EFFECTS OF VISUAL CONDITIONS AND PREY DENSITY ON FEEDING KINETICS OF PARALARVAE OF *OCTOPUS VULGARIS* FROM A LABORATORY SPAWNING

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ABSTRACT

Consumption rate and feeding success of newly hatched paralarvae of the cephalopod *Octopus vulgaris* preying on *Artemia* larvae were investigated in relation to visual conditions and prey density. Each paralarva was tested individually using a small-scale experimental setup; consumption over one day was measured at 20°C. A factorial experiment was designed to investigate the effects on the consumption rate of two predictor variables: illumination/background (three levels: 7.5 W m^{-2} white light + white background, 7.5 W m^{-2} white light + blue background, darkness) and prey density (four levels: 2.35, 4.70, 9.40 and 14.10 *Artemia* metanauplii ml^{-1}). Consumption rate varied significantly between different conditions of illumination and prey density. Light enhanced consumption rate, but different backgrounds yielded similar rates. The maximal consumption rate under illumination was close to 16 *Artemia* paralarva^{-1} day^{-1}, and it was around 5 *Artemia* paralarva^{-1} day^{-1} for assays in darkness. The predatory efficiency, measured as the proportion of prey consumed, was significantly affected by prey density, pointing to a type III functional response. The number of nonfeeding paralarvae was significantly higher in darkness and at low prey density.

INTRODUCTION

The functional response concept, defined as the relation between the numbers of prey consumed within a fixed time and prey density, was first developed in the context of predation ecology theory (Hassell, 1978). Few papers on cephalopods as predators have been devoted to the investigation of functional responses (Borer, 1971; Mather, 1980) and, to our knowledge, none of them to paralarval or juvenile stages.

The number of captures per time unit and predator individual is limited by processes like seeking and handling the prey, or interacting with conspecific predators. It could be enhanced when the range of any pertinent factor (prey density, visual conditions or temperature) maximizes the sense organs efficiency for prey detection, the movement power or the attack decision. Four main types of functional response have been described for predators, including planktonic ones (Gentleman *et al*., 2003): types I (linear with saturation), II (hyperbolic) and III (sigmoidal) show a saturation of the number of captures; type IV has an optimum prey density (or an optimum range) for consumption rate, but the first part of the curve can be hyperbolic or sigmoidal.

Even a slight relaxation of the predatory efficiency at low prey densities can be important to food web stability (Dunne *et al*., 2005). This is a characteristic of type III functional responses. Thus, a first aim of this investigation was to look for such a relaxation of the predatory efficiency.

In spite of the keen vision of octopuses (Messenger, 1981), tactile stimuli seem to be important cues for the foraging strategy of adults of some species in the genus *Octopus*: (1) *Octopus vulgaris* (Cuvier, 1797) adults use arms to probe into holes, or spread arms and web over the substratum while foraging in seagrass environments (Gilchrist, 2003); in addition, fresh remains of burrowing bivalves can be found around dens of *O. vulgaris* individuals inhabiting sandy substrata (Caverivière, 2002); (2) *O. cyanea* adults use long arms to find hidden prey in natural environments (Forsythe & Hanlon, 1997); (3) similar behaviours have been reported for *O. maorum* when preying on lobsters hidden in pots (Brock, Saunders & Ward, 2003). On the other hand, predation success of octopus paralarvae is supposed to be largely dependent on visual abilities (Guerra & Pérez-Gándaras, 1984; Boletzky, 2003), thus, illumination should play an important role in prey detection and capture success. A purpose of the present investigation is to test for the importance of illumination on the consumption rate of *O. vulgaris* paralarvae, under laboratory conditions.

Octopus vulgaris adults are visually monochromatic, but able to discriminate brightness and polarization (Messenger, 1981). Spectral sensitivity curves of several adult specimens of *O. briareus* and *O. vulgaris* have been investigated by Hamasaki (1968): a peak at 480 nm was found and adaptation to white or coloured lights yielded a narrowing and depression of the curve, but no peak shifting was reported. To our knowledge, data on spectral sensitivity, or on brightness-contrast sensitivity, of common octopus paralarvae are not available. A blue plastic sheet as background plus white light (∼4 W m^{-2}), have been successfully used for studying the kinematics of paralarval attacks on a blue-photon absorbing prey – the *Artemia* nauplius (Villanueva, Nozais & Boletzky, 1996). In the present work, the effect of background on consumption rate was tested.

Finally, as starvation of planktonic paralarvae of cephalopods during the first days of life can be a critical factor determining early survival rate (Vidal *et al*. 2002), the effects of illumination and prey density on the probability of starvation of *O. vulgaris* paralarvae was investigated.

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MATERIAL AND METHODS

Biological material

Two batches of *Octopus vulgaris* adults were collected during November 2003 and November 2004 along the Huelva coastal region (SW Spain) by an artisanal fishing boat using cephalopod pots. Adults were stocked at a density of nine individuals per tank (volume = 5000 l, sex ratio ~1:1) at the CIFPA 'Agua del Pino' aquaculture facilities. A flow-through system of seawater filtered to 25 μm was established with a turnover rate of 144% of the tank volume per day. Water temperature ranged from ~15°C to 21°C, salinity from 35 to 39 psu, and photoperiod was natural and attenuated during the broodstock rearing and spawning period (November to July). Octopuses were fed squid in excess every morning. Spawning females were isolated individually until hatching. Two females were used for the present research: female 1 was collected during November 2003 and fed *Illex* sp. squid; female 2 was collected during November 2004 and fed *Loligo* sp. squid. During the hatching period of each spawning, one day's production of neonatal paralarvae was gently extracted from isolation tanks by siphoning into a cylindrical methacrylate tube; paralarval age ranged from 0 to 24 h.

Artemia production methods

EG *Artemia* Cysts (Inve Aquaculture NV) were used. Cysts were decapsulated by immersion for ~7 min with a dilution of commercial hypochlorite solution, and incubated at a density of 1 g of dry cysts per litre of seawater at a temperature of 27°C. A lipidic emulsion (Selco, Inve Aquaculture NV) was added to the incubation tanks during the following two days ($14\ g\ l^{-1}$ the first day and $10\ g\ l^{-1}$ the second day). *Artemia* larvae were harvested on the second day. Thus they ranged in age from 0 to 2 days old at harvesting time. The mean length was 850 μm.

Experimental design

Cellstar rectangular packs (12.7 × 8.5 cm) (Greiner Bio-One) of six plastic Petri dishes of ~14 ml (3.5 cm diameter) were used as experimental containers. Twelve Petri dishes were filled with tap water to a depth of ~1 cm, and then the water volumes were measured using a syringe: the mean experimental volume was 9.2 ± 0.45 ml. A small assay volume was chosen because of the precision of the counting proceedings in assessing individual consumptions, as showed by other investigations on ingestion rate of cultured larvae of *Macrobrachium rosenbergii* (Barros & Valenti, 2003). Experimental seawater was filtered through a 25 μm cartridge filter; salinity was 38 psu, temperature was kept at 20°C and the duration of the assay was 24 h.

To test for the relative importance of light on the functional response of *O. vulgaris* paralarvae, assays under white light and in darkness were compared; for a visual predator, a higher functional response is expected under illumination conditions. To test for a potential effect of background on the functional response shape, we chose two backgrounds: (1) blue foam, coloured near the peak of spectral sensitivity of adults (blue-green range) and (2) rough white blotting paper as a wide-spectrum background. The prey used, 0–2 day old *Artemia*, is orange in colour, thus it is blue-photon absorbing.

All the assays were carried out inside a room equipped with a thermostat and white-light, 18-W fluorescent tubes (Mazdafluor, Lumière du jour) as a light source. Illuminance was measured with a luxometer (Koban KL 1332) and illuminance units (lx) were converted to irradiance units ($W\ m^{-2}$), according to the expression: 100 lx (white light) ≈ $1\ W\ m^{-2}$ (De la Rosa *et al.*, 1990). Experimental packs were placed on the floor under $7.5\ W\ m^{-2}$. Light incidence was from above and from the sides. Darkness was achieved by wrapping dish packs with a piece of aluminium foil. For the background assays, the packs were placed on a layer of rough, white blotting paper or, alternatively, on blue foam. Three combinations of illumination and background were tested: (1) light ($7.5\ W\ m^{-2}$) + white background, (2) light ($7.5\ W\ m^{-2}$) + blue background and (3) darkness. Four prey densities, 20, 40, 80 and 120 *Artemia* $dish^{-1}$ (2.17, 4.35, 8.70 and 13.04 *Artemia* ml^{-1}, respectively) were tested for each of the three light/background conditions.

To determine the survival rate of prey in the absence of predator for 24 h, 12 control replications of each prey density were performed: mean numbers of survivors were 19.67, 38.83, 78.33 and 116.92 for initial densities of 20, 40, 80 and 120 *Artemia* $dish^{-1}$, respectively.

Paralarvae swimming towards the water surface of the collecting tube were selected for the experimental assays: those resting or swimming near the bottom were discarded. A single paralarva was placed at each dish. *Artemia* were counted under a stereomicroscope. Predators and prey remained active at the end of the experience, except in one Petri dish, at the 2.17 prey ml^{-1} (20 prey $dish^{-1}$) density and blue foam background, where the paralarva was found dead; this datum was discarded. A single observation of the ingestion process was made since one of the paralarvae was still feeding at the time of prey counting.

Six experimental replicates were performed for each of the 12 combinations of the two factors – illumination/background and prey density (barring blue background and 2.17 *Artemia* ml^{-1}, for which only five replicates remained useful). The number of living *Artemia* was counted under stereomicroscope after 24 h. For each experimental replicate, a consumption rate, C, was calculated as: $C = A_0 - A_S$, where A_0 is the initial number of prey minus the average predation-independent mortality (i.e. approx. 20, 39, 78 and 117 $dish^{-1}$), and A_S is the number of surviving prey after 24 h for the given replicate. To avoid meaningless results, the consumption rate was set to zero when the former calculation yielded negative numbers due to counting errors.

Statistical analyses

Data on individual consumption rates (Table 1) or proportions of prey consumed (not shown) failed the normality (Kolgomorov-Smirnov) and/or homoscedasticity (Levene) tests. A nonparametric two-way analysis of variance (Zar, 1984) was chosen to analyse the effects of prey density and illumination on consumption rates. To study the existence of a predatory efficiency relaxation at low prey densities, the proportion of prey consumed was also analysed using a nonparametric two-way ANOVA.

To investigate the effect of illumination conditions or prey density on the proportion of starved (nonfeeding) paralarvae (Table 1), the following procedure was used: (1) some levels of the predictor variables (illumination and prey density) were combined into a single one; for illumination conditions two categories were used: light (both backgrounds) *vs.* darkness; another two categories were chosen for prey density: low density (2.35 prey ml^{-1}) *vs.* high density (4.70 + 9.40 +14.10 prey ml^{-1}); (2) 2 × 2 contingency tables (without cells with less than five items) were compiled, the first cross-classified each individual paralarvae by feeding success (nonfeeding or feeding) and prey density (low or high), the second cross-classified them by feeding success and illumination (darkness or light); (3) a χ^2 statistic was calculated for each table (Quinn & Keough, 2002).

Table 1. Effect of illumination conditions and prey density on the predatory kinetics of newly-hatched *Octopus vulgaris* paralarvae preying on *Artemia* sp. metanauplii.

Prey density	Consumption rate			Feeding success (NF/F)		
	Light + white BG	Light + blue BG	Darkness	Light + white BG	Light + blue BG	Darkness
2.35	0.83 (0.98)	1.00 (1.22)	0.00 (0.00)	3/3	2/3	6/0
4.70	6.83 (5.19)	4.67 (4.55)	1.33 (2.80)	0/6	1/5	4/2
9.40	16.50 (3.45)	10.50 (9.54)	1.00 (2.45)	0/6	1/5	5/1
14.10	7.83 (6.94)	12.17 (7.47)	5.33 (7.47)	1/5	1/5	3/3

Abbreviation: BG, background.
Means and SD (numbers in parentheses) are shown for consumption rates. For feeding success, absolute numbers of nonfeeding (NF) and feeding (F) paralarvae are given. Units are prey ml^{-1} for prey density and prey $paralarva^{-1}$ day^{-1} for consumption rates.

RESULTS

Disparity in first feeding success

No paralarvae from female 2 fed during the experiment. Even at saturating prey densities, there were some paralarvae from female 1 that did not feed. Paralarvae from female 1 showed a highly variable consumption rate and nearly all the coefficients of variation (CV) were around 1 (Table 1). When data on consumption rate from animals assayed under illumination and at the two higher prey densities (to avoid the effects of low prey density and darkness on feeding success, see below) were pooled, the associated histogram was bimodal with the first peak at the (0–3) (prey $paralarva^{-1}$ day^{-1}) consumption rate interval (Fig. 1). The CV for such a distribution was reduced by one half when the (0–3) class was excluded.

Effects of illumination conditions and prey density

A nonparametric two-way ANOVA (Zar, 1983), showed that illumination conditions and prey density had a significant statistical effect on consumption rate; however, no significant interaction between the two factors was detected (Table 2).

A Dunn's multiple comparisons test sorted the data into two groups in relation to illumination conditions: light (both backgrounds) and darkness (Table 2). The mean consumption rate was always higher under illumination than in darkness (Table 1). The mean consumption rates for illuminated assays increased from 1 to more than 10 prey $paralarva^{-1}$ day^{-1} for prey densities between 2.35 and 14.10 *Artemia* ml^{-1} ($n = 47$; Spearman rho = 0.525, $P < 0.001$; Kendall tau = 0.435, $P < 0.001$). This increase reached a plateau level at 9.40 *Artemia* ml^{-1} (Table 1), so 9.40 and 14.10 prey ml^{-1} can be described as saturating prey densities. A weaker positive correlation between consumption rate and prey density was found for assays in darkness ($n = 24$; Spearman rho = 0.372, $P = 0.074$; Kendall tau = 0.325, $P = 0.026$).

A nonparametric two-way Anova yielded a significant effect of prey density and illumination on the proportion of prey consumed (Table 2). The proportion of prey consumed for 2.35 prey ml^{-1} was significantly lower than the one for 9.40 prey ml^{-1} (Dunńs test, Table 2), suggesting a relaxation of the predatory efficiency for the lowest prey density tested.

The analyses of the contingency tables (see Statistical Analyses) showed that the numbers of nonfeeding and feeding individuals (Table 1) were not independently distributed with respect to prey density ($\chi^2 = 6.75$, df = 1, $P = 0.009$) or illumination conditions ($\chi^2 = 21.03$, df = 1, $P < 0.001$). The odds of failing to feed were 4.35 times higher for paralarvae tested at 2.35 *Artemia* ml^{-1} than for the ones tested at higher prey densities. Similarly, the odds of failing to feed were 12.7 times higher for paralarvae tested in darkness than for the ones tested under illumination.

Ingestion mechanism

Prey ingestion was observed for one paralarva at the moment of *Artemia* counting. Although *Octopus vulgaris* paralarvae can

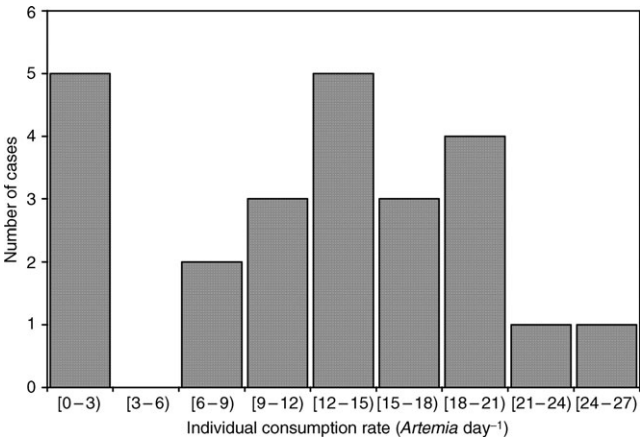

Figure 1. Combined distribution of the consumption rate for paralarvae under illumination with both backgrounds and at the two higher prey density levels (9.40 and 14.10 prey ml^{-1}).

Table 2. Nonparametric two-way ANOVA of consumption rates and proportions of prey consumed by isolated common octopus paralarvae, by illumination conditions and prey density and Dunn's test for both factors.

Source		SS	df	H	*P*	Dunn's test
Cons. rate	PD	6640	3	15.6	0.001	2.35, 4.70 *vs* 4.70, 9.40, 14.10
	L/B	5810	2	13.6	0.001	Darkness *vs* L + W-BG, L + B-BG
	Int.	2406	6	5.6	0.469	–
Prop. cons.	PD	7766	3	18.7	<0.001	2.35, 4.70, 14.10 *vs* 4.70, 9.40, 14.10
	L/B	3863	2	9.3	0.010	Darkness *vs* L + W-BG, L + B-BG
	Int.	2562	6	6.2	0.401	–

Abbreviations: Cons. rate, consumption rate; Prop. cons., proportion of prey consumed; PD, prey density; L/B; light/background; Int., interaction; L + W-BG, light plus white background; L + B-BG, light plus blue background.

externally digest brachyuran zoeae (Hernández-García, Martín & Castro, 2000), the observed paralarva ingested a metanauplius by a chewing mechanism, while holding another one in its arms. The *Artemia* metanauplius was gradually broken up into pieces but the different moving structures of the buccal mass could not be clearly distinguished during the ingestion process and more observations are needed to investigate their functions. The process took no more than a few minutes.

DISCUSSION

Disparity in feeding success

Variability in individual consumption rates is not a new finding: for instance, it has been reported for larvae of a number of crustacean species (Barros & Valenti, 2003), for the fish *Gasterosteus aculeatus* within a narrow size range (Salvanes & Hart, 1998) and for adults of *Octopus joubini* (Mather, 1980). In the case of crustacean larvae, this variability results from individual differences in the ability to detect or pursue prey or from the stage of the moulting cycle (Barros & Valenti, 2003). For this reason, the feeding behaviour of some predators is not completely described by the mean consumption rate. A measure of variability among animals (not merely among experimental replicates) should be given when possible. For planktonic predators with a chewing ingestion mechanism or for those able to digest the prey externally, such as cephalopod paralarvae, separate trials for each predator can be performed to assess individual consumption rates.

Successful feeding was not observed for paralarvae from female 2. This fact was not researched further, but it seems unlikely that it was due to unsuitability of environmental conditions since: (1) paralarvae from female 1 did feed; and (2) similar experimental setups, used by other researchers to describe the swimming behaviour of paralarvae during predation, did not preclude paralarval attacks (Villanueva *et al*., 1996).

Intracohort variability was also apparent within the paralarvae from female 1. The bimodal distribution of consumption rates at saturating prey densities (Fig. 1) contributes to this intracohort variability and suggests heterogeneity in hunting skills of paralarvae. On one hand, evidence exists for disparity in first feeding age in *Sepia officinalis* (Boucaud-Camou, 1982; Boucaud-Camou, Yim & Tresgot, 1985; Domingues *et al*., 2001). Variability in brain development of cuttlefish at hatching has been suggested to cause such disparity in feeding success (Dickel, Chichery & Chichery, 1997). On the other hand, individual differences in size could partially explain the heterogeneity in feeding behaviour, thus collecting data on paralarval dry weight or length during future investigations on functional responses may be useful.

Effects of illumination and prey density on consumption rate and feeding success

An increase in prey density will result in a higher predator-prey encounter rate (Jumars, 1993); this fact explains the rise in consumption rate and feeding success with prey density. As prey density increases the number of prey captures rises and the predator searching time is gradually reduced by time taken during the prey handling processes. This is the reason why consumption rate levels off at high prey densities.

Low prey density not only reduces the mean consumption rate, but also increases the probability of early starvation. Starvation of planktonic paralarvae of *Loligo opalescens* during the first days of life is a critical factor determining yolk depletion rate, hunting skills development, paralarval survival rate and it potentially affects recruitment processes (Vidal *et al*., 2002). In the case of *O. vulgaris* paralarvae in the wild, a relationship between recruitment in Mauritanian waters and environmental variables conditioning food availability has been reported (Faure *et al*., 2000). Our result on the association between low prey density and early starvation for one-day periods (see feeding success, Table 1) is consistent with the potential effect of food abundance fluctuations on *O. vulgaris* recruitment.

The number of prey captures was clearly less in the dark, indicating an important role of vision on capture success. This result suggests a potential effect of photoperiod on consumption rate of paralarvae in natural environments; in that case, diel oscillations of consumption rate could arise. Nevertheless, light may not be essential for capturing and ingesting prey, since a marginally significant, positive correlation was found between prey density and consumption rate under darkness. The relevance of the irradiance contrast, between the background and the prey surface, on the predation success has been studied by some authors (Dendrinos, Dewan & Torpe, 1984; Johnsen, 2001). However, the absence of a significant difference between the two tested backgrounds is compatible with a similar spectral sensitivity peak for paralarvae and adults (at the blue-green range), both backgrounds reflecting enough light intensity within the blue-green region of the spectrum, although more research is necessary.

The functional response of Octopus vulgaris *paralarvae*

Borer (1971) found a type I functional response for *O. briareus* adults, but temperature was not controlled (it ranged from 17°C to 23°C) and an investigation on *O. joubini* adults (Mather, 1980) possibly pointed to a type II functional response. On the contrary, combining the decrease of the proportion of prey consumed at the lower prey density with the absence of a significant peak for consumption rate at the higher ones, it follows that a type III functional response can be suggested for *O. vulgaris* paralarvae. A type III functional response implies an increase of attack rate with prey density. For invertebrate predators, this result is usually explained by a more active search for prey as prey density rises (Hassell, 1978).

Studies on the behaviour of food webs support that even a slight relaxation of predatory efficiency at low prey densities promotes overall food web stability (Dunne *et al*., 2005). *Artemia* larvae are not native prey for cephalopod paralarvae, but the present investigation suggests that *O. vulgaris* paralarvae show such a relaxation of the predatory efficiency under some conditions. This fact allows us to speculate on octopus paralarvae as potential stabilizing predators in planktonic food webs. Temperature should be explored as a factor conditioning the existence of a type III functional response, since in *Crangon septemspinosa* preying on *Pseudopleuronectes americanus* juveniles, functional response is Type II at 16°C and Type III at 10°C, (Taylor & Collie, 2003). Authors have suggested a general mechanism, relevant to all ectotherms, as an explanation for this shifting: temperature-induced acceleration of foraging activity and metabolic rate (Clarke & Fraser, 2004).

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