

The cost of copepod reproduction: increased susceptibility to fish predation

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Summary. 1. We describe a laboratory investigation to determine how the possession of egg sacs by a freshwater copepod influences the likelihood of its capture by both efficient (bream) and inefficient (roach) zooplanktonivorous fish.

2. For both predators the reaction distance was greater for the larger, more visible ovigerous prey than for non-ovigerous copepods.

3. Copepods spent more time stationary, in contact with the substrate, when a fish was present. The more susceptible ovigerous individuals were generally less active than non-ovigerous individuals even in the absence of predators. The likely adaptive significance of this behaviour in the natural environment is discussed.

4. The inefficient zooplanktonivorous fish had a significantly increased attack efficiency on ovigerous prey because their egg sacs reduced acceleration and manoeuvrability. Attack efficiency was only marginally enhanced in the case of the more efficient predator.

5. The energy value of ovigerous prey, expressed in terms of biomass consumed per unit handling time, was greater than for non-ovigerous individuals.

Introduction

Zooplanktonivorous fish may exert a considerable influence on their prey communities (Hrbacek 1962; Brooks and Dodson 1965; Hall et al. 1976). Through the selective nature of their feeding behaviour they can cause dramatic changes in species composition and size-frequency distribution.

Prey selection is known to be influenced, among other things, by visibility (Zaret and Kerfoot 1975; Confer and Blades 1975 (a)) and motion, including both normal locomotion and active escape movements of the plankter (Zaret 1980; Drenner et al. 1978; Wright and O'Brien 1982). Such factors are not necessarily constant through the life cycle: in particular reproduction may be accompanied by important changes. Thus, ephippial individuals of the cladoceran *Daphnia galeata mendotae* have been shown to be selectively predated by zooplanktonivorous fish because of their increased visibility (Mellors 1975). It has been suggested that the possession of egg sacs by copepods may have an analogous effect, altering visibility and locomotory ability and

rendering ovigerous females more susceptible to predation than their non-reproducing conspecifics (Sandstrom 1980).

We have investigated how the possession of egg sacs by the freshwater copepod *Cyclops vicinus* Uljanin influences the likelihood of its capture by both efficient (under-yearling bream, *Abramis brama* (L.)) and inefficient predators of copepods (under-yearling roach, *Rutilus rutilus* (L.)) (Winfield et al. 1983). Studies were made in the laboratory of the attack behaviour of these two fish against ovigerous and non-ovigerous individuals. Observations were also made of the normal locomotory activity of the prey both in the presence and absence of a predator.

Methods

The interaction between predator and prey

The experimental procedures have been described previously (Winfield, 1983; Winfield et al. 1983). Under-yearling bream and roach (total body length 55–60 mm) were taken from a stock held at $14 \pm 2^\circ$ C in aquaria for at least 7 days before use. During this period the fish were fed solely on a commercial pellet food and consequently were not exposed to any zooplankton. Ovigerous and non-ovigerous individuals of *Cyclops vicinus* (size range 1.5–1.8 mm excluding caudal setae) were collected not more than 3 days before their use in experiments. Laboratory observations were made on the four possible single predator – single prey combinations, eight replicates of each.

An individual fish was introduced to the arena (an aquarium 300 mm long, 200 mm wide and 200 mm deep) at least 90 min before the trial commenced. After this settling period, 10 prey were introduced and the behaviour of the fish was recorded for 15 min. At the end of the trial the fish was removed and kept alone with an excess of food pellets for 24 hours. The procedure was repeated for a series of 5 days to investigate the effects of learning.

The behaviour of the fish was recorded in terms of 9 mutually exclusive behavioural units. This analysis only considered data from attacks made against prey swimming actively in the open water of the arena.

Approach. The fish makes its approach with its eyes directed at the prey item.

Chase. The fish follows a prey item as it moves away.

Unsuccessful strike. The fish simultaneously sucks and lunges at the prey but fails to make physical contact.

Successful strike. As above, but contact is successfully made.

Capture. The prey item is taken completely inside the fish's mouth.

Emergence. The prey comes out of the mouth. This may be due to the prey escaping or the predator actively ejecting it.

Mastication. The fish exhibits buccal and opercular movements characteristic of mastication.

Swallow. This is assumed to have occurred when mastication ceases and the prey has not emerged.

End of attack. The fish ceases attacking a particular prey item, or a captured prey is swallowed.

In addition, measurements were made of both handling time and reaction distance for each attack. Handling time, measured to the nearest second using a stopwatch, is defined as the period between the fish's initial approach and swallowing of the prey item. After swallowing, the fish is immediately ready for another attack. Unsuccessful attacks were also timed.

Reaction distance is defined as the distance between the fish's snout and the prey when an approach is initiated. The cyprinids used in this study do not display any particularly distinct behaviour when prey is sighted, unlike species of American sunfish (*Lepomis* spp) which may stop and erect their dorsal fins (Confer and Blades 1975 (b)). In addition, the distances involved were short. Our estimates of reaction distance (to the nearest cm) can only be considered approximate.

The locomotory activity of ovigerous and non-ovigerous copepods

20 *Cyclops vicinus* (size range 1.5–1.8 mm excluding caudal setae) and 30 *Daphnia magna* Straus (size range 1.5–1.8 mm excluding caudal spine) were introduced to an arena and left undisturbed for 60 minutes.

The number of *Cyclops* stationary on the sides or bottom of the arena was counted at 30 second intervals for a period of 20 minutes. A single bream was then introduced and the observations on *Cyclops* continued. The predator had previously been satiated with excess zooplankton prey so that it would show little actual feeding behaviour during the trial. The function of the easily captured *Daphnia* was to draw any predation attempts away from the copepods. Thus copepods, while not actually being depleted in numbers themselves, were exposed to a predator. After 20 minutes the predator was removed. The observations were continued for a further 40 minutes. This procedure was performed once with ovigerous copepods and once with non-ovigerous copepods.

Results

The interaction between predator and prey

Figure 1 illustrates the attack efficiencies (defined as number of swallows/number of approaches $\times 100\%$) exhib-

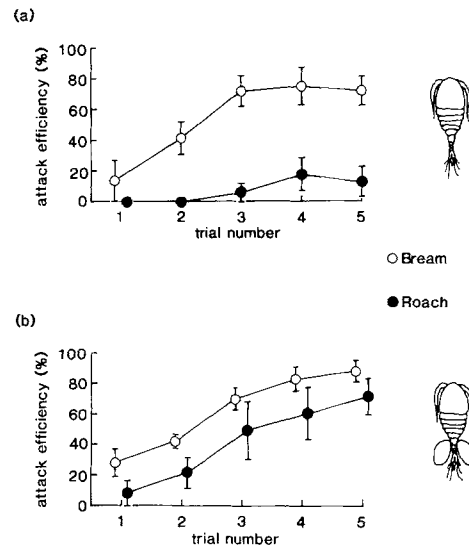


Fig. 1a, b. The effect of increasing experience on attack efficiency by underyearling bream and roach on **a** non-ovigerous copepods, and **b** ovigerous copepods (mean ± 1 S.E.). Bream are represented by open circles and roach by closed circles

ited by bream and roach towards the two forms of copepods. In contrast to roach, after a short period of learning bream were able to capture non-ovigerous copepods quite efficiently and thus quickly became the more efficient predator on this prey type (proportion of attacks which were successful on days 4 and 5: bream $38/55 = 69\%$, roach $9/50 = 18\%$; 2×2 contingency table $\chi^2_{(1)} = 27.61$, $P < 0.001$). Bream showed a very similar pattern of attack efficiency against the ovigerous copepods. Attack efficiencies of the most experienced bream did not differ significantly between the two prey types (non-ovigerous $38/55 = 69\%$, ovigerous $53/70 = 76\%$; $\chi^2_{(1)} = 0.68$, $P > 0.10$). In contrast, roach performed much more efficiently on ovigerous than non-ovigerous copepods and eventually performed as well as bream on these prey (roach $50/71 = 70\%$, bream $53/70 = 76\%$; $\chi^2_{(1)} = 0.50$, $P > 0.10$). Thus the possession of egg sacs by the copepods greatly increased the attack efficiency of roach, an otherwise inefficient predator of the elusive copepods (roach against non-ovigerous $9/50 = 18\%$, against ovigerous $50/71 = 70\%$; $\chi^2_{(1)} = 32.27$, $P < 0.001$).

The detailed character of the attacks made by the most experienced bream and roach is shown in Fig. 2. As was found with attack efficiency, the nature of attacks made by bream was similar for both prey types. Strike efficiencies (defined as number of successful strikes/total number of strikes $\times 100\%$) were not significantly different ($38/61 = 62\%$ for non-ovigerous, $53/83 = 64\%$ for ovigerous; $\chi^2_{(1)} = 0.04$, $P > 0.10$). Chases were quite common against both types of prey and while slightly more were exhibited against the ovigerous copepods this trend was neither very marked nor was it statistically significant (proportions of attacks involving chases: non-ovigerous $12/55 = 22\%$, ovigerous $25/70 = 36\%$; $\chi^2_{(1)} = 2.85$, $0.10 > P > 0.05$). However, bream showed relatively less chasing behaviour against both types of prey when compared with roach (against non-ovigerous, bream $12/55 = 22\%$, roach $26/50 = 52\%$ $\chi^2_{(1)} = 4.85$, $P < 0.05$; against ovigerous, bream $25/70 = 36\%$, roach $46/71 = 65\%$ $\chi^2_{(1)} = 3.98$, $P < 0.05$).

In contrast, the increased attack efficiency of roach

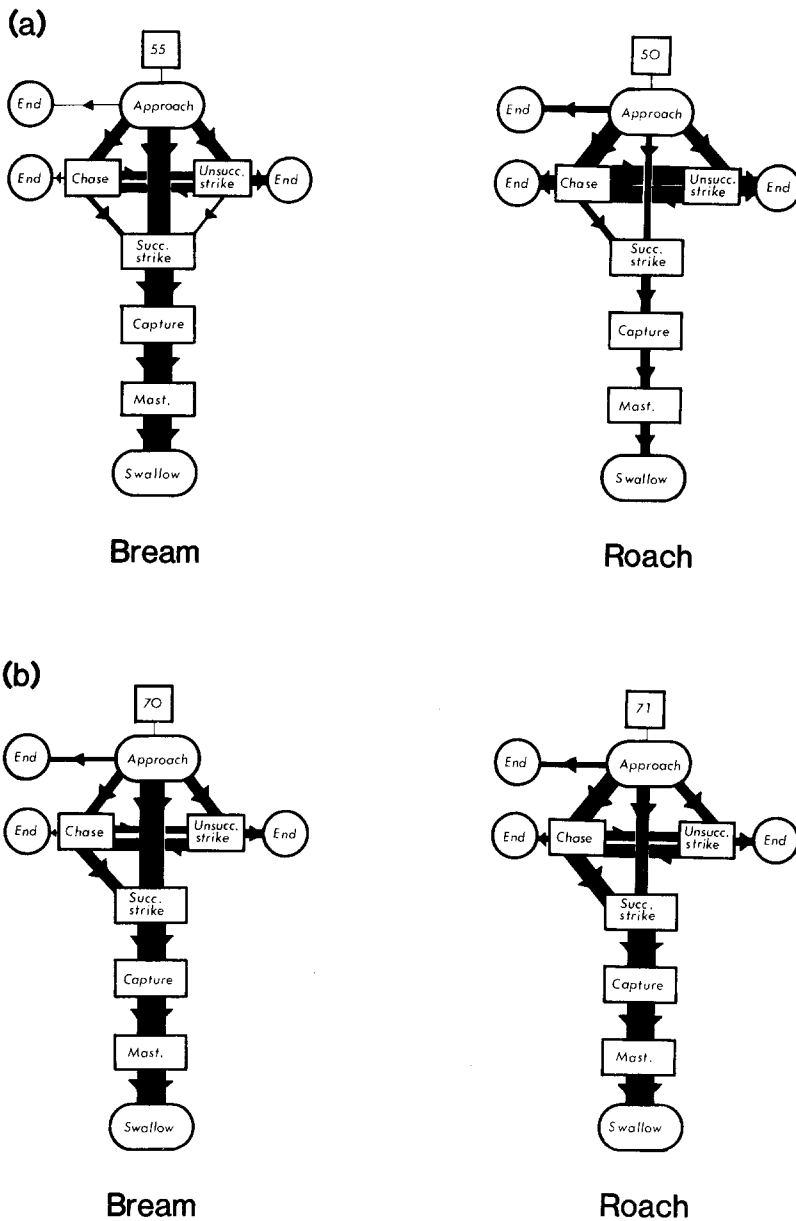


Fig. 2a, b. Flow charts showing the attack pattern exhibited against **a** non-ovigerous copepods, and **b** ovigerous copepods by experienced bream and roach (data combined from days 4 and 5). The units are joined together by lines of width proportional to the frequency with which that transition was exhibited by the fish. Arrow-heads show the direction of each transition. The number of approaches observed is shown at the top of each flow chart

against ovigerous prey was accompanied by other changes in the nature of the attacks. Strike efficiency was more than 3 times better than it was against non-ovigerous individuals (non-ovigerous $9/52 = 17\%$, ovigerous $50/79 = 63\%$; $\chi^2_{(1)} = 26.76$, $P < 0.001$). The proportion of attacks involving a chase, as with bream, did not differ significantly (non-ovigerous $26/50 = 52\%$, ovigerous $46/71 = 65\%$; $\chi^2_{(1)} = 1.99$, $P > 0.10$). However, the proportion of unsuccessful strikes which were immediately followed by the end of the attack did drop significantly (non-ovigerous $23/44 = 52\%$, ovigerous $6/29 = 21\%$; $\chi^2_{(1)} = 7.28$, $P < 0.01$). Roach were able to follow up an unsuccessful strike against an ovigerous copepod with chases which led to further strikes on 83% of occasions.

Handling times showed significant differences between fish species and prey types. Thus, the time taken by roach to handle ovigerous prey was significantly longer than that taken to handle non-ovigerous prey (8.10 ± 0.33 s (mean \pm 1 S.E.) compared with 6.67 ± 0.94 s, Mann-Whitney U test,

$P < 0.05$) as it was for bream (5.72 ± 0.21 s compared with 5.18 ± 0.33 s, Mann-Whitney U test, $P < 0.01$). The mean handling times of bream and roach for non-ovigerous prey did not differ significantly (Mann-Whitney U test, $P = 0.080$) but bream dealt with the ovigerous form significantly more quickly than did roach (Mann-Whitney U test, $P < 0.001$).

Handling time, as defined above, suffers from the serious disadvantage of not considering the time wasted in unsuccessful attacks. This problem may be overcome by the calculation of attack time. Attack time is defined as the total amount of time spent attacking prey during a trial divided by the number of prey swallowed.

Attack times differed significantly between predator and prey types. Mean roach attack time for non-ovigerous copepods was longer than that for ovigerous copepods (26.77 ± 12.53 s compared with 9.80 ± 0.90 s, Mann-Whitney U test, $P = 0.05$). In contrast, bream displayed the converse with attack time being longer for the ovigerous form

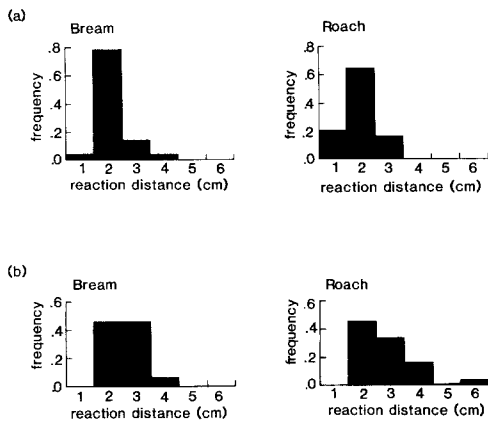


Fig. 3 a, b. Length frequency distributions of reaction distances against **a** non-ovigerous copepods, and **b** ovigerous copepods by experienced bream and roach

although the difference was much less marked (5.61 ± 0.45 s compared with 6.37 ± 0.36 s, Mann-Whitney U test, $P < 0.05$). The mean attack times of bream for both ovigerous and non-ovigerous prey were significantly smaller than those of roach (Mann-Whitney U test, $P < 0.01$ and $P < 0.001$ respectively).

Reaction distances of the most experienced fish are plotted as length frequency distributions in Fig. 3. Reaction distances towards the ovigerous prey were larger than those towards the non-ovigerous prey for both predators, though not significantly in the case of bream (bream non-ovigerous 2.18 ± 0.07 cm, ovigerous 2.67 ± 0.09 cm, Mann-Whitney U test, $P = 0.072$: roach non-ovigerous 1.96 ± 0.08 cm, ovigerous 2.86 ± 0.12 cm, Mann-Whitney U test, $P = 0.001$).

The locomotory activity of ovigerous and non-ovigerous copepods

During these observations the predator consumed only a few (< 8) *Daphnia* on each occasion and did not consume, nor attack, any *Cyclops*.

Changes in the level of locomotory activity of the *Cyclops* populations during the course of the manipulations are shown in Fig. 4. Before the introduction of the predator the ovigerous copepods were significantly less active than the non-ovigerous copepods (mean ± 1 S.E. of population inactive on sides or bottom during last 10 minutes prior to introduction of predator; ovigerous $59.50 \pm 1.14\%$, non-ovigerous $37.45 \pm 1.50\%$, Mann-Whitney U test, $P < 0.001$). Introduction of the predator resulted in both forms of copepod becoming less active. This effect was not instantaneous but gradually increased in strength over a 5–10 minute period until 75–80% of both prey types were inactive (ovigerous prey $59.50 \pm 1.14\%$ inactive prior to predator introduction compared with $79.25 \pm 1.46\%$ in presence of predator, Mann-Whitney U test, $P < 0.001$. Non-ovigerous prey, $37.45 \pm 1.50\%$ compared with $75.50 \pm 1.40\%$, Mann-Whitney U test, $P < 0.001$. Data taken from the last 10 min of each period). On the removal of the predator the non-ovigerous copepods gradually became more active until after 30 minutes they were as active as they had been before the introduction of the predator (before predator

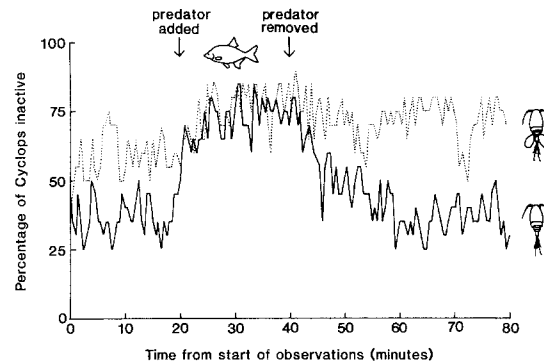


Fig. 4. Changes in the level of activity of non-ovigerous (solid line) and ovigerous (dotted line) copepods in relation to the absence and presence of a predator

$37.45 \pm 1.50\%$ inactive, after predator $37.50 \pm 1.43\%$, Mann-Whitney U test, $P > 0.10$. Data from the last 10 min of each period). The ovigerous copepods showed a similar gradual return to a higher activity level but they never reached that level exhibited in the pre-predator phase (before predator $59.50 \pm 1.14\%$ inactive, after predator $69.75 \pm 2.00\%$, Mann-Whitney U test, $P < 0.001$. Data from the last 10 min of each period). It is possible that the original level of activity would have been regained had the observations been continued for long enough.

Discussion

The interaction between the fish and their copepod prey can be broken down into two independent processes: (a) the rate of encounter with prey and (b) the efficiency with which encountered prey are captured. When alternative prey are available a third factor comes into play, namely (c) preferences shown by the predator for some prey categories over others (Eggers 1977).

The rate of encounter with prey is dependent upon reaction distance within which prey are detected and this depends in turn on prey visibility and prey behaviour (Wright and O'Brien 1982). The reaction distance for the larger, more visible ovigerous copepods was greater whether bream or roach are considered. In fact, the increase in reaction distance was of the same magnitude as that observed when these fish feed on 0.7 mm and 1.7 mm cladocerans (unpublished data). If the fish are assumed to have a hemispherical reaction volume of radius equal to the reaction distance (O'Brien et al. 1976; Confer et al. 1978) then the volume within which they respond to ovigerous copepods is twice as great as for non-ovigerous prey. An increase in visibility of this magnitude will have a significant effect on relative encounter rates between young cyprinids and their contrasting prey.

Zaret (1980), presenting evidence from several previous studies, suggested that prey species in motion are more vulnerable to fish predation because of an increase in conspicuousness. Observations made in the present study support this contention since, despite comprising the majority of individuals (75–80% from the observations of copepods),

stationary prey were the target of only 17–38% of attacks of the most experienced fish. In fact, these attacks against inactive prey were more successful than those against free-swimming individuals but this result is certainly an artefact of the very simple conditions of the laboratory arena; stationary prey were conspicuous against a light background. In the natural habitat the substrate (sediments, macrophytes) provides a better camouflage for the copepods. In this context Wierzbicka (1962) reported that as well as spending considerable periods in association with the surface of a mud substrate in culture tanks, *Cyclops vicinus vicinus* frequently entered the substrate and was able to travel freely under the surface. In addition, both males and females, and especially ovigerous females, of *Cyclops bohater* spent long periods in the mud. The copepods observed in this study frequently came to rest, particularly in the presence of a predator, and it is likely that had a sediment been present they would have burrowed into it.

The lower activity of egg-bearing individuals when compared to non-ovigerous conspecifics could be an adaptive response which reduces the chance of detection; alternatively it may simply be due to the animal being hampered by the weight and bulk of its two large egg sacs. The differences in activity may cause the two prey categories to have different microdistributions in the natural habitat. Such a phenomenon occurs with females of the copepod *Eurytemora hirundoides* Nordqvist which carry their eggs in a single large egg sac (Vuorinen et al. 1983). While non-ovigerous females were found distributed throughout the water column, ovigerous females almost totally avoided the surface layer where the danger of predation by fish was maximal.

Underyearling bream are much more efficient at capturing the rapid and erratically moving non-ovigerous copepods than are roach, probably because bream have a more protrusible mouth and can both develop a greater suction pressure and bring their mouth more rapidly towards the prey before it can dart away (Winfield et al. 1983). The attack efficiency of bream was only slightly, and not significantly, enhanced when ovigerous copepods are compared with non-ovigerous ones. However, the presence of egg sacs will increase the probability of predation in general because of the increased reaction distance and encounter rate.

Attack efficiency of roach was significantly greater on ovigerous copepods. This was mainly due to a threefold increase in strike efficiency and is a consequence of the egg sacs impairing the copepod's acceleration and manoeuvrability. The fact that roach were able to follow up unsuccessful strikes with further attack behaviour in the case of ovigerous prey also suggests that copepods are slowed down significantly by the burden of their egg sacs.

In our experiments on predation behaviour we presented each predator with only a single prey category and we cannot comment in detail on the topic of predator selectivity. However, it is worth noting that not only are ovigerous females encountered more frequently (at equivalent densities), and more efficiently captured (particularly by roach), they also constitute energetically more profitable prey items and are likely to be preferred over non-ovigerous copepods. Length/dry weight regressions derived by Dumont et al. (1975) reveal that a 1.65 mm adult cyclopoid copepod (middle of the size range used here) weighs 23.70 μg . The same paper also gives the dry weight of one cyclopoid copepod egg sac as 5.65 μg . Thus an ovigerous female totals 35.00 μg which is 1.48 times the weight of

a non-ovigerous copepod of similar length. In the parlance of optimal foraging theory we can define the *energy value* of copepods in each category (energy content or biomass divided by handling time – Townsend and Hughes 1981). These are for bream – non-ovigerous 4.58 $\mu\text{g}\cdot\text{s}^{-1}$, ovigerous 6.12 $\mu\text{g}\cdot\text{s}^{-1}$; and for roach – non-ovigerous 3.55 $\mu\text{g}\cdot\text{s}^{-1}$, ovigerous 4.32 $\mu\text{g}\cdot\text{s}^{-1}$. A more accurate determination of the energy values of the two prey types may be gained by the use of attack time (which takes unsuccessful attacks into account) rather than handling time. Values obtained by this method are for bream – non-ovigerous 4.22 $\mu\text{g}\cdot\text{s}^{-1}$, ovigerous 5.49 $\mu\text{g}\cdot\text{s}^{-1}$; and for roach – non-ovigerous 0.88 $\mu\text{g}\cdot\text{s}^{-1}$, ovigerous 3.57 $\mu\text{g}\cdot\text{s}^{-1}$.

Feifarek et al. (1983) revealed that ovigerous *Mesocyclops edax*, a freshwater copepod, survived environmental stress at a lower rate than unmated females which do not reproduce. The present paper shows that reproduction has another cost for copepods in that it increases their susceptibility to predation by fish.

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