Vol. 59: 55–61, 1990 | MARINE ECOLOGY PROGRESS SERIES Mar. Ecol. Prog. Ser. | Published January 11

Predation and food limitation as causes of mortality in larval herring at a spawning ground in British Columbia

Jennifer E. Purcell[1], Jill J. Grover[2]

[1] University of Maryland, Horn Point Environmental Laboratories, PO Box 775, Cambridge, Maryland 21613, USA
[2] Oregon State University, Hatfield Marine Science Center Newport, Oregon 97365, USA

ABSTRACT: We quantified both in situ predation on Pacific herring (*Clupea harengus pallasi*) larvae by soft-bodied zooplankton, and microzooplankton prey of herring larvae in Kulleet Bay, Vancouver Island, British Columbia. Samples were collected at 0 to 5 m depth daily at peak larval hatching from 14 to 21 April 1985. The hydromedusa *Aequorea victoria* was the only soft-bodied zooplankter that ate herring larvae. Densities of *A. victoria* reached as much as 17 m^{-3}, and averaged 1 to 5 m^{-3}. Predation on the herring larvae was severe, averaging 57 ± 29 % d^{-1} of the larvae during each sampling period. Microzooplankton prey of post-yolksac herring larvae were mainly copepod nauplii and eggs, shelled protozoans, and bivalve veligers, and averaged 40.8 ± 21.5 l^{-1} in the environment. Thirty-five percent of the larvae contained between 1 and 30 prey items. Feeding by soft-bodied zooplankton equalled only 0.2 % of the standing stock of microzooplankton and could not reduce their populations. We conclude that predation was a major source of mortality of herring larvae in Kulleet Bay in 1985, and that food limitation was not important.

INTRODUCTION

Many species of soft-bodied zooplankton (pelagic cnidarians, ctenophores, and chaetognaths) have been shown to feed on larval fishes (reviewed in Alvariño 1985 and Purcell 1985). Predation rates on Atlantic herring larvae by the scyphomedusa *Aurelia aurita* were estimated at 4.4 and 2.6 % d^{-1} of the standing stock in 1979 and 1980, respectively (Möller 1980). Predation by the hydromedusa *Aequorea victoria* on Pacific herring larvae was calculated at 0.7 % d^{-1} in 1983 (Purcell 1989), and at 0 to 12.5 % d^{-1} in 1984 (Purcell in press). These estimates differed between years because of differences in the population sizes of the predators.

Starvation has been thought to be a major cause of mortality in larval fishes, because the results of many laboratory experiments indicated that prey densities needed for larval survival were greater than found in situ (reviewed in McGurk 1984 and Leggett 1986). Recently, the importance of starvation has been questioned for 2 reasons. First, results from large enclosures have shown good survival of Atlantic herring larvae at prey densities 10 to 100 times lower than earlier estimates (Gamble et al. 1981, Øiestad & Moksness 1981, Kiørboe et al. 1985). Second, techniques developed to recognize starving larvae in situ generally have found low numbers of larvae in poor condition (O'Connell 1980, Theilacker 1985, Buckley & Lough 1987).

Soft-bodied zooplankton are potentially predators of fish larvae and competitors with them for food. Möller (1980) showed overlap in the diets of the scyphomedusa *Aurelia aurita* and herring larvae, but he quantified only predation on the larvae. Frank (1986) estimated ingestion of zooplankton and haddock *Melanogrammus aeglefinus* eggs and larvae by the ctenophore *Pleurobrachia pileus*, and concluded that the only possible effect on the fish larvae was reduction of food densities. Taggart & Leggett (1987) found no significant correlations of larval capelin *Mallotus villosus* mortality with the densities of chaetognaths and jellyfish, or with microzooplankton prey of larvae. The above studies do not show that foods of larval fishes are reduced by soft-bodied zooplankton, and the possible importance of competition for food remains uncertain.

The present study was the third year of a project on predation by soft-bodied zooplankton on fish larvae. Weekly sampling in the first year from March to June,

1983 in Kulleet Bay, Vancouver Island, British Columbia, Canada, showed feeding by the hydromedusa *Aequorea victoria* on fish larvae in 8 families and on pelagic fish eggs (Purcell 1989). In the second year, population densities of soft-bodied zooplankton varied by 1000-fold, and microzooplankton densities varied by 10-fold, indicating that recently-hatched herring larvae *Clupea harengus pallasi* encountered very different predator and food conditions in 28 locations sampled in April 1984 in British Columbia (Purcell in press). In the present study, we undertook intensive sampling from 14 to 21 April 1985 in Kulleet Bay to address the following objectives that were stimulated from the earlier research: (1) to determine daily variations in predation impact by *A. victoria* on herring larvae, and (2) to determine the likelihood of larval food limitation through analysis of the gut contents of herring larvae and in situ microzooplankton densities. The importance of predation by *A. victoria* on herring larvae in Kulleet Bay is compared among the 3 years.

MATERIALS AND METHODS

Study area. Kulleet Bay is a shallow embayment along the southeastern coast of Vancouver Island (Fig. 1 in Purcell 1989). Pacific herring spawn consistently each spring in the area between Yellow Point and Coffin Point, which includes Kulleet Bay (Hourston 1981). In 1985, the annual spawning occurred in Kulleet Bay on April 1. Three stations within the 1 km wide bay were sampled: (1) near the northern shore (rocky, steep slope, < 10 m depth), (2) mid-bay, 23 m depth, and (3) near the southern shore (sandy, gradual slope, < 5 m depth).

Plankton collection. Plankton samples were collected daily from 14 to 21 April 1985 for data on crustacean zooplankton, fish larvae, and soft-bodied predator densities. A 0.75 m diameter, 333 μm mesh conical plankton net fitted with a flowmeter was towed horizontally at 1 m depth at all stations and also at 5 m depth at Stns 1 and 2. Two tows were made of 0.5 to 1 min duration at each depth in order to prevent clogging of the net (mean volume filtered = 9.22 m^3 ± 2.6 [SD]). After each tow, the net was rinsed thoroughly into the cod end. Formaldehyde buffered with sodium borate was added to the samples to bring the final concentration to 5% formalin. Sampling was restricted to the surface 5 m for accuracy in estimating predation rates, as discussed in Purcell (1989).

In the laboratory, *Aequorea victoria* medusae were removed from the samples and counted before subsampling with a Folsom plankton splitter. All specimens of each taxonomic group were counted from one or more subsamples. All gelatinous predators were identified to species, fish larvae other than herring identified to family, and other zooplankton identified to order. Densities of plankton organisms are expressed as their mean number m^{-3} ± SD for all tows of a sample set.

Microzooplankton were sampled with a 0.5 m diameter, 63 μm mesh conical plankton net that was dropped mouth first to 5 m depth and retrieved, filtering 2 m^3. One sample was taken at each station daily. These samples were preserved with buffered formaldehyde. In the laboratory, they were split using a Folsom plankton splitter, and one eighth sample was diluted with seawater to 1 l volume. All zooplankton were counted in 3 subsamples taken with a 5 ml Hensen stempel pipette.

Dietary analysis. For gut content analysis, *Aequorea victoria* was collected individually in order to prevent either gut evacuation or ingestion of prey during collection in plankton net tows. Collections were made at 0 to 1.5 m depth at the same times and stations as the plankton tows, by use of a 0.5 l beaker with a mesh bottom. Samples were immediately preserved in 5 to 10% buffered formaldehyde solution. The gut contents of all hydromedusae collected in the plankton samples were examined for herring larvae and other prey. In the laboratory, all organisms that had been eaten by the medusae were identified and counted under a dissecting microscope at 8 to 35 × magnification. The gut contents of all post-yolksac larvae were examined as above from whole plankton samples or from one split of the whole. Larvae from all daytime samples were examined.

Feeding rates. An estimate of *Aequorea victoria* ingestion of herring larvae over a given sampling interval was calculated for each field sample as follows:

$$I = H/D \times T \times M$$

where I = number of herring larvae ingested $m^{-3}\ T^{-1}$; H = number of herring larvae $medusa^{-1}$; D = digestion time (h); T = sampling interval (h); and M = number of medusae m^{-3}. This estimate of ingestion was then divided by the total number of herring larvae m^{-3} (sum of the number of larvae eaten m^{-3} and the number of larvae m^{-3}) in order to calculate the percentage of the larvae eaten at 0 to 5 m depth over the sampling period. Digestion time (D) was determined from the regression equation in Purcell (1989), i.e. $D = 2.13 - 0.14\ X_1 + 0.20\ X_2 + 0.16\ X_3$, where X_1 = temperature (°C), X_2 = mean herring larva size in gut [standard length in mm corrected for shrinkage according to Eq. (2) in Purcell et al. (1987)], and X_3 = number of larvae $Aequorea^{-1}$. In order to determine diel patterns in feeding rates and predation effect, samples were collected during daytime (T = 14 h) and night-time (T = 10 h) on 3 dates. No night-time sampling was carried

out on other dates (T = 24 h). Feeding rates were assumed to be constant within the sampling intervals.

Rates of hydromedusae feeding on microzooplankton were estimated from the number of prey in the gut divided by the digestion time, and multiplied by 24 h, assuming constant feeding over 24 h. *Aequorea victoria* digested copepods in 5.4 h at 9 °C (Purcell 1989). A digestion time of 4 h, which is representative for other gelatinous species (Larson 1985), was assumed for other medusa species in the absence of species-specific data.

RESULTS

Predation on herring larvae

Aequorea victoria was the most abundant hydromedusa in Kulleet Bay in 1985 (Table 1). Densities of hydromedusae averaged 4.7 m^{-3} (range 2.2 to 8.8 m^{-3}) over 8 d of sampling, and *A. victoria* averaged 46.3 % of this total. The maximum density of *A. victoria* measured was 17 m^{-3} in one tow at Stn 1. The mean preserved diameter of *A. victoria* medusae was 50.1 ± 7.0 mm. Hydromedusae other than *A. victoria* were 2 to 8 mm in preserved diameter or height. No siphonophores or ctenophores were found in the plankton tows, and chaetognaths occurred in densities of 0.1 to 0.3 m^{-1}. No specimens of any species other than *A. victoria* contained herring larvae.

Individually collected *Aequorea victoria* medusae contained many herring larvae, with a maximum average of 148 larvae $medusa^{-1}$ on 16 April. Although a variety of zooplankton taxa were present in the environment, the gut contents of *A. victoria* contained mostly herring larvae, and some larvaceans (Fig. 1). The predominance of soft-bodied prey in the diet of this species has been discussed earlier (Purcell 1989).

The predation rates of *Aequorea victoria* feeding on herring larvae were calculated based on the number of larvae in the gut contents, the digestion time, and abundances of larvae and medusae (Table 2). The numbers of herring larvae found in each medusa were highest from 14 to 18 April, and much reduced from 19 to 21 April (Table 2). This was related to the densities of larvae, which were markedly reduced by 19 to 21 April after hatching had ended. The numbers of larvae $medusa^{-1}$, the densities of larvae, and the densities of medusae were generally greater at Stns 1 and 3 than at Stn 2 in mid-bay (Tables 2 and 3). When the larvae were very numerous, the medusae contained a maximum average of 148 larvae $medusa^{-1}$. When densities of herring larvae had decreased by 19 April, there were ≤ 4 larvae $medusa^{-1}$. At the surface water temperature of 10 °C, digestion times were around 24 h when ca 130 herring had been consumed, but diges-

Table 1. Densities (mean ± SD) of soft-bodied zooplankton, numbers of microzooplankton eaten by hydromedusae, numbers of all prey in the gut contents and numbers of medusae examined, and the numbers of microzooplankton eaten m^{-3} d^{-1} in Kulleet Bay, 14 to 21 April 1985. Numbers of damaged medusae not used for gut analyses are in parentheses

Taxon	Abundance (No. m^{-3})	No. of prey $medusa^{-1}$				# Prey/ # medusae	Prey eaten m^{-3} d^{-1}
		Tintinnids	Veligers	Copepod nauplii	Copepodites		
Leptomedusae							
Aequorea victoria	2.16 ± 1.20	P	P	P	1.0	20 523/322	3.3
Obelia sp.	0.03 ± 0.02	0.1	0	0	0	1/7	0.9
Unidentified	0.35 ± 0.21						
Anthomedusae							
Sarsia tubulosa	1.27 ± 0.86	0	0	0	0.5	42/56 (292)	5.7
Miscellaneous	0.60 ± 0.06						
Limnomedusae							
Proboscidactyla flavicirrata	0.23 ± 0.21	2.3	0.9	0.03	0	99/30 (39)	4.6
Trachymedusae							
Aglantha digitale	0.06 ± 0.04	6.0	0	0.25	0.5	27/4 (13)	2.4
Total medusae	4.66 ± 1.90						
Siphonophores	0						
Ctenophores	0						
Chaetognaths	0.17 ± 0.10						

P: present in small numbers

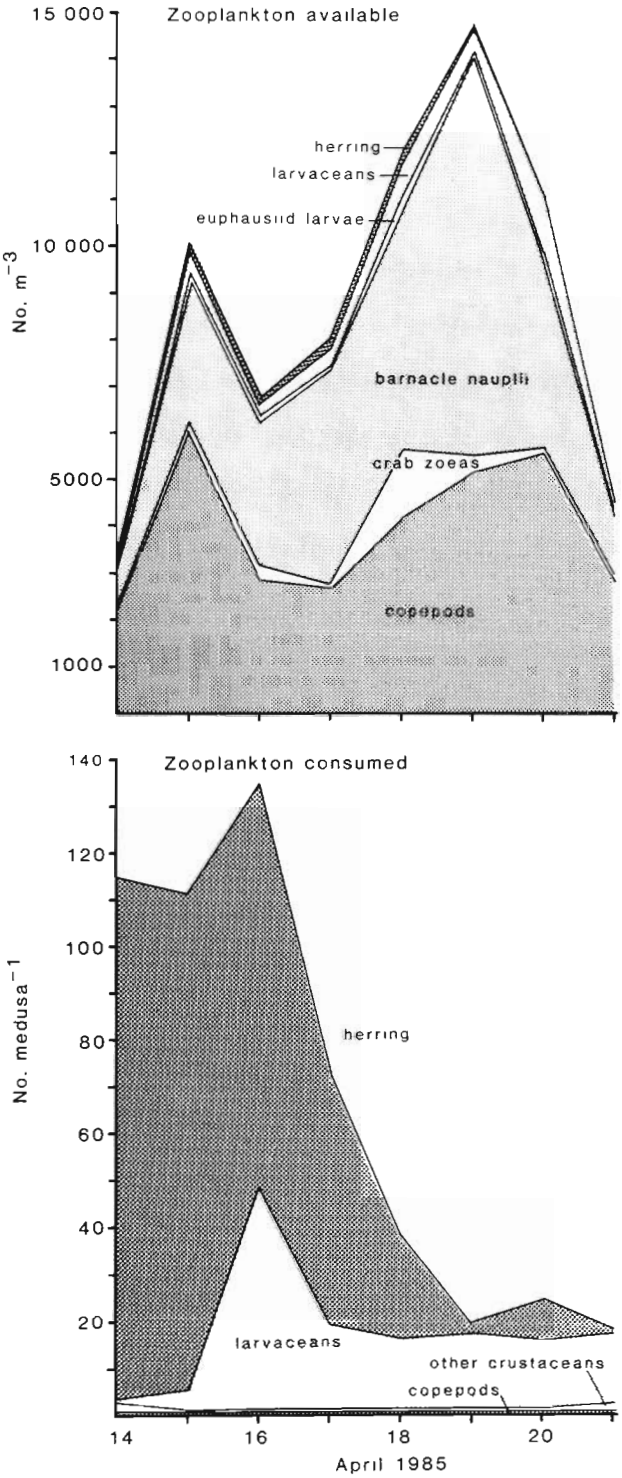

Fig 1 Top Zooplankton densities (333 µm mesh net) in Kulleet Bay during 14 to 24 April 1985 Bottom Zooplankton retrieved from the gut contents of *Aequorea victoria* medusae collected individually at the same times Averages for 3 stations

tion took only about 3 h for ≤ 4 larvae (Table 2) This suggests that large numbers of larvae had accumulated in the guts from 14 to 18 April. Medusae in the field were observed to be feeding continuously at all times, suggesting that feeding did not stop in response to high prey capture.

The percentages of larvae consumed daily in the surface 0 to 5 m varied from 4 to 97 %. These percentages were sometimes low at Stn 1, where larval densities were great. The percentages of larvae consumed were often greatest at Stn 3, where medusa densities were highest. However, the differences among stations in the percentages of larvae consumed were not statistically significant (Table 3).

Predation on microzooplankton

The gut contents of the early post-yolksac herring larvae in Kulleet Bay included mostly diatoms, protozoans (primarily tintinnids and some radiolarians), bivalve veligers, and copepod eggs, nauplii, and copepodites (Table 4). Copepod nauplii comprised nearly 60 % of the prey items, and 57 % of the larvae with prey contained nauplii. Copepod nauplii and tintinnids predominated in the environment (Table 4). Over the sampling period, 1320 post-yolksac larvae were examined. Of these, 24.1 % had underdeveloped lower jaws and were considered unhealthy and unable to feed (Purcell et al. unpubl.). Of the healthy post-yolksac larvae, 26 ± 17 % contained prey, varying from 1 to 30 items.

Microzooplankton prey comprised nearly 100 % of the prey items found in 3 species of hydromedusae, *Obelia* sp., *Proboscidactyla flavicirrata,* and *Aglantha digitale* (Table 1) These medusae measured 1 to 2 mm in preserved swimming bell diameter or height. Microzooplankton were incidental prey of *Aequorea victoria.* Copepodites were eaten by *A. victoria, Sarsia tubulosa,* and *A digitale* (Table 1). Thus, the diet of herring larvae overlapped greatly with the diets of *Obelia* sp., *P. flavicirrata,* and *A. digitale.* According to estimates from feeding rates and the densities of medusae, a total of 7.5 microzooplankton were eaten m^{-3} d^{-1}, and 9.4 copepodites were eaten m^{-3} d^{-1} by hydromedusae in Kulleet Bay Densities of these prey in the environment were 4.08×10^4 m^{-3}. Therefore predation by medusae would not have affected densities of these organisms.

DISCUSSION

Importance of predation

The hydromedusa *Aequorea victoria* consumed from 4 4 to 95.8 % d^{-1} of the herring larvae in the surface 5 m of Kulleet Bay 14 to 21 d after the herring had spawned. The variation in predation was due to differences in

Table 2. *Aequorea victoria*. Predation rates of medusae on herring larvae at 0 to 5 m depth in Kulleet Bay in 1985. Densities (means ± SD) are from 4 samples at Stns 1 and 2, and from 2 samples at Stn 3 and at night (N) (average)

Date	Station	No. of medusae examined	No. of larvae medusa^{-1}	Larval length (mm)	Digestion time (h)	Interval (h)	No. of medusae m^{-3}	No. of larvae eaten m^{-3} T^{-1}	No. of larvae m^{-3}	% of larvae consumed T^{-1}
14 Apr	1	11	135.3	8.5	25.3	14	0.3 ± 0.4	22.5	64 ± 12	26
	1N	14	7.7	8.6	3.7	10	0.2	4.2	688	1
	2	0	–	–	–	24	0.2 ± 0.3	–	21 ± 16	–
	3	10	88.4	9.3	17.5	24	9.0	1091.1	83	93
15 Apr	1	19	123.4	8.8	23.4	24	3.8 ± 2.7	480.9	174 ± 74	73
	2	0	–	–	–	–	0.2 ± 0.1	–	75 ± 25	–
	3	19	88.4	8.8	17.4	24	1.4	170.7	173	50
16 Apr	1	10	133.3	7.2	24.7	24	2.9 ± 0.9	375.6	247 ± 72	60
	2	14	6.4	7.6	3.3	24	0.6 ± 0.4	27.9	38 ± 26	42
	3	14	147.6	7.2	27.2	24	3.6	468.9	195	71
17 Apr	1	10	82.7	7.5	16.2	24	0.2 ± 0.3	24.5	534 ± 460	4
	2	5	6.4	6.5	3.0	24	0.3 ± 0.3	15.4	39 ± 18	28
	3	18	73.2	7.8	14.6	24	4.3	517.4	54	91
18 Apr	1	16	48.3	7.7	10.4	14	0.4 ± 0.2	26.0	568 ± 425	4
	1N	13	22.1	8.8	6.2	10	0.8 ± 0.5	28.5	836 ± 812	3
	2	10	3.4	8.3	2.9	24	2.3 ± 0.9	64.7	23 ± 8	74
	3	14	9.9	8.2	4.0	24	1.6	95.0	138	41
19 Apr	1	13	1.5	8.7	2.6	24	0.3 ± 0.3	4.2	23 ± 19	16
	2	13	2.0	8.8	2.8	24	1.9 ± 0.9	32.6	15 ± 6	68
	3	15	3.7	8.5	3.0	24	8.8	260.5	12	96
20 Apr	1	14	24.1	7.2	6.2	14	0.9 ± 0.6	49.0	18 ± 7	73
	1N	13	4.8	8.0	3.1	10	2.8 ± 0.7	43.4	33 ± 30	57
	2	11	0.5	8.5	2.4	24	1.8 ± 0.6	9.0	17 ± 16	35
	3	13	0.9	9.0	2.6	24	1.8	15.0	5	76
21 Apr	1	9	0.9	9.1	2.6	24	7.7	64.0	2	97
	2	0	–	–	–	24	1.1 ± 1.3	–	7 ± 5	–
	3	8	0.2	8.5	2.4	24	5.4	10.8	3	79

N: night-time, T: time period in hours

larval and medusa densities. The predation effect in 1985 was much greater than that observed in 1983 and 1984. At Stn 3, predation by *A. victoria* on herring larvae 14, 18 and 14 d after spawning in 1983, 1984, and 1985 respectively, was estimated to be 0.7, 12.5, and 92.9 % d^{-1}. Densities of *A. victoria* used for those estimates were 0.04 m^{-3} in 1983 (Purcell 1989), 0.28 m^{-3} in 1984 (Purcell in press), and 9.0 m^{-3} in 1985. These figures indicate roughly order of magnitude increases in both medusa density and predation from 1983 to 1984 and from 1984 to 1985.

The reasons for changes in the population size of *Aequorea victoria* among the 3 years in Kulleet Bay are not understood. The differences are probably true variations in population size in the bay, because of the relatively consistent abundances of *A. victoria* throughout the spring in 1983, and during 8 consecutive days in 1985. The benthic hydroid generation would maintain the local populations of *A. victoria*. Zavodnik (1987) showed how the effects of wind, current, and bottom topography can result in aggregations of medusae, especially in water less than 10 m deep. Such factors may act to concentrate medusae and larvae in Kulleet Bay, especially in shallow areas. Vertical tows at all depths outside the mouth of Kulleet Bay showed densities of *A. victoria* much lower than in the bay (Purcell unpubl.). Purcell (1989) showed that more herring larvae were captured by the medusae than necessary to balance metabolism, providing energy that could go to increased reproduction. Consumption of large numbers of herring larvae might have led to increased reproduction in *A. victoria* medusae, resulting in large hydroid populations, and in subsequent months, to increased medusa populations.

The vertical overlap of medusa and herring larva populations is critical to the overall predation impact (Frank & Leggett 1982). Vertical plankton tows with a closing net in Kulleet Bay on 28 and 29 March 1985,

Table 3. Distribution of herring larvae and *Aequorea victoria* in Kulleet Bay. Comparisons of densities at 1 m depth at Stns 1, 2, and 3 are based on Wilcoxon Signed Ranks Tests

Comparison of stations	Herring larvae m^{-3}	*Aequorea* medusae m^{-3}	Larvae eaten $medusa^{-1}$	% of larvae consumed
1 vs 2	1 > 2 $p < 0.005$	NS	1 > 2 $p < 0.04$	NS $p = 0.17$
1 vs 3	NS	3 > 1 $p < 0.005$	3 > 1 $p < 0.05$	NS $p = 0.06$
2 vs 3	3 > 2 $p < 0.002$	3 > 2 $p < 0.007$	3 > 2 $p < 0.02$	NS $p = 0.11$

NS: not significant

Table 4. Microzooplankton in the guts of post-yolksac, herring larvae (6 to 11 mm standard length) and in the surface waters (0 to 5 m) of Kulleet Bay. Data for each day were similar, so combined results are presented for 14 to 21 April 1985

	Diatoms	Protozoa	Bivalve veligers	Copepod eggs	Copepod nauplii	Copepodites	Other	Total
% of prey	14.1	6.3	2.4	14.9	59.8	0.3	0.2	1141 prey
Frequency of occurrence (%)	16.7	12.1	5.4	17.7	56.6	0.6	0.6	382 larvae
In environment (No. l^{-1})	NQ	17.4 ± 21.1	0.9 ± 1.1	NQ	27.0 ± 12.1	1.5 ± 0.8	NQ	40.8 ± 21.5

NQ: not quantified

before the herring spawned, indicated that more *Aequorea victoria* occurred at 0 to 10 m depth than at 10 to 20 m (12 vs 2 in 4 tows, Purcell unpubl.). Unfortunately, no discrete-depth sampling was possible during 14 to 21 April 1985 when both medusae and larvae were present. Previous results indicate that newly hatched herring larvae stay near the surface and that older larvae undergo a diel vertical migration (e.g. Blaxter & Hunter 1982, Purcell 1989). Therefore, predation by *A. victoria* on the recenctly hatched larvae in the present study would be greatest in surface waters. Predation impact at depths below 5 m, which were not sampled in the present study has not been estimated.

Recruitment variability and its causes are key issues in studies of fish populations (Sissenwine 1984). Stocker et al. (1985) showed that recruitment to the Strait of Georgia herring population varies maximally by 4-fold and concluded that the variation can be explained to a reasonable degree by spawning stock size, sea-surface temperature (affecting development), and Fraser River discharge (affecting food production). These environmental factors could also affect predator population sizes. Abundances of soft-bodied zooplankters that are potential predators and food competitors of larval herring ranged over 2 orders of magnitude among 14 locations sampled in the Strait of Georgia in 1984 (Purcell in press). Abundances of *Aequorea victoria* in Kulleet Bay differed by 2 orders of magnitude between 1983 and 1985. Such large differences in predator populations may contribute to variations in recruitment.

As in 1983 and 1984, the hydromedusa *Aequorea victoria* was the only soft-bodied zooplankter that consumed herring larvae in Kulleet Bay in 1985. Other medusa species, siphonophores, and ctenophores are eaten by *A. victoria* (Arai & Hay 1982, Purcell 1989), and the large population of this species may have kept densities of other species low. Some medusae, ctenophores and chaetognaths had captured yolksac herring larvae in other locations sampled in British Columbia in 1984 (Purcell in press).

Importance of food limitation

Published data on the incidence of feeding of wild herring larvae vary from 0 to 70% (reviewed in Blaxter 1965). Much of this variation may be due to the methods of collection. Hay (1981) found that the percentage of reared larvae with food decreased from 97 to 27% after a 1 min tow in a plankton net and formalin preservation. We conclude that 26% of the larvae with

prey in our samples indicates good feeding by post-yolksac larvae.

Microzooplankton that could be prey of herring larvae were very abundant, averaging 40.8 ± 21.5 l^{-1} over the 8 d study. Purcell (in press) calculated from metabolic needs of first-feeding herring larvae and their search abilities that prey must occur in densities of at least 0.5 to 0.8 l^{-1} for the larvae to survive. Gamble et al. (1981), Øiestad & Moksness (1981), and Kiørboe et al. (1985) found good feeding, survival, and growth of herring larvae at prey densities as low as 5 to 12 l^{-1}. Therefore, prey in Kulleet Bay were clearly abundant enough for survival of herring larvae.

Acknowledgements. We thank G. O. Mackie and the Biology Department of the University of Victoria, Canada, for their gracious cooperation, D. Grosse for his excellent assistance in the field, J.-A. Gordon for counting plankton samples, and V. S. Kennedy for comments on the manuscript. This research was supported by Natural Sciences and Engineering Research Council strategic grant GO871 to Dr. Mackie, a Department of Fisheries and Oceans, Canada, subventions grant to G. O. Mackie and J. E. Purcell, and funds from the Oregon State University Sea Grant Program to J. E. Purcell. UMCEES Contribution No. 2039.

LITERATURE CITED

Alvariño, A. (1985). Predation in the plankton realm: mainly with reference to fish larvae. Investigaciones Marinas Centro Interdisciplinario de Ciencias Marinas 2: 1-122

Arai, M. N., Hay, D. E. (1982). Predation by medusae on Pacific herring (*Clupea harengus pallasi*) larvae. Can. J. Fish. Aquat. Sci. 39: 1537–1540

Blaxter, J. H. S. (1965). The feeding of herring larvae and their ecology in relation to feeding. Rep. Calif. coop. ocean. Fish. Invest. (CalCOFI) 10: 79–88

Blaxter, J. H. S., Hunter, J. R. (1982). The biology of clupeoid fishes. Adv. mar Biol. 20: 3–223

Buckley, L. J., Lough, R. G. (1987). Recent growth, biochemical composition and prey field of larval haddock (*Melanogrammus aeglefinus*) and Atlantic cod (*Gadus morhua*) on Georges Bank. Can. J. Fish. Aquat. Sci. 44: 14–25

Frank, K. T. (1986). Ecological significance of the ctenophore *Pleurobrachia pileus* off southwestern Nova Scotia. Can. J. Fish. Aquat. Sci. 43: 211–222

Frank, J. H., Leggett, W. C. (1982). Coastal water mass replacement: its effect on zooplankton dynamics and the predator-prey complex associated with larval capelin (*Mallotus villosus*). Can. J. Fish. Aquat. Sci. 39: 991–1003

Gamble, J. C., MacLachlan, P., Nicoll, N. T., Baxter, I. G. (1981). Growth and feeding of Atlantic herring larvae reared in large plastic enclosures. Rapp. P.-v. Réun. Cons. int. Explor. Mer 178: 121–134

Hay, D. E. (1981). Effects of capture and fixation on gut contents and body size of Pacific herring larvae. Rapp. P.-v. Reún. Cons. int. Explor Mer 178: 395–400

Hourston, A. S. (1981). British Columbia herring spawn deposition data for the 1970's. Can. Data Rept. Fish. Aquat. Sci. No. 257: 1–200

Kiørboe, T., Munk, P., Støthrup, J. G. (1985). First feeding by larval herring *Clupea harengus* L. Dana 5: 95–107

Larson, R. J. (1985). Trophic ecology of gelatinous predators (Cnidaria and Ctenophora) in Saanich Inlet, Vancouver Is., B. C., Canada. Ph. D. Thesis, Univ. of Victoria

Leggett, W. C. (1986). The dependence of fish larval survival on food and predator densities. In: Skreslet, S. (ed.) The role of freshwater outflow in coastal marine ecosystems. Springer-Verlag, Berlin, p. 117–137

McGurk, M. D. (1984). Effects of delayed feeding and temperature on the age of irreversible starvation and on the rates of growth and mortality of Pacific herring larvae. Mar. Biol. 84: 13–26

Möller, H. (1980). Scyphomedusae as predators and food competitors of larval fish. Meeresforsch. 28: 90–100

O'Connell, C. P. (1980). Percentage of starving northern anchovy, *Engraulis mordax*, larvae in the sea as estimated by histological methods. Fish. Bull. U.S. 78: 475–489

Øiestad, V., Moksness, E. (1981). Study of growth and survival of herring larvae (*Clupea harengus* L.) using plastic bag and concrete basin enclosures. Rapp. P.-v. Réun. Cons. int. Explor. Mer 178: 144–149

Purcell, J. E. (1985). Predation on fish eggs and larvae by pelagic cnidarians and ctenophores. Bull. mar Sci. 37: 739–755

Purcell, J. E. (1989). Predation on fish larvae and eggs by the hydromedusa *Aequorea victoria* at a herring spawning ground in British Columbia. Can. J. Fish. Aquat. Sci. 46: 1415–1427

Purcell, J. E. (in press). Soft-bodied zooplankton predators and competitors of larval herring (*Clupea harengus pallasi*) at herring spawning grounds in British Columbia. Can. J. Fish. Aquat. Sci.

Purcell, J. E., Siferd, T D., Marliave, J. B. (1987). Vulnerability of larval herring (*Clupea harengus pallasi*) to capture by the jellyfish *Aequorea victoria*. Mar. Biol. 94: 157–162

Sissenwine, M. P. (1984). Why do fish populations vary? In: May, R. M. (ed.) Exploitation of marine communities. Springer-Verlag, Berlin, p. 59–94

Stocker, M., Haist, V Fournier, D. (1985). Environmental variation and recruitment of Pacific herring (*Clupea harengus pallasi*) in the Strait of Georgia. Can. J. Fish Aquat. Sci. 42 (Suppl. 1): 174–180

Taggart, C. T., Leggett, W. C. (1987). Short-term mortality in post-emergent larval capelin *Mallotus villosus*. I. Analysis of multiple in situ estimates. Mar. Ecol. Prog. Ser. 41: 205–217

Theilacker, G. H. (1985). Starvation-induced mortality of young sea caught jack mackerel, *Trachurus symmetricus*, determined with histological and morphological methods. Fish. Bull. U.S. 84: 1–17

Zavodnik, D. (1987). Spatial aggregations of the swarming jellyfish *Pelagia noctiluca*. Mar. Biol. 94: 265–270

This article was presented by Professor K. Banse, Seattle, Washington, USA

Revised version accepted: September 21, 1989