choosing these categories included taxonomic distinctiveness, relative importance to the diet (% weight) during 1 or more cruises and consideration of prey identification limitations of stomach contents.

For comparison of diet, redfish were divided into 1 of 3 size classes to represent larval redfish (≤ 9 mm), redfish undergoing metamorphosis (10–19 mm), and pelagic juvenile redfish sampled mostly during the summer period (≥ 20 mm). For these comparisons redfish diet was summarized into a smaller number of prey categories: copepod eggs (both calanoid and cyclopoid), calanoid nauplii, calanoid copepodites, cyclopoid nauplii and cyclopoid copepodites. Two other prey items that occurred abundantly during some cruises were euphausiid furcilia larvae and the shelled gastropod *Limacina* sp. All other prey types

occurred in low proportions and were classified as 'Other'.

Feeding comparisons among years were possible for 4 different periods ranging from late March to early August. In the first comparison (20–24 March 1979 versus 6–13 April 1980) the cruise dates differed by approximately 3 wk. However, both cruises occurred before the seasonal increase in redfish larval abundance and the mean and size range of larvae were similar. The second comparison (23–27 April 1979 versus 2–9 May 1981) occurred just after the time of peak redfish release (Anderson 1984, Penney & Evans 1985), for 2 cruises that differed in time by only 1.5 wk. However, the mean size of redfish was 6.3 mm in 1979 compared to 8.3 mm in 1981 although the range of lengths was similar: 4 to 12 mm and 6 to 13 mm, respectively. For this comparison redfish were compared for 2 size classes: ≤ 9 mm and 10–19 mm. For the third comparison (20–26 May 1980 versus 22–27 May 1981) redfish size was not different. The final comparison which included all 3 redfish size classes was among 4 yr during the period mid-July to the first week of August (Table 1). Statistical analyses for feeding differences among cruises were based on the Kolmogorov-Smirnov test (Siegel 1956).

As a relative measure of the amount of food redfish ate, stomach weights of redfish were standardized by summing the contents of each fish, dividing by the length of the fish cubed and then computing standard statistics for each cruise. For cruises which occurred later in the season, mean standardized stomach weights were determined for both small (larvae ≤ 11 mm) and large (juveniles ≥ 12 mm) length groups. A direct comparison between years of stomach weight to fish weight was possible for 20–26 May 1980 versus 22–27 May 1981. Statistical differences were determined for each mm length group based on Wilcoxon's test (SAS, Inc. 1985).

Diurnal feeding patterns were determined within each cruise by summing the stomach weights of all redfish sampled and then averaging these weights for each 2 h period over the entire cruise. Sunset and sunrise were based on a standard table used by the St. John's weather station.

Estimates of food preference by redfish were based on Chesson's (1978) α_i index. With Chesson's α_i , selectivity is standardized for the relative abundance of all prey types, allowing direct comparison among samples when abundance varies (Lechowicz 1982, Pearre 1982). Selectivity (α_i) for each prey type was calculated as

$$\alpha_i = \frac{r_i/p_i}{\sum_{k=1}^n r_k/p_k}$$

where r_i = proportion of prey type i in the diet and p_i = proportion in the water.

Redfish diet, r_i , was calculated from stomach contents for all fish examined within each mm size class at each station sampled within a cruise. Calculation of p_i for zooplankton prey in the environment was based on 0.080 mm mesh samples for 4 cruises (GAD035, GAD037, GAD050, GAD051) and 0.165 mm mesh samples for 2 cruises (HAWPAN, ATC331). Prey types were the same 15 prey categories used to describe feeding. Feeding selectivity was based on plankton that were both eaten by redfish and sampled by the plankton nets. An overall estimate of prey preference was calculated for each cruise by averaging the α_i s for each mm size class. Neutral selection was calculated as $1/n$, where n = no. of prey types which occurred in the intersection set for all redfish within each redfish size class for each cruise.

Sampling and processing methods for the zooplankton samples are outlined in Anderson (1990). In both cases, diet and environment, samples were based on integrated tows from 0 to 200 m for bongo samples and 0 to 100 m for the ring net samples. However, larval redfish are known to occur in the upper 50 m of the water column which typically will be above the pycnocline (Kenchington 1991, K. Frank, Bedford Institute of Oceanography, Dartmouth, Nova Scotia, Canada, unpubl. data). In addition, it is known that early stages of copepods (Krause & Trahms 1982, Williams et al. 1987, Williams & Conway 1988) and *Limacina* sp. (Perry & Neilson 1988) are concentrated in the upper mixed layer as well. Therefore, it is assumed that the fish larvae co-occurred with their prey, at least during the early part of the season from March through June. By July–August the degree of co-occurrence is less well known. However, it is typical of fish in their first year of life to begin diurnal migrations as they grow, which may put them in association with a greater variety of food items.

Relative condition was based on redfish dry wt mm^{-1} length, comparing redfish sampled during the end of May 1980 and 1981. This allowed a direct comparison between years during the end of the larval period. Wilcoxon's non-parametric test was used to evaluate differences between each mm size category.

RESULTS

Seasonal patterns in diet

Observations of redfish diet for the period April to August during 1979–81 demonstrated significant differences with the changing biological season, characterized by an increasing number of prey types during all 3 yr. For example, during 20–24 March 1979 and 6–13 April 1980 2 and 3 food types made up 98 and 99.8% of the diet by weight respectively (Table 2). By

Table 2. *Sebastes* spp. Summary of redfish diet expressed as percent occurrence based on both weight and numbers. Here diet is summarized for each cruise for all sizes of redfish, and cruises are listed chronologically by season (see Table 1). Diet is ranked from highest to lowest in each case. Each prey item represents the best possible taxonomic identification from stomach samples. NS: not staged; cop.: copepodite; F: female. Numbers in parentheses indicate size ranges of cyclopoid copepodites (420: ≤ 0.4 mm; 421: 0.4 to 0.8 mm) and calanoid nauplii (351: ≤ 0.2 mm; 352: 0.3 to 0.4 mm; 353: ≥ 0.5 mm)

Cruise	Prey species	Frequency (% wt)	Prey species	Frequency (% no.)
GAD019 (1979)	Copepod nauplii	66.6	<i>Limacina</i> sp.	41.1
	Copepod eggs	17.5	Copepod eggs	37.2
	<i>Limacina</i> sp.	13.8	Copepod nauplii	19.8
	<i>Gibberina</i> sp.	2.0		
GAD035 (1980)	Copepod eggs	85.8	Copepod eggs	97.5
	Copepod nauplii	14.0	Copepod nauplii	2.2
	<i>Limacina</i> sp.	0.1	<i>Limacina</i> sp.	0.2
GAD020 (1979)	Copepod nauplii	47.8	Copepod eggs	79.7
	Copepod eggs	30.0	Copepod nauplii	17.8
	Euphausiid nauplii	13.5	Euphausiid nauplii	1.0
	Copepods NS	5.6	<i>Limacina</i> sp.	0.5
	Euphausiid eggs	1.5		
GAD050 (1981)	Cyclopoid nauplii	32.2	Cyclopoid nauplii	77.3
	<i>Oithona</i> spp. cop. (420)	20.3	Calanoid nauplii	6.5
	<i>Oithona</i> spp. cop. (421)	15.5	<i>Oithona</i> spp. cop. (420)	5.1
	Calanoid nauplii (352)	7.6	Copepod eggs	4.9
	Calanoid nauplii (353)	4.2	<i>Oithona</i> spp. cop. (421)	2.3
			<i>Limacina</i> sp.	1.2
GAD037 (1980)	Copepod nauplii	72.1	Copepod eggs	50.0
	Copepod eggs	12.2	Copepod nauplii	41.2
	<i>Oithona</i> spp. cop. NS	3.6	<i>Oithona</i> spp. cop. NS	3.0
	Calanoid NS	3.2	<i>Limacina</i> sp.	1.3
	<i>Oithona</i> spp. NS	2.1	Dinophyta	1.0
	<i>O. similis</i> CVI	1.4	<i>Oithona</i> spp. NS	0.9
GAD051 (1981)	Cyclopoid nauplii	39.4	Cyclopoid nauplii	79.7
	<i>Oithona</i> spp. cop. (420)	32.9	<i>Oithona</i> spp. cop. NS	9.5
	<i>Oithona</i> spp. cop. (421)	20.1	Copepod eggs	4.2
	Copepod eggs	3.4	Dinophyta	4.2
			<i>Limacina</i> sp.	1.4
HAWPAN (1981)	<i>Oithona</i> spp. cop. (421)	34.0	Cyclopoid nauplii (351)	47.0
	<i>Oithona</i> spp. cop. (420)	32.7	Calanoid eggs	25.6
	Cyclopoid nauplii	10.6	<i>Oithona</i> spp. cop. (420)	15.3
	Calanoid eggs	9.5	<i>Oithona</i> spp. cop. (421)	9.4
	<i>O. similis</i> CVI F	3.0	<i>Limacina</i> sp.	0.7
	<i>C. hyperboreus</i> CIII	2.0	Calanoid nauplii (352)	0.7
	<i>C. finmarchicus</i> CIV	1.7		
	<i>C. finmarchicus</i> CV	1.2		
	<i>Calanus</i> sp.	0.7		
DAW079 (1979)	<i>O. similis</i> cop. NS	36.1	Copepod nauplii	45.3
	<i>O. similis</i> CV	28.9	<i>O. similis</i> cop. NS	20.2
	<i>O. similis</i>	8.5	<i>O. similis</i> CV	16.2
	Copepod copepodites	8.3	<i>Limacina</i> sp.	4.8
	<i>O. similis</i> CIV	6.9	Copepod eggs	4.2
	<i>C. finmarchicus</i> cop. NS	3.2	<i>O. similis</i> CIV	3.8
	Copepod nauplii	2.7	<i>O. similis</i> CVI	3.6
	<i>C. finmarchicus</i> CIV	2.0		
ZAG004 (1980)	<i>O. similis</i> cop. (421)	47.9	<i>O. similis</i> cop.	50.1
	<i>O. similis</i> cop. (420)	6.0	Calanoid eggs	16.4
	<i>O. similis</i> CVI M	5.8	Cyclopoid eggs	11.7
	<i>C. glacialis</i> CV	5.1	Calanoid nauplii	5.9
	<i>O. similis</i> CVI F	4.2	<i>O. similis</i> CVI M	3.8
	<i>C. finmarchicus</i> CVI F	3.9	Calanoid nauplii	3.6
	Fish eggs	3.5	<i>O. similis</i> CVI F	2.8
	<i>C. finmarchicus</i> CV	2.8	Cyclopoid nauplii	2.3
	<i>C. finmarchicus</i> CIV	2.7	<i>C. finmarchicus</i> CI	0.7
	<i>C. glacialis</i> CVI F	2.2	<i>C. finmarchicus</i> CII	0.3
	<i>C. glacialis</i> CIII	2.1		
	Calanoid eggs	2.0		
	<i>Oithona</i> spp.	1.8		
	Calanoid nauplii	1.5		
	<i>C. finmarchicus</i> CI	1.5		
	<i>C. finmarchicus</i> CII	1.5		
	<i>C. finmarchicus</i> CIII	1.4		
HAW002 (1981)	<i>C. finmarchicus</i> CV	31.3	<i>Oithona</i> spp. cop. (421)	35.1
	<i>Oithona</i> spp. cop. (421)	23.2	<i>Oithona</i> spp. cop. (420)	31.0
	<i>C. finmarchicus</i> CVI F	14.1	Cyclopoid nauplii	11.6
	<i>Oithona</i> spp. cop. (420)	12.2	Calanoid eggs	8.2
	<i>Thysanoessa</i> NS	5.5	Calanoid nauplii	4.3
	<i>O. similis</i> CVI F	2.4	<i>O. similis</i> CVI F	2.7
	Calanoid NS	1.8	<i>M. pygmaeus</i> NS	1.3
	<i>M. pygmaeus</i> CVI F	1.5		
	Euphausiid furcilia	1.2		
	<i>C. finmarchicus</i> CIII	1.2		
	<i>M. pygmaeus</i> NS	1.0		
	<i>C. finmarchicus</i> CII	0.9		
ATC331 (1982)	<i>O. similis</i> cop. (421)	33.2	<i>O. similis</i> cop. (421)	35.1
	<i>C. finmarchicus</i> CV	22.0	<i>O. similis</i> cop. (420)	31.4
	<i>O. similis</i> cop. (420)	17.6	Cyclopoid nauplii	23.9
	<i>C. finmarchicus</i> CIV	14.5	Calanoid eggs	4.2
	<i>Thysanoessa</i> furcilia	3.5	<i>O. similis</i> CVI F	2.2
	<i>O. similis</i> CVI F	2.7		
	Euphausiid furcilia	2.5		
	Cyclopoid nauplii	1.4		

Table 3. *Sebastes* spp. preying on *Calanus finmarchicus* and *Oithona similis*. Estimates of prey width for selected prey types as a percent of maximum mouth width for different redfish sizes. NI & NVI: nauplii stages I & VI; CI & CVI: copepodite stages I & VI. Width was estimated for *C. finmarchicus* nauplii and copepodites as 75 and 33% of total length respectively. For *O. similis* nauplii and copepodites, width was estimated as 67 and 34% of total length respectively. Width estimates approximated inclusion of folded antennae

Redfish length (mm)	Mouth width (mm)	Eggs	<i>C. finmarchicus</i>				<i>O. similis</i>			
			NI	NVI	CI	CVI	NI	NVI	CI	CVI
6	0.63	21.4	26.2	72.7	32.2	112.7	12.2	22.9	12.4	27.8
10	1.54	8.8	10.7	29.7	13.2	46.1	5.0	9.4	5.2	11.4
15	2.67	5.1	6.2	17.2	7.6	26.6	2.6	5.4	2.9	6.6
20	3.80	3.5	4.3	12.1	5.3	18.7	2.0	3.8	2.1	4.6
25	4.93	2.7	3.4	9.3	4.1	14.4	1.6	2.8	1.6	3.6

the end of May this had increased to 12 food types making up 98.7% of the diet in 1980 (GAD037) and 9 food types making up 98.7% of the diet in 1981 (GAD051). By July–August during 1979–1982 there were 12 to 27 food types which made up 98.9 to 99% of the diet by weight. In addition, food types tended to increase in size as the fish grew, with a shift from eggs and nauplii to cyclopoid and later calanoid copepodites. However, the differences in diet observed in 1981 compared to 1979 and 1980 make it difficult to generalize about the diet of Flemish Cap redfish.

During March–May 1979–80 copepod nauplii dominated by weight, except 6–13 April 1980 when eggs accounted for 85.8% of the diet, compared to 14% for nauplii (Table 2). In 1981, the dominant food item was cyclopoid copepodites followed by nauplii. A detailed examination of diet differences among years is presented in the next section.

Comparison of the diet of redfish larvae (≤ 9 mm) demonstrated differences in prey availability both seasonally and between years. In March–May 1979 and 1980 copepod eggs and nauplii (primarily calanoid) comprised 78.5 to 99.8% of the diet by weight. During this period in 1981 copepod eggs and nauplii (primarily cyclopoid) comprised 56.1 and 63.3%, respectively, whereas cyclopoid copepodites accounted for 34.6 to 42.6% of the diet. The predominance of cyclopoid prey in the diet during 1981, particularly copepodites, demonstrates interannual differences in prey availability, as prey selectivity did not change (see below). During the July–August period eggs and nauplii made up 30.7 to 43.1% of the diet in 1980–82 and only 4.5% in 1979. In contrast, *Oithona* spp. copepodites made up 51.8 to 81.6% of the diet. These results demonstrate a seasonal change in diet from calanoid eggs and nauplii to cyclopoid copepodites for redfish larvae.

Limacina sp. was a component of the diet of small redfish in most cruises. However, in only 2 instances did it constitute a notable proportion of the diet. During 20–24 March 1979 and 1–3 August 1982 it made up 13.8 and 17.5% of the diet by weight respectively. It is

noteworthy that these 2 cruises represented the earliest and latest observations available, indicating that *Limacina* sp. may be relatively more important in the diet both prior to the onset of spring copepod production and possibly late in the summer period. In all other cruises it ranged from 0 to 2% of the diet by weight.

Maximum mouth width for redfish 6, 10, 15, 20 and 25 mm in length was compared to sizes of *Calanus finmarchicus* eggs, and *C. finmarchicus* and *Oithona similis* nauplii and copepodites (Table 3). The range of preferred prey sizes relative to maximum mouth width ranged from 2 to 73%, based on the diet and preferred prey types (see below) for larvae of these lengths sampled at different times. These values represent the extremes of 6 mm larvae feeding on *C. finmarchicus* NVI and 25 mm juveniles feeding on *O. similis* NI (Table 3). Comparison of mouth width to standard length indicates that mouth width increases at a greater rate. For example, at 6 mm length mouth width is 10% of body length while at 25 mm it is 20%. A relatively rapid increase in mouth size would favour successful feeding in a changing environment with an ever increasing variety and size of the prey field.

Interannual differences in diet

Among year differences in diet were apparent during April–May 1979–81, while by July most differences had disappeared. The greatest difference was a predominance of cyclopoid nauplii and copepodites during May 1981, and of calanoid eggs and nauplii in 1979 and 1980.

Redfish diets differed significantly between 20–24 March 1979 and 6–13 April 1980 ($D_{\max} = 0.683$, $p < 0.001$, $n_1 = 135$, $n_2 = 218$). In March 1979 copepod nauplii dominated (66.7% by weight) followed by copepod eggs (17.5%) and *Limacina* sp. (13.8%). In April 1980 copepod eggs dominated (85.8%) followed by nauplii (14%) (Fig. 1). *Calanus finmarchicus* spawning apparently was more advanced by the end of March 1979 than in the second week of April 1980.

Copepod nauplii (47.8%), copepod eggs (30%) and euphausiid nauplii (13.5%) dominated the diet during 23–27 April 1979, whereas *Oithona* spp. copepodites (35.8%) and nauplii (32.3%) dominated during 2–9 May 1981 (during which calanoid nauplii comprised only 11.8%) (Fig. 1). Diets of redfish ≤ 9 mm and 10–13 mm were significantly different in both cases ($D_{\max} = 0.657$, $p < 0.001$, $n_1 = 692$, $n_2 = 237$) and $D_{\max} = 0.313$, $p < 0.05$, $n_1 = 56$, $n_2 = 42$, respectively).

Diets also differed between May 1980 and 1981 ($D_{\max} = 0.804$, $p < 0.001$, $n_1 = 861$, $n_2 = 248$). During 20–26 May 1980, most redfish ate copepod nauplii (calanoid) (72.1%), eggs (12.2%) and *Oithona* spp. copepodites (7.1%). During 22–27 May 1981 redfish larvae ate rela-

tively older cyclopoid stages (*Oithona* spp. copepodites, 53%; cyclopoid nauplii 39.4%; Fig. 1).

No overall pattern of dietary differences was observed for larvae in the 3 size classes (≤ 9 , 10–19, ≥ 20 mm) among years in July–August. In all 3 years ≤ 9 mm redfish ate mainly *Oithona* spp. copepodites, (51.8 to 53.8% by weight). Redfish 10–19 mm ate mainly *Oithona* spp. copepodites (1980, 72.3% by weight; 1981, 53.8%; 1982, 89.3%). Only redfish ≥ 20 mm exhibited a difference among years. Their diet was dominated in all years by copepodites of *Oithona* spp. and *Calanus finmarchicus*. However, *Oithona* spp. dominated by weight in 1980 and *C. finmarchicus* dominated in 1981 and 1982. The diets were not statistically different among years.

Only the diets of redfish ≤ 9 mm sampled in July 1979 differed statistically from July 1980 ($D_{\max} = 0.386$, $p < 0.01$, $n_1 = 232$, $n_2 = 24$) and August 1981 ($D_{\max} = 0.354$, $p < 0.1$, $n_1 = 232$, $n_2 = 13$). These differences were due to small redfish eating fewer copepod eggs and nauplii ($< 5\%$ by weight) in 1979 compared to 1980 and 1981 ($> 40\%$ by weight).

Diurnal patterns in feeding

Redfish fed primarily during daylight. Peak stomach weights consistently occurred before sunset (Fig. 2) after which they decreased to a minimum around sunrise. Some variation occurred among cruises: during 20–26 May 1980 the minimum occurred 0.5 h after sunrise, after which stomach weights began to increase (Fig. 2); during 26–30 June 1981 the minimum occurred 0.5 h after sunrise but no increase occurred until 4 h later (Fig. 2); combined results for the 4 cruises in July–August cruises yielded a minimum 2 h after sunrise and no increase until 6 h after sunrise (Fig. 2). A steady increase in stomach weight occurred during daylight hours once feeding commenced.

The diurnal pattern was less pronounced on the remaining sampling dates (20–24 March and 23–27 April 1979 and 2–9 May and 22–27 May 1981) which sampled redfish larvae ≤ 11 mm (Fig. 2), and in which feeding was generally poorer. It is possible that feeding was suboptimal, such that normal diurnal feeding patterns were not established at these times.

Seasonal and interannual differences in feeding

The amount of food redfish ate varied both among years and for different periods within years. In general, the index (based on standardized stomach weights) increased later in the season. This was most apparent in 1981 where the index increased from a low of 0.085

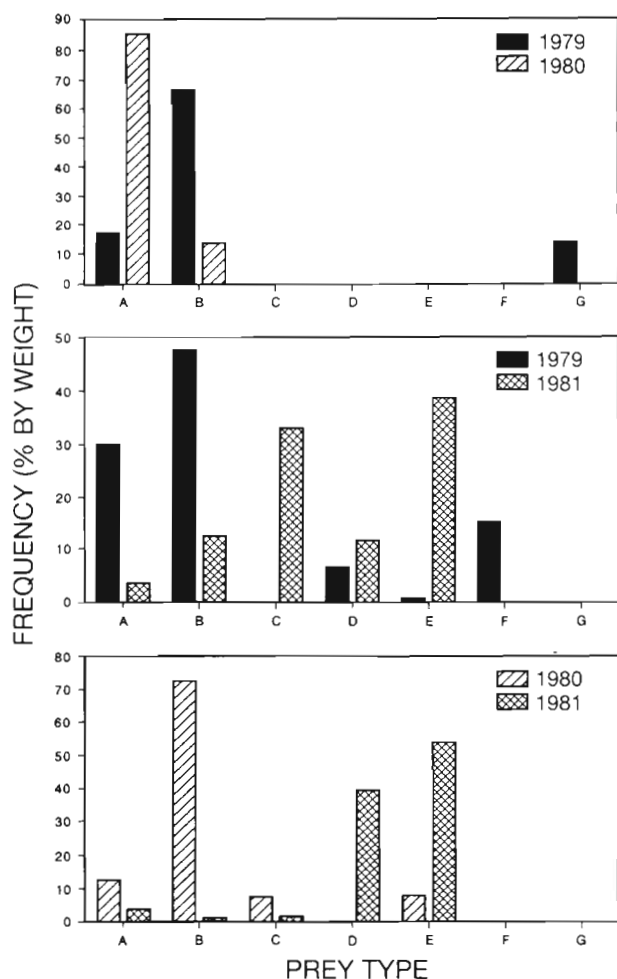


Fig. 1. *Sebastes* spp. Direct comparisons of diet differences for redfish larvae sampled in different years at approximately the same time: 20 to 24 March 1979 versus 6–13 April 1980; 23–27 April 1979 versus 2–9 May 1981; 20–26 May 1980 versus 22–27 May 1981. Prey type labels – A: copepod eggs; B: copepod nauplii; C: copepod copepodites; D: cyclopoid nauplii; E: cyclopoid copepodites; F: euphausiids; G: *Limacina* spp.

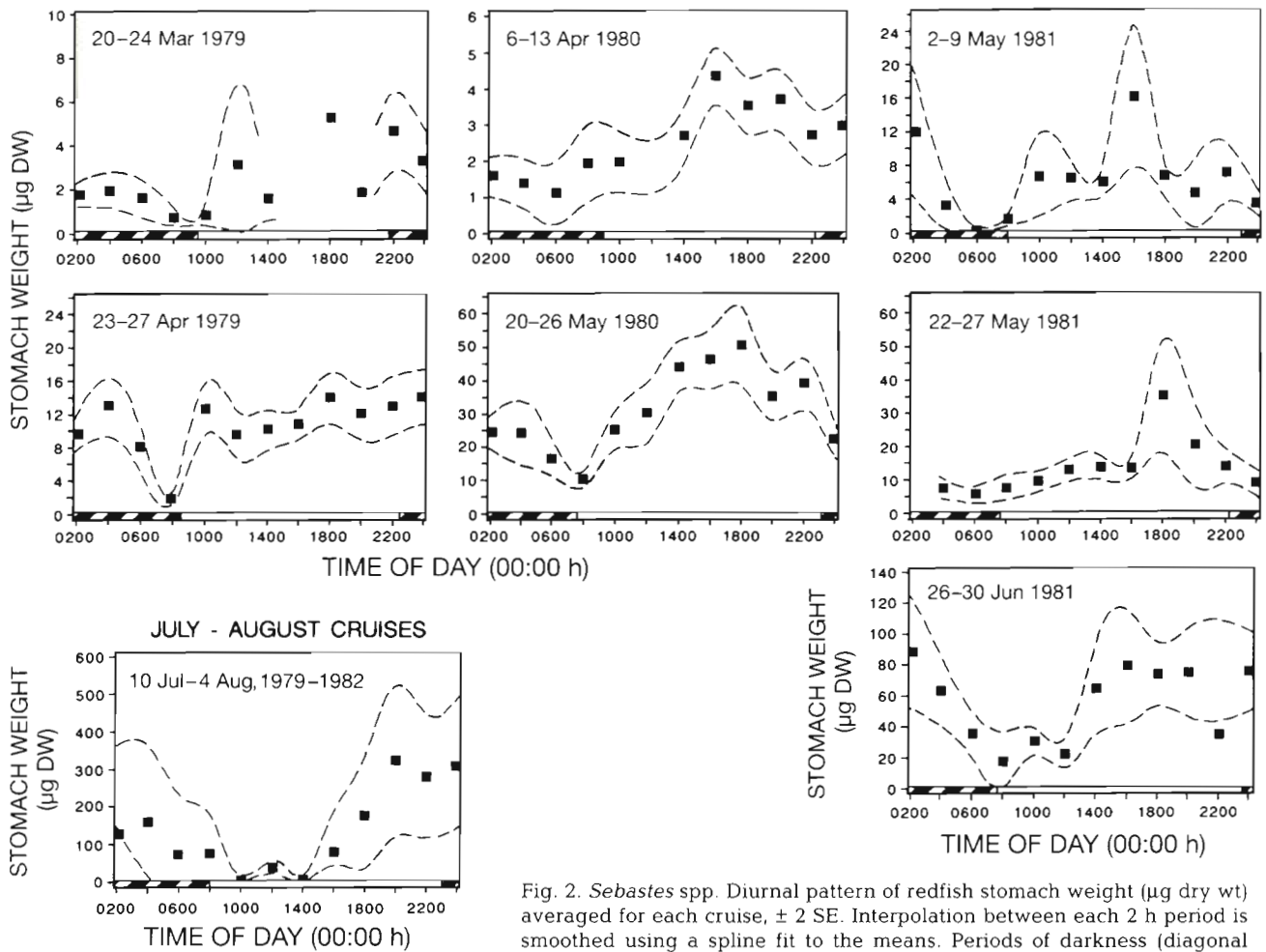


Fig. 2. *Sebastes* spp. Diurnal pattern of redfish stomach weight (μg dry wt) averaged for each cruise, ± 2 SE. Interpolation between each 2 h period is smoothed using a spline fit to the means. Periods of darkness (diagonal shading) and light (open) are indicated at the bottom of each panel

Table 4. *Sebastes* spp. Mean stomach weight (μg) standardized for fish size (mm^3) for redfish larvae sampled on Flemish Cap. Mean standardized stomach weights were calculated for each size class within each cruise and then an overall mean was calculated from these mean estimates. SD: standard deviation; CV: coefficient of variation

Cruise	Sampling dates	Redfish sizes (mm)	Mean ($\mu\text{g mm}^{-3}$)	SD	CV (%)
GAD019	20–24 Mar 1979	4–7	0.124	0.0441	35.6
GAD020	23–27 Apr 1979	5–11	0.281	0.0836	29.8
DAW079	10–14 Jul 1979	4–11	0.344	0.0749	21.8
GAD035	6–13 Apr 1980	5–7	0.109	0.0040	3.7
GAD037	20–26 May 1980	6–14	0.381	0.0753	19.8
ZAG004	22–28 Jul 1980	5–11	0.055	0.0437	79.5
		12–24	0.449	0.1581	35.2
GAD050	2–9 May 1981	6–11	0.085	0.0369	43.4
GAD051	22–27 May 1981	6–11	0.109	0.0378	34.7
HAWPAN	26–30 Jun 1981	6–7	0.070	0.0170	24.3
		8–16	0.351	0.0378	10.8
HAW002	1–4 Aug 1981	7–11	0.088	0.0504	57.3
		13–24	0.311	0.1921	61.8
ATC331	1–3 Aug 1982	6–11	0.242	0.1839	76.0
		16–23	0.642	0.2422	37.7

to values >0.3 from 2–9 May to 1–4 August 1981 (Table 4). A similar seasonal increase was also observed in 1979 and 1980.

A seasonal increase in the amount of food redfish ate per unit size would occur if pelagic juvenile redfish are better feeders than larvae. There are 3 lines of evidence in support of this observation. First, the index increased from 0.109 during 22–27 May to 0.351 during 26–30 June 1981, which relates to feeding for larvae and juveniles respectively. Second, differences in the index were observed among 4 cruises which sampled both small (larvae) and large (juveniles) redfish. In each case the index of standardized stomach weights was considerably less for larvae (range 0.055 to 0.242) than for pelagic juveniles (range 0.311 to 0.642) (Table 4). Third, comparison between May 1980 and 1981 demonstrated that differences in feeding which occurred between larvae were not evident between juveniles (Fig. 3). All length groups from 7 to 11 mm had significantly greater standardized stomach weights in 1980 (Table 5). The mean difference tended to decrease with increasing fish length and by 12 mm the means were no longer statistically different (Table 5). At 12 mm length most redfish had metamorphosed to pelagic juveniles.

In general, standardized stomach weights of juveniles were consistently high, whereas those for larvae were high only for 20–26 May 1980, when redfish larvae were growing relatively fast and were in better condition. Feeding was relatively poor in redfish larvae from all other cruises.

Feeding selectivity

During 4 cruises which occurred in different years and seasons, redfish larvae consistently selected copepod eggs and larvae, but did not select copepodites (Fig. 4). This observation is based on the mean value of selectivity compared to neutral selection. Mean values of selectivity were greater for copepod nauplii than for eggs in 3 of 4 cruises. During 2–9 May 1981, cyclopoid eggs were not selected by redfish larvae, with all values falling below neutral selection. However, 3 wk later larvae were actively selecting cyclopoid eggs. The larger calanoid copepodites (predominantly *Calanus* sp.) on average had lower selectivity than small cyclopoid copepodites (predominantly *Oithona* spp.).

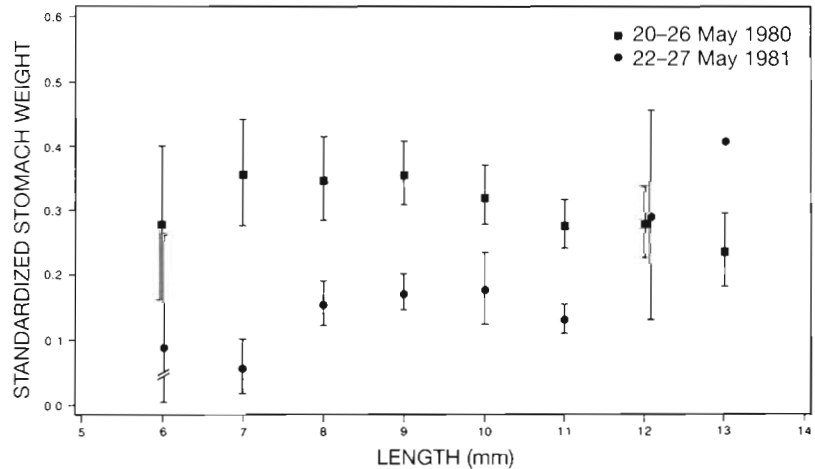


Fig. 3. *Sebastes* spp. Redfish stomach weights standardized by redfish dry wt (± 2 SE) versus redfish length (mm) for 20–26 May 1980 and 22–27 May 1981

Limacina sp. was neutrally selected. Prey types classified as 'Other' generally were not selected by redfish larvae (i.e. less than neutral). The 'Other' prey types that occurred in the diet for these 4 cruises were exclusively Protozoa. The most common food types were tintinnids, *Globigerina* sp. and radiolarians, although radiolarians were only abundant as an 'Other' food type in the 20–26 May 1980 cruise (73 % of 'Other' prey types). *Globigerina* spp. typically range in size from 0.270 to 0.800 mm (Newell & Newell 1977), and would be retained by both the 0.080 mm and 0.165 mm nets (see below). Protozoans dominated 'Other' food types in the diet for all other cruises. Later in the season 'Other' food types which also occurred in the diet included *Oikopleura* spp. (ZAG004), *Parathemisto* spp. (HAWPAN), fish eggs (ZAG004) and Isopoda (HAW002). Prey types classified here as 'Other' were always a small component of the overall redfish diet by weight (Table 2).

Table 5. *Sebastes* spp. Wilcoxon's test of difference between standardized stomach weights (weight of stomach per weight of redfish) for each mm length group sampled May 1980 versus 1981. n_1 and n_2 : 20–26 May 1980 and 22–27 May 1981 respectively. z : Wilcoxon's test statistic

Length group (mm)	n_1, n_2	z	p
6	44, 2	-0.9965	0.3190
7	123, 12	-4.0012	0.0001
8	146, 55	-4.2499	0.00001
9	153, 78	-5.3535	0.00001
10	145, 26	-2.7553	0.0059
11	105, 48	-4.8148	0.00001
12	52, 10	-0.2010	0.8407

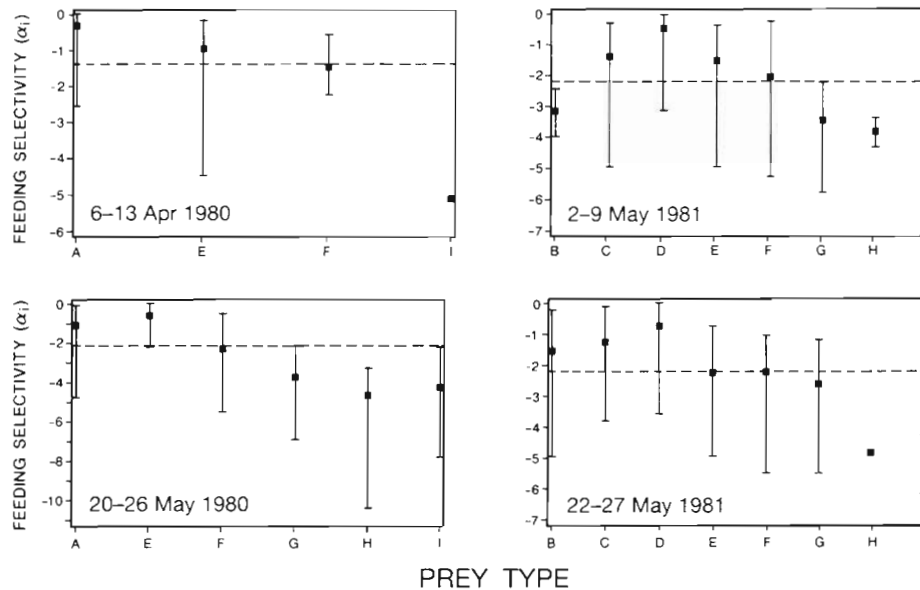


Fig. 4. *Sebastes* spp. Redfish feeding selectivity calculated for 8 food types for 4 cruises using 0.080 mm mesh zooplankton samples. Mean selectivity is plotted with minimum and maximum values calculated for each food type within a cruise. α_i : Chesson's alpha index for prey species i , plotted here as $\log e$. The dashed line references the estimate of neutral selectivity. Prey type – A: copepod eggs; B: cyclopoid eggs; C: calanoid eggs; D: cyclopoid nauplii; E: calanoid nauplii; F: *Limacina* sp.; G: *Oithona* spp. copepodite; H: *Calanus finmarchicus* copepodite; I: other prey types

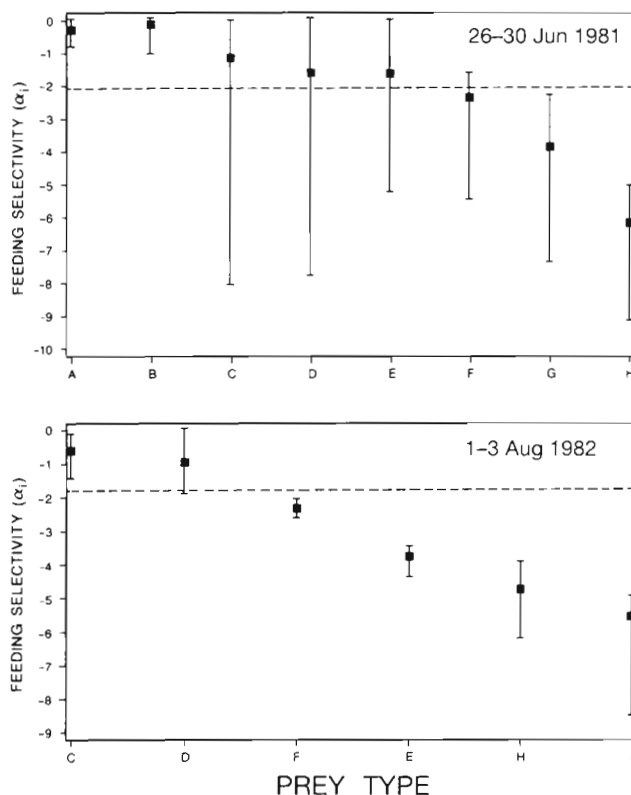


Fig. 5. *Sebastes* spp. Redfish feeding selectivity calculated for 8 food types for 2 cruises using 0.165 mm mesh zooplankton samples. α_i : Chesson's alpha index for prey species i , plotted here as $\log e$. Redfish analyzed 26–30 June 1981 ranged in length from 9 to 15 mm and 1–4 August 1982 from 16 to 23 mm. The dashed line references the estimate of neutral selectivity. Prey type – A: calanoid eggs; B: cyclopoid nauplii; C: calanoid nauplii; D: *Oithona* spp. copepodite; E: *Limacina* sp.; F: euphausiids; G: *Calanus finmarchicus* copepodite; H: other copepod copepodites; I: other prey types

It was also possible to calculate prey selectivity for 2 cruises later in the season (26–30 June 1981 and 1–3 August 1982) when zooplankton were collected using 0.165 mm mesh nets. Selectivities calculated from these samples are biased by the fact that 0.165 mm mesh nets will not quantitatively sample copepod eggs and nauplii (Davis 1980). However, these nets will retain at least *Pseudocalanus* spp. stage CI (0.4 mm TL), and possibly smaller (Davis 1980). A statistical approximation gave a mean retention of 0.26 ± 0.08 mm, which corresponds closely with the size of *Oithona* spp. CI of 0.23 ± 0.07 mm (Murphy & Cohen 1978). Therefore, prey selectivity would be overestimated for copepod eggs and nauplii but not for the copepodite stages which would be quantitatively sampled by 0.165 mm mesh nets.

Redfish sampled during June 1981 and August 1982 were predominantly pelagic juveniles ranging in length from 9 to 15 and 16 to 23 mm respectively. During June these juvenile redfish were, on average, selecting cyclopoid copepodites, in addition to selecting copepod eggs and nauplii (Fig. 5). By August all selectivities for cyclopoid copepodites were above the level of neutral selection. However, the larger calanoid copepodites, which were predominantly *Calanus finmarchicus* stage CV (Anderson 1990), were not actively selected by juvenile redfish. During both cruises euphausiid furcilia larvae were neutrally selected (Fig. 5) although they were an unimportant component of the diet accounting for <1% by both weight and number. During both cruises copepodites dominated the diet (Table 2). Therefore, there appeared to be a switch in prey selectivity to cyclopoid copepodites later in the season after the redfish metamorphosed to the pelagic juvenile stage.

Redfish larvae (6 to 8 mm) were also captured during the June and August cruises, and were most likely the later spawning species *Sebastes fasciatus* (Barsukov & Zakharov 1972, Templeman 1976, Penney 1987). Selectivity results for the smaller fish (larvae) differed from those for the larger fish (juveniles), as the larvae did not select *Oithona* spp. copepodites. These results are similar to those for larval redfish analyzed for the April–May period in 1980 and 1981 where the total size range was 6 to 12 mm (Fig. 4). Therefore, selectivity results were similar for all larval redfish ≤ 12 mm for the period spanning early April to early August.

Redfish condition

Redfish were in better condition in 1980 than in 1981, based on a comparison at the end of May each year. Comparison over all length groups demonstrated that redfish 6 to 11 mm in length weighed significantly more in 1980 than in 1981. Only at 12 mm length was there no difference (Table 6). Comparison of percent differences in weight demonstrated that 1980 redfish 6 to 10 mm in length weighed 34.4 to 50.1% more, after which the difference in weight decreased to 10 to 16%. Redfish > 10 mm were undergoing, or had undergone, metamorphosis (see below) indicating that the difference in weight which occurred between these years occurred only for the larval stage. The rapid recovery in weight for larger redfish represents those fish which survived to metamorphosis, which may represent differential size-dependent survival or increased growth for these juveniles.

Metamorphosis from larvae to pelagic juveniles

Comparison of size at metamorphosis was made at the end of May, which coincided with the end of the

Table 6. *Sebastes* spp. Wilcoxon's test of differences in redfish dry wt (μg) for each length group (mm) between 20–26 May 1980 versus 22–27 May 1981. n_1 and n_2 : sample size for 1980 and 1981 respectively. z : Wilcoxon's test statistic; Percent diff.: difference between years relative to 1980 data

Length group (mm)	n_1, n_2	z	p	Percent diff.
6	39, 3	-2.3935	0.0167	34.3
7	136, 15	-5.8011	0.00001	50.1
8	155, 58	-8.6939	0.00001	36.6
9	160, 82	-9.5851	0.00001	36.1
10	151, 27	-6.3198	0.00001	34.4
11	110, 49	-4.8624	0.00001	16.3
12	37, 9	-1.4122	0.1579	11.0

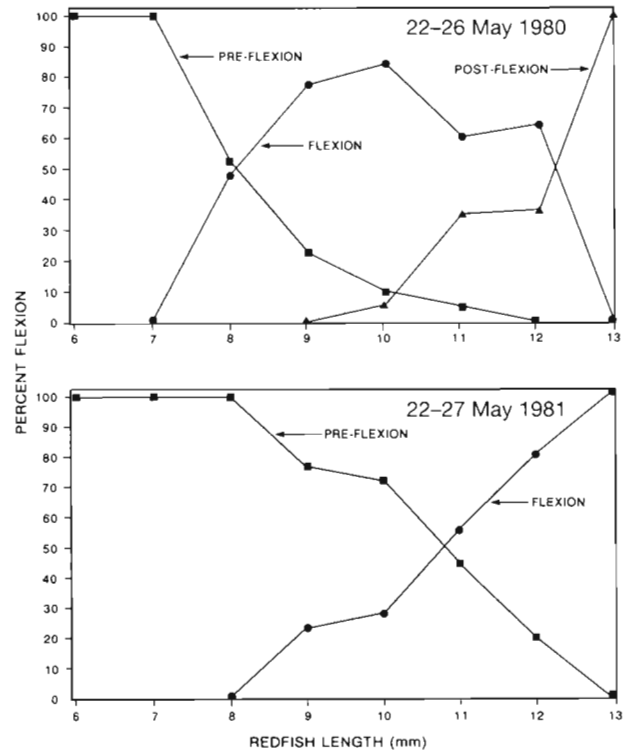


Fig. 6. *Sebastes* spp. Metamorphosis of redfish from larvae to pre-juveniles determined by the degree of flexion at different lengths (mm) for 20–26 May 1980 and 22–27 May 1981. Pre-flexion, flexion and post-flexion refer to flexion stages 1 to 3 respectively

larval period. In 1980 flexion had begun in 47.5% of redfish at 8 mm, 77.3% at 9 mm and was complete by 13 mm (Fig. 6). In 1981 no redfish at 8 mm had begun flexion while only 23.4% of the 9 mm larvae and 55.4% of the 11 mm larvae had begun flexion and all of the 13 mm larvae were in flexion (Fig. 6). Not only did redfish begin flexion at a larger size in 1981 but it occurred over a larger size range compared to 1980. Comparison of the percent of larvae that were in flexion as a function of length was statistically different ($p < 0.0001$, Kolmogorov-Smirnov test). Considering growth and metamorphosis of redfish size as a continuous process, then the size at which 50% of the redfish were in flexion differed by 2.72 mm between 1980 and 1981. Based on growth rates for these fish (Penney & Evans 1985), this equates to a time difference of 17 d at 1980 growth rates and 25 d at 1981 growth rates.

DISCUSSION

Diet and feeding of larvae

Both the maximum prey size and the variety of prey types increased in the diet, as redfish increased in size,

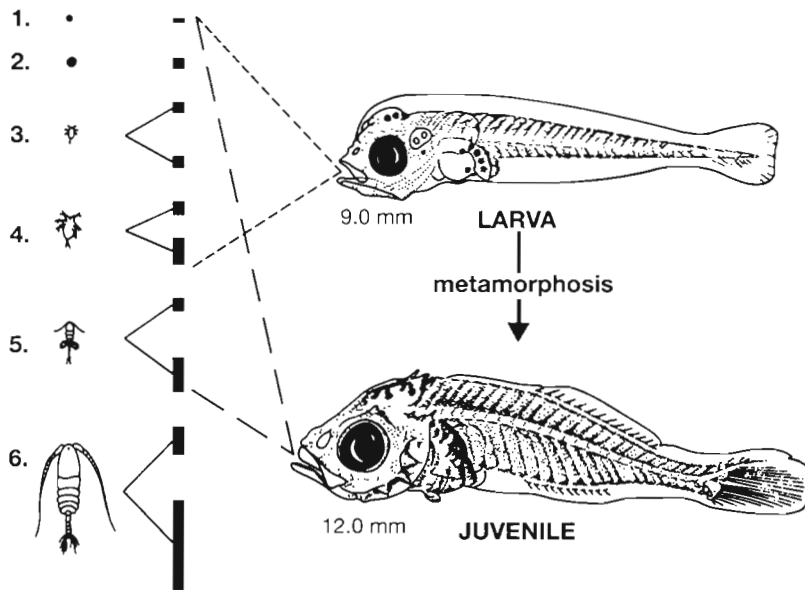


Fig. 7. *Sebastes* spp. Schematic representation of prey preferences for a 9.0 mm larva and a 12.0 mm pelagic juvenile redfish. The prey are represented as eggs, nauplii and copepodites for *Calanus finmarchicus* (Nos. 2, 4 and 6) and *Oithona similis* (Nos. 1, 3 and 5), with the bars representing their sizes, drawn to scale with respect to the redfish. The dashed lines enclose the preferred prey types. The figure emphasizes that *O. similis* copepodites are not a preferred prey, even though they are very similar in size to *C. finmarchicus* nauplii

from March to August. These observations are characteristic of fish larvae. Examples include redfish (Bainbridge & McKay 1968, Marak 1974), cod and haddock (Kane 1984), flounder, sole and dab (Last 1978), Atlantic herring (Cohen & Lough 1983), mackerel (Peterson and Ausubel 1984, Ware & Lambert 1985), sand lance (Ryland 1964, Monteleone & Peterson 1986), northern anchovy, Pacific sardine and jack mackerel (Arthur 1976). Only in highly selective feeders such as plaice (Shelbourne 1962, Ryland 1964, Last 1978) and English sole (Gadomski & Boehlert 1984) that feed exclusively on *Oikopleura* sp. does the variety of prey types not increase with increasing fish size, although the size does.

A change in diet will result from changes in prey availability, when prey selectivity has not changed. Seasonal differences in prey availability were more apparent for redfish larvae (≤ 9 mm), as the diet of these larvae differed while prey selectivities did not. Larval diet early in the season was dominated by copepod eggs and nauplii whereas by July–August the diet was dominated by *Oithona* spp. copepodites. Regardless of the season, larvae always selected copepod eggs and nauplii but did not select *Oithona* spp. copepodites, in spite of size ranges which are very similar (Fig. 7). *Calanus finmarchicus* eggs are approximately 0.135 mm in diameter (Bainbridge & McKay 1968)

while the nauplii range from 0.22 to 0.61 mm in length (Ogilvie 1956). By comparison, *Oithona similis* nauplii range in length from 0.115 to 0.215 (Gibbons & Ogilvie 1933) and copepodites from 0.230 to 0.515 mm total length (Conway & Minton 1975).

Other studies have demonstrated that fish larvae can have strong prey preferences for one or more species selected from a variety of prey types that are all within the same size ranges (Shelbourne 1962, Ryland 1964, Checkley 1982, Gadomski & Boehlert 1984, Monteleone & Peterson 1986). For example, cod and haddock larvae did not select *Oithona* spp. but preferred eggs, nauplii and copepodites of a small calanoid copepod (*Pseudocalanus* spp.) of comparable size (Kane 1984). Reasons why fish larvae prefer a particular prey type are not known. It has been hypothesized that fish larvae prefer relatively sessile prey that would be easily captured (Drenner et al. 1978). Alternatively, it has been hypothesized that larvae prefer moving, relatively active prey because

they are easier to see (Peterson & Ausubel 1984). In studies reporting the avoidance of *Oithona* spp. as a prey item it was hypothesized that the copepodites of this cyclopoid species hold their antennae at right angles to their body, effectively increasing the prey width thereby making them difficult to ingest (Cohen & Lough 1983, Kane 1984).

Seasonal cycles

The seasonal shift in diet of redfish larvae can be interpreted with respect to the seasonal production cycles of *Calanus finmarchicus* and *Oithona similis*, the 2 dominant copepod species on Flemish Cap (Anderson 1990). The seasonal dynamics of these 2 species are very different. *C. finmarchicus* is characterized as a large, herbivorous calanoid that spawns in spring in direct proportion to the spring bloom of diatoms (Krause & Trahms 1983, Runge 1988). While it may produce more than one generation each year, it is essentially univoltine in terms of its annual production (McLaren & Corkett 1986). It develops rapidly at rates directly dependent on water temperatures (Corkett et al. 1986), and stage development within the nauplii and copepodite stages results in relatively large increases in biomass at each stage (McLaren & Corkett 1986). On

Flemish Cap spawning began in March and peaked sometime in April. By the end of June the spring production of eggs and nauplii was complete, with copepodites (CV) predominating (Anderson 1990).

In contrast, *Oithona similis* is a small, omnivorous cyclopoid. It spawns independently of the spring bloom and is multivoltine, producing a number of generations with more or less continuous development for at least half the year (McLaren & Corkett 1986). Its relatively small size for all stages result in small biomass increases as each stage develops within each generation (op. cit.). While its development rate is temperature dependent, the increase in development rate is slow compared to *Calanus finmarchicus*, based on development rates given by McLaren (1978) for *O. similis* and Corkett et al. (1986) for *C. finmarchicus*. For example, at 7°C it takes *C. finmarchicus* 18 d to develop from an egg to stage CI, whereas it takes *O. similis* 37 d.

The seasonal diet change of redfish larvae with respect to the zooplankton indicates that available prey in the preferred size range of these larvae typically shifts from eggs and nauplii of *Calanus finmarchicus* to nauplii and copepodites of *Oithona similis*. Because redfish larvae did not actively select *Oithona* copepodites, the seasonal replacement in the diet of *C. finmarchicus* nauplii with *Oithona* copepodites may be disadvantageous to feeding, growth, and possibly survival of redfish larvae. This observation is supported, in part, by standardized stomach weights for redfish larvae. Values during April and May were always high compared to values in June–August which ranged from high to low in different years. Differences in the seasonal timing of the spring production of *C. finmarchicus* and the release of redfish larvae may result in poor larval feeding conditions.

Differences in larval diets, and therefore prey availability, also occurred for 1981 compared to 1980 and 1979. Redfish sampled in May 1981 predominantly ate cyclopoid nauplii and copepodites, compared to redfish in 1979 and 1980 which ate calanoid eggs and nauplii. As noted previously, the size ranges of these prey types are approximately equal. The low selection of *Oithona* copepodites by redfish larvae, together with the significantly lower feeding rates and relative condition of larvae in 1981, suggests that this food type was an inadequate replacement for *Calanus* sp. nauplii.

Prey concentrations

Differences observed between years in larval feeding rates and condition did not relate directly to prey concentrations. Densities and total biomass of cope-

pods were greater in May 1981 (Anderson 1990) than May 1980 even though feeding rate was lower. *Oithona* spp. and *Calanus finmarchicus* were approximately 3.7 and 2.4 times more abundant in 1981, respectively. While total copepod concentrations were higher in 1981 compared to 1980, *Oithona* spp. was relatively more abundant than *C. finmarchicus*. In addition, copepod nauplii were 4.2 times more abundant in 1981, although 94 % of these nauplii were classified as cyclopoids. These results indicate that total prey concentrations were greater in 1981 and this was especially true for *Oithona* spp. This difference in prey availability was reflected in the diet of redfish larvae that was dominated numerically by small cyclopoid nauplii and in biomass by *Oithona* spp. copepodites in 1981. However, even though prey concentrations were higher in 1981, the amount of food eaten, as weight per unit fish, was lower than in 1980, as was the relative condition of the redfish larvae. Feeding on many small prey items (cyclopoid nauplii) versus a few large items (calanoid nauplii) is generally considered to be disadvantageous to growth and survival (Pyke 1984). These results suggest that feeding conditions in 1981 were poor, not because of lower prey concentrations, but because these prey were, on average, one-tenth the size of the predominant prey eaten in 1980.

Metamorphosis

The diet of pelagic juvenile redfish was increasingly dominated by copepodites of *Oithona* spp. and *Calanus finmarchicus* as the season progressed and the fish grew. This coincided with an increased selectivity for *Oithona* spp. copepodites. Chronologically, the switch in diet from *C. finmarchicus* eggs and nauplii to *Oithona* spp. copepodites appears to begin sometime in June. This coincides with the metamorphosis of redfish from larvae to pelagic juveniles, the end of the spring development cycle when *C. finmarchicus* reaches stage CV (i.e. diapause), and the increased biomass of *Oithona* spp. relative to *C. finmarchicus* in the zooplankton community (Anderson 1990). Bainbridge & McKay (1968) reported a similar shift in the diet of redfish from *Calanus* eggs and nauplii to copepodites at 14 to 16 mm, which corresponds to redfish that have recently metamorphosed. The transition from larva to juvenile is probably an important phase in the life history of redfish. When they metamorphose redfish acquire fin rays and vertebrae which are expected to increase their swimming performance. In addition, they also develop gill rakers at this time which should aid in the retention of small food particles (Einarrson 1960, Bainbridge & McKay 1968), such as the nauplii of *Oithona* spp.

Coincident with the change in diet at metamorphosis there appeared to be an increase in feeding rate, based on standardized stomach weights. This was true when comparing values for larvae in early and late May 1981 (0.085 and 0.132 $\mu\text{g mm}^{-3}$ respectively) versus juveniles sampled in late June and early August (0.351 and 0.311 $\mu\text{g mm}^{-3}$ respectively) of the same year. During each cruise in 1981, the diet was dominated by copepodites (Table 2). Improved feeding following metamorphosis might occur due to an increased ability to capture *Oithona* spp. copepodites, which dominate the prey field at this time of year.

There was a consistent difference between years, where larval redfish ate more, were in better condition and metamorphosed at smaller sizes in 1980. In addition, these redfish grew significantly faster (Penney & Evans 1985). These results indicate that size at metamorphosis is adaptive, shortening the larval period when conditions for feeding and growth are favourable. Experimental studies have demonstrated that fish larvae which grew faster went through metamorphosis earlier, at smaller sizes, and were larger than fish that metamorphosed later, when compared at a common age (Chambers & Leggett 1987, Chambers et al. 1988). Given the seasonal succession of zooplankton on Flemish Cap, it is reasonable to hypothesize that an earlier metamorphosis is generally advantageous for feeding, and subsequently growth and survival of redfish.

Match/mismatch of redfish and their prey

Redfish release larvae predominantly in association with the spring spawning of *Calanus finmarchicus*, when the preferred prey of redfish larvae are plentiful. When the timing of appearance of first-feeding larvae is relatively constant but annual phytoplankton and zooplankton production varies there will be good and poor matches of fish larvae and their food, as outlined by Cushing (1975, 1990). Results of this study indicate that redfish larvae occurred in association with the annual spawning and production cycle of *C. finmarchicus* in 1980, but not in 1981.

Analysis of the zooplankton on Flemish Cap demonstrated that the seasonal production cycle of *Calanus finmarchicus* was earlier in 1981, a year of significantly warmer temperatures (Anderson 1990). The difference between 1980 and 1981 could be explained by temperature-dependent development but also may have been due to an earlier spawning of *C. finmarchicus*. In contrast, the time of peak release of redfish larvae was not different in 1980 and 1981 (Penney & Evans 1985). Therefore, it appears a poor match occurred between redfish larvae and their preferred prey in 1981. Such a

mismatch is supported by observations on larval diet and relative feeding rates. Further, these observations suggest that the match of redfish larvae with their preferred prey is dependent on both the onset of copepod spawning and their rate of temperature dependent development during spring. It is also noteworthy that the higher overall concentrations of copepods (primarily nauplii and copepodites of *Oithona* spp.) in 1981 did not compensate for availability of the preferred prey of redfish larvae.

Ellertsen et al. (1989) have reported a similar match/mismatch of cod larvae and their prey. They reported that the time of peak cod spawning only varied by 1 wk over many years, in contrast to peak spawning of *Calanus finmarchicus* which varied by almost 7 wk. Poor matches of cod larvae with their prey occurred during both warmest and coldest years, with early spawning of *C. finmarchicus* occurring during warm years. Finally, they reported that the food of cod larvae is predominantly eggs and nauplii of *C. finmarchicus* but that during the warmest year recorded (1960) cod larvae fed predominantly on *Oithona* spp. (Sysoeva & Degtyareva 1965) which lead to a poor year-class of cod. The similarity of these observations to those observed for Flemish Cap redfish suggest that the timing of spring spawning of *C. finmarchicus* and its subsequent temperature dependent development is a critical determinant of larval fish feeding, growth and ultimately survival in marine systems dominated by this large herbivorous zooplankton.

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