Food Consumption of Squids (*Illex illecebrosus* and *Loligo pealei*) off the Northeastern United States

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Abstract

Estimates of the seasonal and annual food consumption by *Illex illecebrosus* and *Loligo pealei* in NAFO Subareas 5 and 6 of the Northwest Atlantic were made from samples collected during spring, summer and autumn surveys of the continental shelf from the Gulf of Maine to Cape Hatteras. Euphausiids made up a considerable proportion of the diets of both species in the spring offshore, but fish and squid were the major components of the stomach contents in summer and autumn. Overall, predation on fish was greater for *Loligo* and cannibalism was greater for *Illex*. Consumption estimates varied with predator size, feeding intensity and predator biomass.

Introduction

Two species of squid, the short-finned *Illex illece-brosus* and the long-finned *Loligo pealei*, are of commercial importance in the Northwest Atlantic. In 1981-82, the average annual catch of short-finned squid was 39,800 (metric) tons, of which 17,400 tons were taken off the United States in NAFO Subareas 5 and 6. The average catch of long-finned squid during the same period was 21,400 tons, all of which were taken in Subareas 5 and 6. Estimates of minimum abundance have been in the range of 18–124 million short-finned squid and 1.2–4.3 million long-finned squid off the northeastern United States (Lange, MS 1982).

Short-finned squid migrate seasonally onto the continental shelves from the Mid-Atlantic Bight to Newfoundland, where they feed during the summer, and they migrate offshore in late autumn. Long-finned squid migrate seasonally to shallow inshore waters from Cape Cod to Chesapeake Bay in spring and summer to spawn. Spawning usually peaks in spring and autumn, resulting in two distinct cohorts (Summers, 1971; Mesnil, 1977). The juveniles grow rapidly and feed intensively until late autumn when they move offshore (Lange, MS 1982).

This paper focuses on the role of both species as predators. The importance of cannibalism and predation on fish is compared between species and between years from material collected in 1979 and 1980. For brevity, these squid are called *Illex* and *Loligo* in the remainder of this paper.

Materials and Methods

In 1979 and 1980, *Illex* and *Loligo* were collected from trawl catches during spring, summer and autumn

groundfish surveys of inshore and offshore areas from the Gulf of Maine to Cape Hatteras (Fig. 1). Generally, inshore surveys sampled strata less than 40 m deep and offshore surveys sampled strata depths greater than 40 m. At each station, squid were randomly sampled by size and preserved in a formaldehyde solution. In the laboratory, squid were measured (dorsal mantle length to the nearest cm) and stomach contents were identified to the lowest possible taxa and weighed to the nearest 0.001 g. Food items which could not be identified were categorized as animal remains. For the purpose of this analysis, the weight of animal remains was apportioned among the identified prey, and prey categories which accounted for less than 0.1% of the stomach contents by weight were omitted.

Food consumption was calculated by using an exponental model (Elliot and Persson, 1978; Eggers, 1979),

$$\frac{dS}{dt} = R - \alpha S$$

where S is the level of food in the stomach, R is the rate of food intake and α is the instantaneous rate of gastric evacuation. This is a volume-dependent model which has been used extensively to estimate consumption of food by fish (Tyler, 1980; Elliot and Persson, 1978; Durbin and Durbin, MS 1980; Cohen and Grosslein, 1981).

Very little information exists on the evacuation rates of squid. Fange and Grove (1979) found that the time of evacuation was related to temperature when fish were grouped by feeding types. Known stomachevacuation times were plotted in fig. 4 of Fange and Grove (1979) (Fig. 2). Values which were reported for *Illex* at 10°C (Boucher-Rodini, 1975; Wallace *et al.*, 1981) and for *Loligo opalescens at 18*°C (Karpov and Caillet, 1978) fall within the area of evacuation times for



Fig. 1. Stations where Illex and Loligo were sampled for analysis of food habits, 1979-80.

microphagous fish. A line connecting the most commonly cited evacuation time at 10° C (12 hr) and the point for *L. opalescens* at 18° C (6.6 hr) is similar in slope to that of Jones (1974) for fish. If the relationship of Fange and Grove (1979) for fish is assumed to be valid for squid, the gastric evacuation time (t) can be described by

$$t = 25.3353 e^{-0.0747T}$$

or, following Durbin and Durbin (MS 1980),

$$\alpha = ae^{bT} = 0.1818 e^{0.0747}$$

where α is the instantaneous gastric evacuation rate and T is temperature (°C). From this relationship, α values were estimated for mean temperatures at which the squid were caught during the surveys (Table 1). Average stomach contents (\overline{S}) were calculated by assuming that samples were random within survey strata and with respect to time. Mean weights of individual food components (prey types) were estimated for 5-cm length groups of squid in samples from each survey. If a size group was undersampled for stomachcontent analysis, it was omitted from the consumption estimate. Because sampling adequacy was related to the estimates of biomass, this procedure probably had a minimal effect on the final estimates of consumption.

Average daily ration (\overline{D}) was estimated from the modified Bajkov equation (Eggers, 1979; Pennington, MS 1981), where $\overline{D} = 24.\alpha.\overline{S}$. Estimates of daily ration were expressed as percent of body weight of squid. Estimates of minimum biomass were calculated for



Fig. 2. Shaded area shows gastric evacuation time (t) in relation to temperature (T) for microphagous fish (after Fange and Grove, 1979), together with known evacuation times for squid (Boucher-Rodoni, 1975; Karpov and Cailliet, 1978, Wallace *et* al., 1981).

TABLE 1. Temperature (T) and instantaneous digestion rates (*a*) used for calculation of daily rations of *Loligo* and *Illex*, 1979–80.

	Lo	oligo	L	llex
Season (area)	T°C	α	Т°С	α
· · · · · · · · · · · · · · · · · · ·	19	79		
Spring (offshore)	9.6	0.3724	9.9	0.3809
Summer (inshore)	16.0	0.6007	-	
Summer (offshore)	11.0	0.4135	9.0	0.3561
Autumn (inshore)	16.5	0.6236		
Autumn (offshore)	11.9	0.4422	10.6	0.4031
	19	80		
Spring (offshore)	9.8	0.3766	10.0	0.3837
Summer (inshore)	15.0	0.5575	-	_
Summer (offshore)	9.5	0.3697	8.5	0.3430
Autumn (inshore)	16.0	0.6007		
Autumn (offshore)	12.8	0.4730	10.1	0.3886

each survey with the computer program which has been in regular use for analysis of groundfish survey data. Length-weight relationships for *Illex* and *Loligo* (Lange and Johnson, 1981) were used to convert predator length to body weight.

Estimates of food consumption were derived by multiplying the daily ration (% of body weight) of each size-group of squid by the appropriate biomass (tons) and expanding to quarterly consumption (\times 90 days). Inshore and offshore estimates of consumption were summed for *Loligo* within the summer and autumn quarters. Estimates of *Illex* consumption were based on offshore surveys only.

TABLE 2. Food of Illex and Loligo (expressed as % of stomach contents by weight) in samples from Subareas 5 and 6 of the Northwest Atlantic, 1979-80.

	. III	эx	Lol	Loligo		
Prey	1979	1980	1979	1980		
Polychaetes		0.1		0.5		
Amphipods (gammarids)			1.3			
Decapods (shrimp)	—	0.7	_			
Euphausiids	9.0	1.0	20.8	4.8		
Copepods (Candacia)			1.3			
Unidentified crustaceans	6.6	30.0	12.1	5.2		
Total crustaceans	15.6	31.7	35.5	10.0		
Squid	45.8	49.3	13.3	28.2		
Fish	38.1	18.8	51.2	61.2		
No. of stomachs examined	692	745	969	673		
No. of stomachs empty	120	190	156	185		
Mean stomach content (g)	1.92	0.74	0.46	0.71		
Mean content (% body wt.)	1.01	0.57	0.85	1.31		
Mean predator size (cm)	21	18	12	12		

Results

Major differences were evident in the overall food habits of *Illex* and *Loligo* in 1979 and 1980 (Table 2). Squid ranked first as prey for *Illex* in both years, followed by fish in 1979 and crustaceans in 1980. The incidence of empty *Illex* stomachs was higher in 1980 (26%) than in 1979 (17%) and the mean stomach content was lower in 1980. *Loligo* fed primarily on fish in both years (50–60%), followed by crustaceans in 1979 and squid in 1980.

For *Illex*, the composition of prey varied considerably with predator size (Table 3). Young animals (6–10 cm) fed predominantly on squid in both years. Squid decreased in importance in the next size-group (11–15 cm), which fed mostly on fish in 1979 and crustaceans in 1980. The primary prey of 16–20 cm *Illex* in both years consisted of crustaceans, which decreased in importance with size of larger predators. Squid prey increased in importance for larger predators and strongly dominated the diet of the larger size-groups. Stomach content weight increased with predator size in both years, with the exception of the poorly sampled 31–35 cm size-group in 1979. The ranges of mean stomach content (% body weight) were 0.04–1.33 in 1979 and 0.18–0.92 in 1980.

For *Loligo*, the composition of prey also varied with predator size (Table 4). In the smaller predators (1–15 cm), squid accounted for 50–58% of the stomach contents by weight in 1979, with crustaceans being 32–42% of the diet. Fish represented less than 50% of the diet of 16–25 cm predators, but it increased significantly with predator size greater than 25 cm. In 1980, fish was dominant (67–100%) in all size-groups except

		Food cons	umption by	predator	ength (cm))
Prey	6-10	11-15	16-20	21-25	26-30	31-35
		1979				
Total crustaceans	_	4.7	71.3	14.7	5.6	
Chaetognaths		0.4				
Squid	57.7	2.6	14.7	32.8	81.0	100.0
Fish	42.3	92.1	14.0	52.5	13.4	
No. of stomachs examined	35	56	132	377	90	1
No. of stomachs empty	18	13	14	50	26	(
Mean stomach content (g)	0.01	0.55	0.98	2.17	3.91	0.5
Mean content (% body wt.)	0.04	1.33	0.68	1.01	1.15	1.1
Mean predator size (cm)	9	12	19	22	26	32
		1980				
Polychaetes		9.5				
Total crustaceans	29.9	48.9	58.3	28.6	22.2	-
Squid	67.1	27.3	20.1	44.9	74.3	-
Fish	2.9	14.2	20.5	25.2	3.4	
No. of stomachs examined	46	161	222	263	44	
No. of stomachs empty	20	46	63	56	5	
Mean stomach content (g)	0.03	0.09	0.32	1.17	3.46	·
Mean content (% body wt.)	0.23	0.18	0.25	0.54	0.92	-
Mean predator size (cm)	8	13	18	22	27	-

TABLE 3. Food composition (% by weight) of *Illex* by size group in samples from Subareas 5 and 6, 1979-80.

TABLE 4. Food consumption (% by weight) of *Loligo* by size group in samples from Subareas 5 and 6, 1979-80.

		Food	l compositi	on by prec	ator length	n (cm)	
Prey	1-5	6-10	11-15	16-20	21-25	26-30	31-35
		197	'9				
Amphipods (gammarids)	4.6	2.8	2.9				
Copepods (Candacia)		11.1			_		
Decapods (shrimp)	1.000		1.0				
Euphausiids		2.3	20.7	17.6	33.6		
Unidentified crustaceans	37.2	15.8	11.8		13.0		
Total crustaceans	41.8	32.0	36.4	17.6	46.6	—	
Chaetognaths		2.3	0.5				
Squid		14.9	5.2	24.3	9.6	19.2	-
Fish	58.1	50.3	57.1	43.6	43.7	80.7	100.0
No. of stomachs examined		390	250	131	90	20	2
No. of stomachs empty	23	62	40	13	14	4	0
Mean stomach content (g)	0.02	0.12	0.35	1.17	1.45	1.05	5.98
Mean content (% body wt.)	0.43	0.55	0.64	1.02	0.72	0.34	1.44
Mean predator size (cm)	4	8	12	17	22	27	31
		198	30				
Polychaetes		7.8					
Euphausiids		5.4	10.3	3.4	_		
Unidentified crustaceans	17.9	26.2	3.6	2.7	6.8		
Total crustaceans	17.9	31.6	13.9	6.1	6.8	<u></u>	
Squid	_	26.8	18.8	47.1	10.1		
Fish	82.1	44.5	67.2	46.7	83.0	100.0	
No. of stomachs examined		227	241	98	45		
No. of stomachs empty	35	47	64	28	8	3	
Mean stomach content (g)	0.03	0.38	0.53	1.47	2.07	3.20	
Mean content (% body wt.)	0.59	1.70	0.83	1.29	1.04	1.04	
Mean predator size (cm)	4	8	13	17	22	27	

			1979	1980						
	Spring Summer		Autumn		Spring	Summer		Autumn		
Prey	OS	IS	OS	IS	OS	OS	IS	OS	IS	OS
Polychaetes			_				2.4			
Euphausiids	95.0	0.5	0.3		10.1		_	1.7		
Other crustaceans	1.1	3.7	11.4	2.8	7.6	90.0	10.0	41.8		20.6
Total crustaceans	96.1	4.2	11.7	2.8	17.7	90.0	10.0	43.5	-	20.6
Squid		3.0	76.1	12.0	67.0	5.0	1.3	40.5		67.5
Fish	3.9	92.7	12.0	85.2	15.3	5.0	86.3	15.9		11.8
No. of stomachs examined	44		236	43	291			354		281
No. of stomachs empty	0	3	11	6	100	7	11	100		72
Mean stomach content (g)	1.83	4.35	1.87	1.21	1.43	0.04	0.60	0.75	_	0.89
Mean content (% body wt.)	2.41	2.29	0.98	0.50	0.75	0.07	0.66	0.52		0.71
Mean predator size (cm)	15	21	21	23	21	13	16	19		18

TABLE 5. Seasonal (quarterly) composition of food, expressed as percent of stomach contents by weight, of *Illex* from inshore (IS) and offshore (OS) areas of Subareas 5 and 6, 1979-80.

 TABLE 6.
 Seasonal (quarterly) composition of food, expressed as percent of stomach contents by weight, of Loligo from inshore (IS) and offshore (OS) areas of Subareas 5 and 6, 1979-80.

			1979			1980					
	Spring Summer		mer	Autumn		Spring	Summer		Autumn		
Prey	OS	IS	OS	IS	OS	OS	IS OS		IS	OS	
Polychaetes							7.2				
Amphipods (gammarids)		6.3									
Copepods (Candacia)			14.4								
Decapods (shrimp)		1.8									
Euphausiids	50.8					15.1					
Unidentified crustaceans	12.7	4.9	28.9		15.3	5.5	19.6	13.3	1.1	2.3	
Total crustaceans	63.5	13.0	43.3	_	15.3	20.6	19.6	13.3	1.1	2.3	
Chaetognaths		0.4		1.0		_	_	_	_		
Squid	4.6	38.3	_	1.6	11.7		7.3	25.5		61.9	
Fish	29.9	47.7	55.5	93.7	72.5	79.4	65.9	61.1	98.8	35.8	
No. of stomachs examined	154	233	113	95	359	148	106	131	27	214	
No. of stomachs empty	5	27	2	28	91	2	34	50	2	71	
Mean stomach content (g)	1.46	0.40	0.42	0.03	0.21	1.77	0.12	0.29	0.07	0.64	
Mean content (% body wt.)	1.70	0.90	1.20	0.20	0.40	2.77	0.19	0.64	0.29	1.41	
Mean predator size (cm)	15	11	10	7	12	13	13	11	10	11	

6–10 and 16–20 cm predators. Crustaceans peaked in importance (32%) as food in 6–10 cm *Loligo* and then decreased in importance with size of larger predators. Cannibalism was greatest (47%) in the 16–20 cm size-group. Stomach content weight increased with predator size, with the exception of one size-group in 1979. The ranges of mean stomach content (% body weight) were 0.34–1.44 in 1979 and 0.59–1.70 in 1980.

A consistent seasonal feeding pattern was evident for *Illex* in both years (Table 5). In 1979, offshore feeding changed almost exclusively from crustaceans (mostly euphausiids, 95%) in the spring to a cannibalistic diet in the summer (76%) and the autumn (67%). A similar pattern occurred offshore in 1980, but crustacenas made up a larger proportion of the summer diet (44%) before the shift to autumn cannibalism (67%). Inshore feeding in both years was dominated by fish (85–93%). The percentages of empty stomachs from the offshore area in summer and autumn were 5% and 34% in 1979 and 28% and 25% in 1980 respectively. In 1979, the mean stomach content (% body weight) was high in the spring (offshore) and summer (inshore) but was much lower in the remaining season-areas. In 1980, this parameter was lowest in spring (inshore).

Consistent seasonal and inshore-offshore feeding patterns were evident for *Loligo* (Table 6). In both years, the spring population fed on crustaceans and fish in the offshore area, with euphausiids (51%) being

			1979			1980					
Prey	Spring	Summer	Autumn	Total	(%)	Spring	Summer	Autumn	Total	(%)	
				llləx							
Crustaceans	4,659	37,695	17,636	59,990	(23)	63	95,559	7,718	103,340	(42)	
Squid	16	141,103	21,501	162,620	(64)	3	75,021	23,895	98,919	(40)	
Fish	574	25,350	7,288	33,212	(13)	3	32,395	11,054	43,452	(18)	
Total consumption (C)	5,249	204,148	46,425	255,822		69	202,975	42,667	245,711		
Illex biomass (B)	271	30,980	42,878			121	63,641	14,026			
Ratio (C/B)	19.4	6.6	1.1			0.6	3.4	3.0			
				Loligo							
Crustaceans	35,650	53,574	5,788	95,012	(52)	21,570	3,586	32,868	58,024	(8)	
Squid	1,196	12,210	554	13,960	(8)		1,693	313,599	315,292	(45)	
Fish	18,838	32,397	22,081	73,316	(40)	63,090	15,776	251,035	329,901	(47)	
Total consumption (C)	55,684	98,181	28,423	182,288		84,660	21,055	597,502	703,217		
Loligo biomass (B)	7,371	10,891	22,369			4,438	6,364	35,148			
Ratio (C/B)	7.6	9.0	1.3			19.1	3.3	17.0			

TABLE 7. Quarterly estimates of prey consumption (tons) relative to estimates of biomass of Illex and Loligo in Subareas 5 and 6, 1979-80.

dominant in 1980. In summer, both inshore and offshore diets were primarily fish (48-66%), and fish (94-99%) remained an important component of the inshore diet in the autumn of both years. During autumn in the offshore area, Loligo fed heavily on fish (73%) in 1979 but became more cannibalistic (62%) in 1980. The highest percentages of empty stomachs occurred during the autumn (29% inshore and 25% offshore) of 1979 and during the summer (32% inshore and 38% offshore) and autumn (33% offshore) of 1980. In 1979, the mean stomach content (% body weight) was highest in the spring (offshore), intermediate in the summer (inshore and offshore) and low in the autumn (inshore and offshore). In 1980, this parameter was highest in the spring (offshore) low in the summer and autumn (inshore) and higher in the autumn (offshore).

The estimates of food consumption by both species reflect major patterns in diet composition and daily ration. The spring consumption of food (mainly crustaceans) by Illex was lowest in both years and contributed less than 2% of the annual estimates. The summer consumption of food was highest in both years and made up over 80% of the annual estimates. During this season, cannibalism was 69% of the quarterly estimate in 1979 and 37% in 1980. Predation on fish was highest in the summer of both years, consisting of 12-15% of the total consumption in that quarter. Consumption in the autumn decreased to about 17% of the annual estimate for both years, with cannibalism accounting for 45% and 54% of the quarterly estimates for 1979 and 1980 respectively. The estimates of total food consumption by Illex in 1979 and 1980 differed by only 5%. Cannibalism and predation on fish accounted for 64% and 13% of the estimate of total consumption respectively in 1979 and for 40% and 18% of the estimate of total consumption respectively in 1980.

The seasonal consumption of prey by *Loligo* in 1979 was strongly dominated by crustaceans and fish (Table 7). Consumption was highest in the summer and lowest in the autumn, and cannibalism followed the same trend. The annual consumption was composed of crustaceans (52%), fish (40%) and squid (8%). In 1980, consumption of prey was lowest in the summer and highest in the autumn, the latter being 84% of the annual estimate. Total consumption in the autumn consisted of crustaceans (5%), fish (42%) and cannibalism (53%). The overall annual consumption was composed of crustaceans (8%), fish (47%) and cannibalism (45%).

Discussion

Estimates of food consumption for Georges Bank (E. B. Cohen and M. D. Grosslein, Northeast Fisheries Center, Woods Hole, Mass., pers. comm.) rank squid (*Illex* and *Loligo*) as major consumers of fish and squid, second only to silver hake in the fish community. They estimated food consumption by squid to be 17.4 Kcal/m²/yr, of which approximately 50% was assumed to be fish and squid. Although data for Georges Bank are not analyzed separately in the present analysis, the percentages of consumed fish and squid were found to be consistently higher (62–83% by *Illex* and 64–89% by *Loligo*) for Subareas 5 and 6 as a whole. The results indicated that *Loligo* is a major fish predator, with fish making up over 50% of the diet in 1979 and 1980.

The consumption of prerecruit fish and squid by *Loligo* can be crudely assessed. If the upper limit of prey size is roughly equal to mantle length of predator (O'Dor *et al.*, 1980), approximately 80% of the total fish and squid consumption in the autumn of 1979 and 75% of the total fish and squid consumption in the autumn

of 1980 were by small *Loligo* (≤ 10 cm). In that quarter, the consumption of prerecruit fish (≤ 10 cm) was estimated to be about 17,600 tons in 1979 and 188,000 tons in 1980, and the consumption of prerecruit squid (≤ 10 cm) was estimated to be 443 tons in 1979 and 235,000 tons in 1980. Fish species, with prerecruits in this size range during autumn, include Atlantic cod, haddock, yellowtail flounder, silver hake, Atlantic butterfish, scup, Atlantic mackerel, Atlantic herring, Atlantic menhaden and sand lance. The high degree of intra-cohort cannibalism that was observed in 1980 was associated with a strong pulse of fast-growing juvenile squid (1–5 cm).

Cannibalism by *Illex* does not appear to be a function of population biomass. In the summer of 1979, when the biomass was 30,000 tons, cannibalism was higher than in the other seasons. However, in the following summer, when the biomass was 63,000 tons, cannibalism was reduced to only half of the 1979 level. This indicates that the availability of alternate prey may be the primary mechanism which controls cannibalism in *Illex*.

The spring samples of *Illex* and *Loligo* were from catches along a narrow band on the outer edge of the survey area. The 100 m isobath along this edge is associated with the 10° C isotherm. Results of the present analysis indicated that both squid species fed intensively on euphausiids, which are prevalent at this time in the mid-Atlantic and southern New England offshore regions. Illex and Loligo fed almost exclusively on euphausiids in both regions (92-98% by weight) in 1979. Amaratunga (1983) reported that the feeding activity of Illex on the Scotian Shelf is closely associated with the seasonal availability of euphausiids. This could be an important consideration if the availability of euphausiids is low, because squid may become more cannibalistic or increase predation on co-occurring fish species. Fish predation by Illex in the spring seems to be negligible, but *Loligo* evidently consumes significant quantities of fish during this period. Species which co-occur with Loligo offshore in the spring include Atlantic butterfish, Atlantic mackerel and silver hake (Lange, MS 1978).

The peak biomass (63,600 tons) of *Illex* in the summer of 1980 was unexpected (Table 7). Past survey records indicated that this species was traditionally more abundant on the shelf in the autumn. This summer abundance in 1980 does not appear to have been linked to prey availability, because the C:B ratio (3.4) is only about half of the 1979 value (6.6) for the same season. All other biomass estimates for 1979 and 1980 fall within traditional limits (Lange, MS 1982).

Several sources of error should be noted. The catchability of squid was assumed to be 100%. However, the pelagic schooling habit of these squid species makes the groundfish survey trawl an inadequate sampling gear. No catchability coefficients are available for squid, but the catchability of haddock is considered to be 45% (Clark and Brown, 1977). Application of this factor to squid would increase the minimum biomass estimates by a factor of 2.2. This is quite conservative when the differences between the behavior of squid and haddock are considered. The timing of the groundfish surveys may not sample the Loligo population each year at the same point in the spawning season. The location of the slope water-shelf water frontal zone in the spring could influence squid abundance in the survey area. The rates of digestion for both species need to be determined experimentally for different sizes of predators, types of prey, sizes of meals, and temperatures. Because very small squid (<5 cm) are not retained completely by the groundfish trawl, they were evidently undersampled for this analysis of food habits.

Experiments are being conducted on stomach contents to determine if electrophoresis can be used as a method of identifying fish prey to the species level. If successful, this method would provide the data which are necessary to assess the effects of squid predation on individual fish stocks, especially predation by juve-nile *Loligo* on larval and postlarval fish. Nevertheless, the rather crude estimates of food consumption in this paper indicate that predation on fish and squid by *lllex* and *Loligo* may be a significant source of prerecruit mortality.

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