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Laboratory study of predation by *Aurelia aurita* on larvae of cod, flounder, plaice and herring: development and vulnerability to capture

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Abstract

Capture success of the medusa *Aurelia aurita* preying on various developmental stages of fish larvae was measured together with larval reactivity and escape speed after being stung. These experiments were conducted in the spring of 1983 with *A. aurita* medusae collected from Loch Etive, Scotland and laboratory-reared larvae of *Gadus morhua* L., *Platichthys flesus* L., *Pleuronectes platessa* L. and *Clupea harengus* L. Capture success of the medusae increased with medusa size, but decreased with advancing larval development. Smaller species of larvae were more vulnerable to capture. Larval reactivity to encounters with medusae increased with advancing development, and larger species of larvae were more reactive to encounters. Larval escape swimming speeds also increased with advancing larval development and size. These results indicate that earlier stages of larvae within a species and smaller species of larvae at a given stage are more vulnerable to predation by medusae since they are less reactive to encounters. Apparently they are more susceptible to the effects of neurotoxins. Predation rates on different developmental stages of herring larvae are documented and compared with rates predicted by a predation model. Predictions fell within the range of observed predation rates, but tended to overestimate rates by larger medusae feeding on larger herring larvae. This indicates the possibility of predator satiation and/or behavioural avoidance.

Introduction

The scyphozoan medusa *Aurelia aurita* has been shown to be an important predator on larval herring, *Clupea harengus* L., by Möller (1980, 1984). Laboratory studies have already demonstrated that predation rates by *A. aurita* on fish larvae decline with increasing larval size (Bailey, 1984). They have also shown that predation rates by medusae on herring larvae depend on encounter rates of the predator and prey, and on capture success (Bailey and Batty, 1983). Whereas the factors that influence encounter rates (size, swimming speed, swimming direction of predator and prey) are well-known, the factors that influence capture success are relatively less studied.

The purpose of this study is to determine why larvae become less vulnerable to predators with increasing size. Previous studies have used a "black box" approach, correlating predation rates with larval size or other factors (Lillelund and Lasker, 1971; Theilacker and Lasker, 1974; Bailey, 1984). By contrast, using video recordings, we measured capture success, larval reactivity to encounters with predators, and escape speeds for various developmental stages of fish larvae. The larvae used were: cod, *Gadus morhua* L.; flounder, *Platichthys flesus* L.; plaice, *Pleuronectes platessa* L. and herring, *Clupea harengus* L. Predation rates by *A. aurita* medusae were measured on developmental stages of herring, and compared with rates predicted by a predation model of encounter rate and capture success (Bailey and Batty, 1983).

Materials and methods

Larvae of flounder (*Platichthys flesus*), plaice (*Pleuronectes platessa*) and herring (*Clupea harengus*) were obtained by artificially fertilizing eggs in the laboratory. Fertilized cod (*Gadus morhua*) eggs were obtained from Dr. J. Gamble, Department of Agriculture and Fisheries for Scotland, Marine Laboratory, Aberdeen, Scotland and from the Sea Life Centre, Barcaldine, Scotland. Fish larvae were reared in aquaria at 8° to 14 °C and fed rotifers, Brazilian *Artemia* sp. nauplii, and natural zooplankton. Ephyrae of *Aurelia aurita* were captured in Loch Etive, Scotland, with a slowly towed plankton net. They were cultured at temperatures of 2° to 12 °C to control development rates, and fed algae, rotifers, *Artemia* nauplii, natural plankton and fish larvae.

Predation experiments were conducted as in Bailey (1984) in air-conditioned rooms, at 10° to 12 °C, under fluorescent room lights of 100 lux intensity. Briefly, larvae were counted into 5-litre glass jars containing filtered seawater, one medusa was then added to each jar, the lids were applied and the jars were placed on a stirring machine that slowly rotated them about their long axes. Experiments were ended after 1 h and the number of larvae in the gut of each medusa was counted under a binocular microscope. Ingested larvae are visible in guts for 3 to 5 h. The number of larvae remaining in the jars was also counted.

Encounters of larvae with medusae in a Perspex dish, 11.5 cm in diameter by 4 cm deep, were recorded using a television camera with transmitted illumination from an infra-red emitting diode (Batty, 1983). Recordings were made both with room lights on and off. No visual avoidance of medusae by larvae was observed, and burst speeds reported here are aggregated observations in light and dark. Maximum observed burst speeds after an encounter were measured between consecutive 20 ms fields of a video-recording. Mean escape speeds were measured through four fields and averaged over from 4 to 11 filmed encounters.

Larval encounters with medusae were also monitored by direct visual observation with room lights on. Ten to twenty larvae were pipetted into a clear glass cylinder of 15 cm diameter containing one medusa and the number of encounters and successful captures were recorded. Ten to twenty encounters for each of 5 to 12 individual medusae were observed. Larvae that were apparently damaged by medusae were pipetted out and replaced with new larvae. The following types of behaviour were noted as follows: encounter, an apparent touch by a medusa; response, a successful escape from a medusa immediately after an encounter; delayed response, a successful escape by a larvae after being held by a medusa for 3 to 5 s; capture, larva held for more than 5 s.

Results

Percent capture success

The percentage of larval encounters with *Aurelia aurita* medusae which resulted in successful capture was determined as a function of larval species, developmental stage and medusa diameter. Capture success increased with medusa size and within each species of larva decreased with increasing developmental stage (Fig. 1). Capture success of first-feeding stages of the different species is

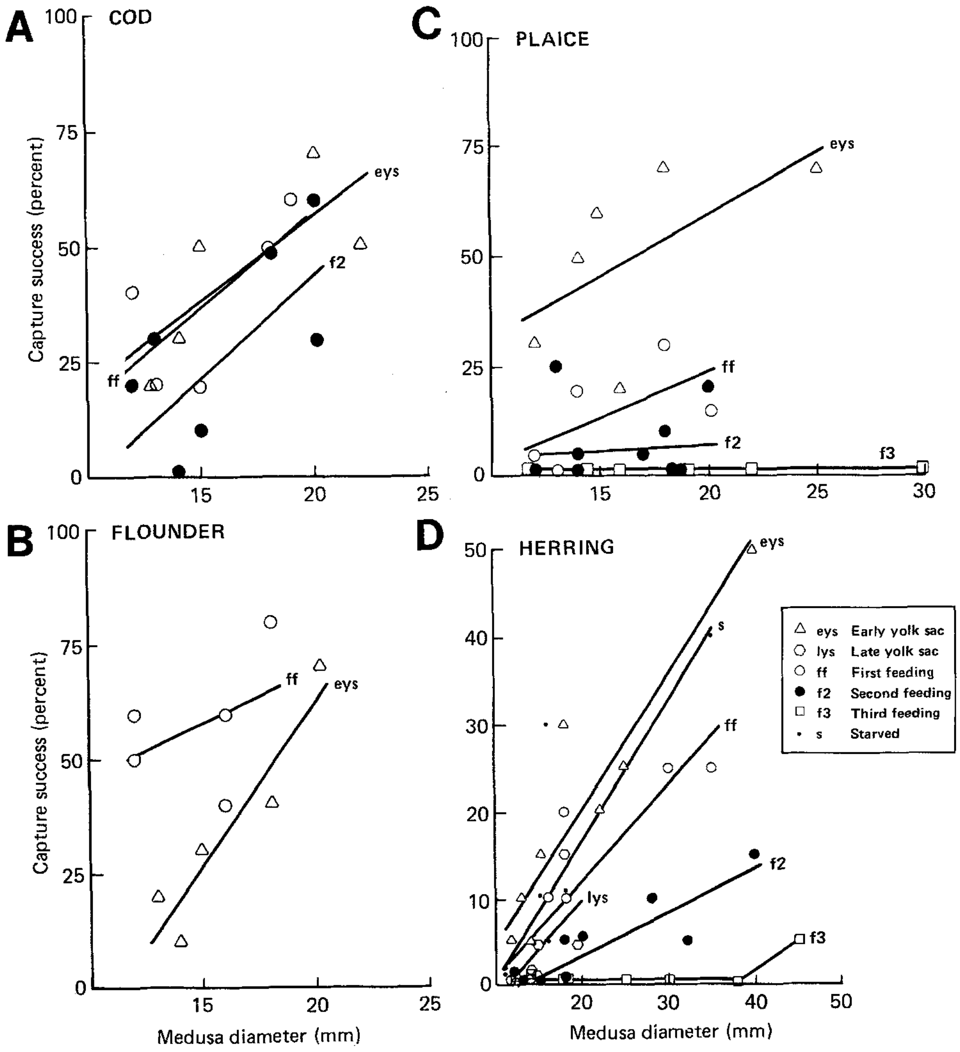

Fig. 1. *Aurelia aurita.* Relationship between medusa diameter and percent capture success on fish larvae of different developmental stages: (A) cod, *Gadus morhua;* (B) flounder, *Platichthys flesus;* (C) plaice, *Pleuronectes platessa;* (D) herring, *Clupea harengus.* Lines are least-squares regression fits for each developmental stage

compared in Fig. 2. In this comparison, flounder (*Platichthys flesus*) larvae were most vulnerable to capture by medusae, followed by cod (*Gadus morhua*), plaice (*Pleuronectes platessa*) and finally herring (*Clupea harengus*).

Encounters not resulting in successful captures were sometimes a result of larvae not adhering to the surface of medusae, but most often, resulted from reactions by larvae. A standardized percentage capture success was determined for an 18 mm diam medusa by interpolating from the regression line of percent capture success against medusa size from Fig. 1; these values were compared with larval reactivity. For the aggregated data on all species, the percentage of encounters resulting in successful captures was closely related to the reactivity of larvae (Fig. 3).

A general relationship also existed between the percentage of larvae reacting to an encounter and larval size (Fig. 4). Percent capture success increased with advancing larval development and size. The one exception to this trend was the flounder, whose yolk-sac larvae were markedly more reactive than first-feeding larvae. In general, plaice larvae were less reactive than predicted by the regression line calculated for all species. Herring greater than 11 mm reacted to nearly all encounters with medusae.

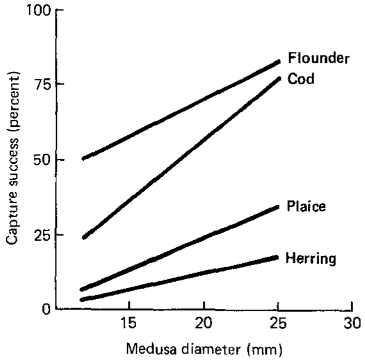

Fig. 2. *Aurelia aurita.* Relationship between medusa diameter and percent capture success on first-feeding fish larvae of the different species. Lines are least-squares regressions from Fig. 1 (A)–(D)

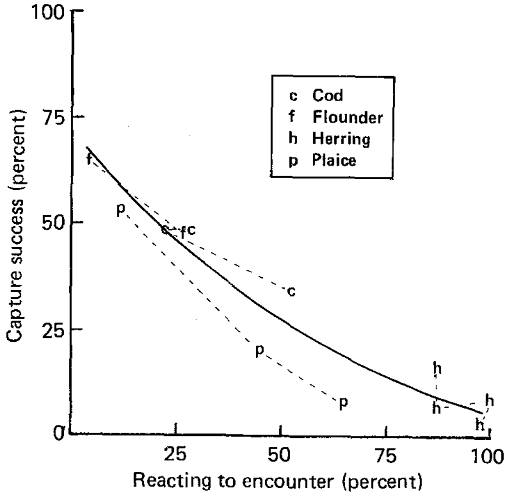

Fig. 3. Relationship of percent fish larvae reacting to encounters with *Aurelia aurita* medusae and percent capture success. Percent capture success was determined as standardized value for an 18 mm medusa, by interpolating from regression lines in Fig. 1 (A)–(D). Dashed lines connect developmental stages within each species; continuous line is the nonlinear least-squares fit to all points

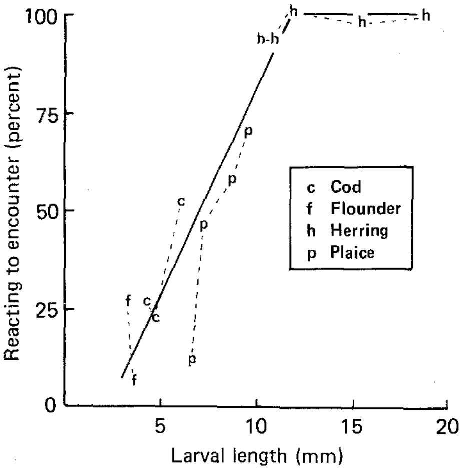

Fig. 4. Relationship of larval length to percent of fish larvae reacting to encounters with *Aurelia aurita* medusae. Dashed lines connect developmental stages within each species; continuous line is linear least-squares fit to all points up to the third developmental stage of herring, after which nearly 100% of larvae reacted to encounters

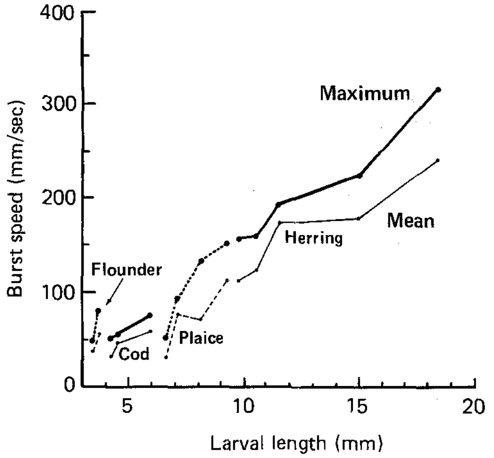

Fig. 5. Relationship of larval length to burst swimming speed of fish larvae. Heavy upper lines connect maximum observed burst speeds for developmental stages within each species; thin lower lines connect mean burst speeds for developmental stages within each species. Mean speeds through four 20 ms fields of a video recording were determined from at least 4 to 11 encounters for each larval stage and species

Escape speeds

Maximum burst speeds and mean burst speeds of larvae after an encounter with a medusa were measured for each stage and species. As found in previous studies (Bailey, 1984), burst speeds generally increased with larval size for a given species (Fig. 5). Maximum burst speeds after encounters with medusae were not significantly different from those after being touched with a probe (Table 1).

Table 1. Maximum and mean burst speeds (mm s^{-1}) of fish larvae after encounters with *Aurelia aurita* medusae and after touch with a probe. Values for means and maximums are averages for 4 to 11 encounters. Dash indicates value not obtained. eys: early yolk-sac; lys: late yolk sac; ff: first feeding; f1, f2 and f3, later feeding stages

Fish species	Stage	Size (mm)	Medusae		Probe	
			max	$\bar{x}$	max.	$\bar{x}$
Cod	eys	4.2	5.1	3.4	5.9	4.7
Gadus morhua	ff	4.5	5.6	4.6	6.5	4.5
	f2	5.9	7.5	5.3	8.4	6.7
Flounder	eys	3.4	4.9	3.8	4.1	2.4
(*Platichthys flesus*)	ff	3.7	–	–	8.3	6.0
Plaice	eys	6.6	5.2	3.1	6.2	4.3
(*Pleuronectes*	ff	7.1	9.4	7.7	10.7	8.4
platessa)	f1	8.2	14.3	7.1	11.6	5.1
Herring	eys	9.8	15.1	11.2	13.9	10.3
(*Clupea*	lys	10.5	15.7	12.2	–	–
harengus)	f1	11.5	19.3	17.1	16.7	13.7
	f2	15.0	22.4	18.0	–	–
	f3	18.4	31.5	24.1	37.1	23.6

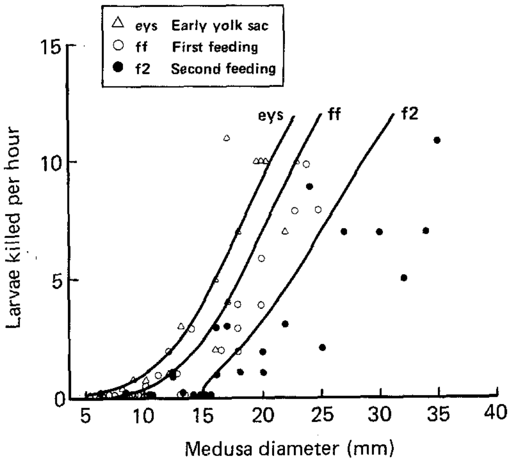

Fig. 6. *Aurelia aurita.* Relationship between medusa diameter and predation rate (number of larvae killed per hour) for different developmental stages of herring larvae. Lines are predation rates predicted by the encounter model of Bailey and Batty (1983) for each stage

Predation rates

One-hour predation rates on herring larvae of different developmental stages by medusae of different sizes were determined. Early yolk-sac larvae were vulnerable to medusae as small as 8 mm in diameter, and first-feeding larvae were vulnerable to medusae of 10 mm in diameter and larger (Fig. 6). Larger larvae showed decreasing vulnerability to the smaller medusae. These results are compared with those predicted by the predation model of Bailey and Batty (1983). In general, for early yolk-sac larvae the predation rates fit the observed data fairly well. For first-feeding and advanced-feeding larvae, the predictions tended to overestimate rates of predation when more than 3 to 5 larvae were captured. These higher rates of predation tend to occur when medusae are greater than 20 to 25 mm in diameter.

Discussion

The objective of this study was to examine in detail the predator-prey interaction between fish larvae and *Aurelia aurita* medusae, and in particular why larger larvae are less vulnerable to predation. It was found that the capture of larvae by medusae was related to larval reactivity to encounters, and that smaller larvae tended to be less reactive. Differences in reactivity of larvae resulted from both growth and species effects. For example, the capture success of medusae was highest on young stages of cod (*Gadus morhua*) and flounder (*Platichthys flesus*) and declined with larval development. These young stages did not usually react to encounters. Yolk-sac plaice (*Pleuronectes platessa*) and herring (*Clupea harengus*) were less vulnerable to capture by medusae than the other species of larvae and became even less vulnerable with advancing development. Larger species of larvae, such as herring, react to almost all encounters, and capture success for these larvae is probably a function of the ability of larvae to shake free from the mucus of medusae after being captured. In general, larger larvae are more successful in doing this.

Webb (1981) also found that the reactivity of different developmental stages of anchovy larvae to a biting fish predator was a function of length. He implicated the development of the visual system of larvae in this reactivity. In our study, we observed no visual response by larvae to the approaching medusae, which are fairly transparent compared with fish predators. Herring larvae, for example, may respond instead to the mechanical stimulation of touch or water movement, possibly using the neuromast organs, or to stings by medusa, i.e., pain reception. Since only about 20% of early yolk-sac herring larvae respond to touch by a probe (Bailey, 1984) compared with about 97% responding to an encounter with medusae, pain reception from stings seems to be a likely mechanism.

Small larvae, such as early stages of cod and flounder, appeared to be more susceptible to nematocyst stings compared with the larger larvae. Small larvae usually showed no visible response to touch by medusae and often were immediately paralyzed after contact. These results indicate the possibility of a toxic dose response, with small larvae receiving a higher dose of toxin per unit of body weight.

Larval burst speeds increased as a function of larval size. In this case, larval escape speeds did not appear to be important in the interaction with medusae, although they may reflect the ability of larvae to free themselves after being captured. Larval escape speeds may be more important in their interaction with pursuing predators, such as fish. Larval reaction time after an encounter may also be an important variable, but it was difficult to determine the precise moment of initial contact of predator and prey using two-dimensional images in video replay.

A decline in laboratory predation rates by medusae of different sizes on herring larvae of increasing developmental stages was found. Predation rates predicted from a predation model (Bailey and Batty, 1983) fell within the range of observed predation rates, and predictions were especially close for medusae feeding on early yolk-sac larvae and for medusae feeding at low rates (less than 3 to 5 larvae captured) on the larger stages of herring larvae. Model predictions tended to overestimate predation rates for medusae capturing more than 5 larger larvae; these were medusae larger than 20 to 25 mm in diameter. As noted by Bailey and Batty (1983), medusae may become satiated after catching several larvae. Furthermore, our definition of capture success in this study, i.e., a larva is held by a medusa for more than 5 s, is different from actual capture success resulting in ingestion. Alternatively, the mechanism of prey capture by larger medusae may differ from that of small medusae. Qualitatively, we did observe that small medusae capture larvae by contact with the exumbrella surface, whereas larger medusae tend to capture prey with their tentacles. Possible variations in capture mechanisms due to medusa size were not accounted for by the predation model, and the encounter radius was assumed to be the radius of the bell of the medusa throughout.

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