



A review of the adaptive significance and ecosystem consequences of zooplankton diel vertical migrations

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Abstract

Diel vertical migration (DVM) by zooplankton is a universal feature in all the World's oceans, as well as being common in freshwater environments. The normal pattern involves movement from shallow depths at night to greater depths during the day. For many herbivorous and omnivorous mesozooplankton that feed predominantly near the surface on phytoplankton and microzooplankton, minimising the risk of predation from fish seems to be the ultimate factor behind DVM. These migrants appear to use deep water as a dark daytime refuge where their probability of being detected and eaten is lower than if they remained near the surface. Associated with these vertical movements of mesozooplankton, predators at higher trophic levels, including invertebrates, fish, marine mammals, birds and reptiles, may modify their behaviour to optimise the exploitation of their vertically migrating prey. Recent advances in biotelemetry promise to allow the interaction between migrating zooplankton and diving air-breathing vertebrates to be explored in far more detail than hitherto.

Introduction

Diel vertical migration (DVM) occurs in a wide range of both freshwater and marine zooplankton taxa and probably represents the biggest animal migration, in terms of biomass, on the planet. It is, consequently, not surprising that ever since the first descriptions of this behaviour a century or more ago, there has been extensive consideration of the adaptive significance and wider ecosystem consequences of this phenomenon (e.g. Forel, 1878; Hardy, 1936; Cushing, 1951; Pearre, 2003). The normal pattern (normal DVM) involves animals occurring deeper in the water column during the day and shallower at night, this being achieved by a dusk ascent and a dawn descent, with the difference between the day and night depths being termed the amplitude of DVM. A number of different aspects of DVM have been studied. For example, there has been considerable discussion of the proximate cues initiating vertical movements, with a strong role being implicated for the relative change in light intensity around dusk and dawn (Ringelberg, 1995, 1999). Over

the last two decades, international programmes such as the Joint Global Ocean Flux Study (JGOFS) have increased awareness of the role of the oceans in global biogeochemical cycles and have led to consideration of the implications of DVM in terms of the net removal of carbon and nitrogen from the ocean surface. By feeding near the surface at night, and then fasting at depth during the day where they continue to defecate, respire and excrete, migrating zooplankton may remove carbon and nitrogen from the surface layers and release it at depth (Longhurst & Harrison, 1989; Hays et al., 1997; Schnetzer & Steinberg, 2002).

In this review, I will first concentrate on the ultimate reasons for DVM and, second, I will examine the wider ecosystem implications in terms of how upper trophic levels adapt their behaviour to exploit vertically migrating prey.

Ultimate reasons for DVM

Given the wide occurrence of DVM in different marine and freshwater environments and in different taxa, it

is naive to hope to find a single ultimate reason to explain this behaviour. For example, DVM may serve to reduce the risk of damage to animals from ultraviolet radiation (Leech & Williamson, 2001), but avoidance of exposure to ultraviolet radiation certainly cannot explain many cases where the vertical movements have an amplitude of many tens or even hundreds of metres. However, the fact that DVM is so widespread and found within practically all taxonomic groups, suggests that, in many cases, there must be a common underlying ultimate driving force. Generally, when considering the ultimate reason for normal DVM, this question is couched in terms of mesozooplankton that feed either herbivorously or omnivorously on phytoplankton and microzooplankton that occur in maximal densities in near surface waters. For these mesozooplankton, there is a clear cost to DVM, in that during the day, animals will be separated spatially from their near-surface food and so cannot feed at high rates. In addition, cold sub-thermocline temperatures may reduce the reproductive fitness of migrants (Aksnes & Giske, 1990; Dawidowicz & Loose, 1994).

Counterbalancing this cost, it is axiomatic that there must be some benefit to DVM. Hypotheses for the ultimate reason for DVM have been divided into two broad categories by Lampert (1989). Firstly, it has been suggested that residing in cold water during the day and feeding in warmer water at night may provide a metabolic advantage for migrants (e.g. McLaren, 1963, 1974; Enright, 1977). However, empirical support of this group of hypotheses is scant and most evidence suggests that the reverse is true: vertical migration is energetically disadvantageous (Lampert et al., 1988; Lampert, 1989; Aksnes & Giske, 1990). Secondly, it has been suggested that normal DVM serves to reduce the risk of predation from visually orientating predators, the so-called predator evasion hypothesis. This hypothesis is elegantly simple and has intuitive appeal. The predator evasion hypothesis suggests that if mesozooplankton remained near the surface during the day, they would have a high chance of being seen by visually orientating predators (principally fish) and hence consumed. Consequently, migrants descend around dawn to use the ocean depths as a dark daytime refuge where the probability of being detected by a visually hunting predator, and hence eaten, is lower than if they remained near the surface (Zaret & Suffern, 1976). Essentially, the benefit of a reduced probability of predation is suggested to outweigh the cost of a reduced potential for daytime feeding, with the maxim being 'better hungry than

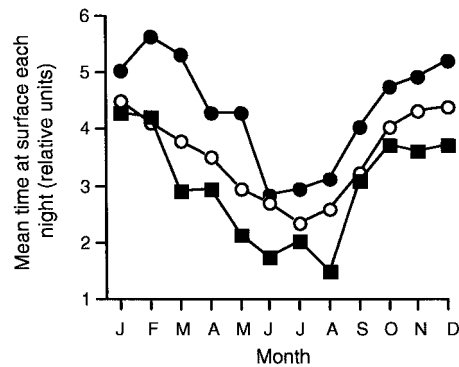


Figure 1. The mean daily length of near-surface occupation by different populations of copepods in the North Atlantic, using samples from the Continuous Plankton Recorder survey. Filled circles = juvenile *Metridia*, open circles = adult *M. lucens*, filled squares = adult *M. longa*. For adult *Metridia longa*, adult *M. lucens* and juvenile *Metridia*, there were seasonal changes in the length of near-surface occupation in line with seasonal changes in the length of the night. For example, in winter, when nights are longer, populations spent longer at the surface each night compared to during the summer. In addition to this seasonal pattern, the length of near-surface occupation varied with body size, being shortest for the largest group, adult *M. longa*, and longest for the smallest group, juvenile *Metridia*. Adapted from Hays (1995).

dead' (Kremer & Kremer, 1988). There is considerable support for the predator evasion hypothesis.

In freshwater environments, there has been particularly elegant work showing how DVM is a plastic behaviour modified in accord with the presence of planktivorous fish or fish kairomones: when fish are present, zooplankton show stronger DVM (Dawidowicz & Loose, 1992, 1994; Dodson et al., 1997; Van Gool E. & J. Ringelberg, 1998, 2002). Comparable evidence also exists for marine systems. For example, at times when planktivorous fish are more abundant, normal DVM may be more pronounced (Bollens & Frost, 1989; Frost & Bollens, 1992). Individual differences in DVM may also be under genetic control leading to long-term evolutionary changes in the DVM behaviour of populations associated with changes in the intensity of predation pressure from fish (Cousyn et al., 2001).

While these types of study show that, for the selected species, normal DVM is coupled to the abundance of planktivorous fish, they cannot be used to suggest that normal DVM serves an anti-predator function in all other cases. One approach to consider whether predator evasion can be used as a general explanation for the occurrence of normal DVM in a range of taxa, is to examine inter-specific patterns in this behaviour. Furthermore, we can use the predator eva-

sion hypothesis to make specific *a priori* predictions about inter-specific patterns in DVM. Specifically, the predator evasion hypothesis predicts that DVM should be more pronounced in those species that are most susceptible to visually orientating predators. Since the visibility, and hence susceptibility, of mesozooplankton to planktivorous fish increases with increasing size and pigmentation, the predator evasion hypothesis predicts that DVM should be most pronounced in larger and more heavily pigmented individuals and species and, indeed, there is very extensive empirical evidence to show that this is the case (Zaret & Kerfoot, 1975; Wright et al., 1980; Wiebe et al., 1992; Hays et al., 1994). Smaller zooplankton arrive at the surface earlier and leave later than larger forms, consistent with the interaction of light levels and prey size on prey perception by planktivorous fish (Hays, 1995; De Robertis et al., 2000). Furthermore, in order to constrain their near-surface foraging to the hours of darkness, we can use the predator evasion hypothesis to predict that, particularly at high latitudes, there will be marked seasonal changes in the length of near-surface residence by migrants in line with seasonal changes in day and night length. Again, this prediction is supported by extensive empirical evidence, with migrants spending longer at the surface each night during the winter when nights are longer (Hays, 1995; Hays et al., 1995) (Fig. 1).

The predator evasion hypothesis can be used also to make predictions about how DVM should vary between individuals of the same species depending on their nutritional state. For example, for individuals that have built up lipid reserves, there may be less need to come to the surface to feed and so lipid-rich individuals can maintain their reproductive output without increasing their risk of predation by near-surface foraging (Fiksen & Carlotti, 1998; Sekino & Yamamura, 1999). Moreover, this prediction is supported by empirical observations that show how lipid-rich individuals may spend less time at the surface than their lipid-poor co-specifics (Sekino & Yoshioka, 1995; Hays et al., 2001).

Interestingly, instances where mesozooplankton reverse their normal pattern of DVM can also be explained by predator evasion. In reverse DVM, a population occurs nearer the surface during the day and deeper at night, and this behaviour has been associated with high levels of invertebrate predators that use tactile stimuli, rather than vision, to locate their prey, i.e. the normal pattern of DVM appears to be reversed when evasion of invertebrate predators, rather than

visually feeding planktivorous fish, is most important (Ohman et al., 1983; Neill, 1990).

While predator evasion is probably the most important ultimate reason for DVM, there are associated consequences of this behaviour. For example, if migrants move between different currents at different depths, then DVM may translate into horizontal movement into new patches of surface water (Hardy, 1936). However, except in the case of some vertical movements that are coupled to tidal flows in coastal regions (Hill, 1998), horizontal movement is probably most often just a consequence of DVM rather than the ultimate reason for DVM. In short, while there are certainly a number of reasons why mesozooplankton undertake DVM, the most likely ultimate reason, is predator evasion.

Implications for higher trophic levels

Invertebrates and fish

With many species of mesozooplankton undertaking daily vertical movements, it is hardly surprising that some predators at higher trophic levels modify their behaviour to exploit this vertically moving food source, while at the same time possibly minimising their own risk of predation from their own visually orientating predators. For example, many carnivorous zooplankton (e.g. copepods of the genus *Euchaeta*, scyphozoan jellyfish and siphonophores) use tactile stimuli, rather than vision, to locate prey and, hence, probably catch mesozooplankton equally well in darkness *versus* daylight. Such predators can simply track the vertical movements of their prey. Indeed, larger pelagic animals, many of them carnivores, are frequently observed on echo-sounders as 'deep scattering layers' (DSLs) or 'sound scattering layers' (SSLs) which can be seen to ascend around dusk and descend around dawn presumably reflecting this predator-prey tracking. Often discrete layers are evident at different depths, each layer composed of different species or developmental stages (e.g. Tarling et al., 2001).

Fish that require high ambient light levels to locate and capture prey may be unable to feed on animals within the SSL, and so confine their foraging to well illuminated shallow depths. However, fish that are able to hunt at low light levels may join the SSLs to feed. For example, many small mesopelagic fish form part of the SSL (e.g. Rasmussen & Giske, 1994), while acoustic tracking of large (25–50 kg)

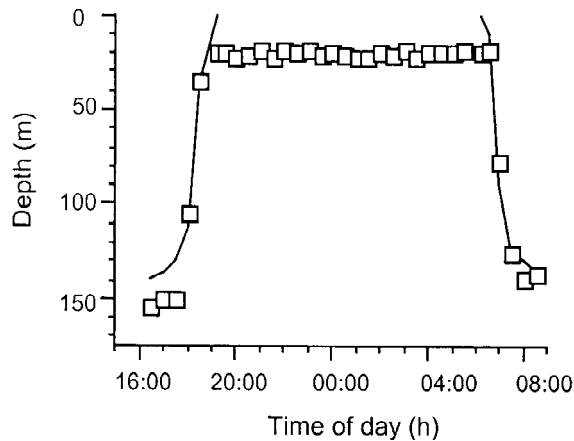


Figure 2. The depth of an acoustically tracked megamouth shark (*Megachasma pelagios*) over 1 day and the estimated depth of the isolume that most closely corresponded with the dawn descent and dusk ascent of the shark. Open squares show depth of the shark, solid line shows depth of the isolume. Adapted from Nelson et al. (1997). This fish followed this isolume, which presumably reflected the depth of its zooplankton prey. At night the isolume 'disappeared', so that ambient light levels experienced by the shark were lower near the surface at night than at depth during the day.

big-eye tuna (*Thunnus obesus*) has shown that there is sometimes a close correspondence between the descent of individuals at dawn and the depth of the SSL (Dagorn et al., 2000). Similar diel vertical movements have been recorded for swordfish (*Xiphias gladius*) (Carey & Robison, 1981). Also, some filter-feeding fish may track the SSL. For example, an acoustically tracked megamouth shark (*Megachasma pelagios*) showed rapid changes in depth around dusk and dawn, presumably associated with this shark attempting to track its zooplankton prey (Nelson et al., 1997) (Fig. 2). However, for all these examples of fish exhibiting diel vertical movements, it would be over simplistic to describe this as an invariant behaviour. On occasion, all species will probably break away from tracking the SSL. For example, tracked bigeye tuna and swordfish have been shown sometimes to move up into shallow water during the day, possibly to re-warm (Carey & Robison, 1981; Dagorn et al., 2000). Similarly, we might expect that vertical movements of such fish might be suspended when prey occur in sufficiently high concentrations near the surface.

Air-breathing vertebrates

Of course, air-breathing vertebrates that feed on animals within SSLs must periodically come to the surface to breathe. This requirement to breathe, means that

the commuting costs (i.e. from the surface to the prey) will vary over a diel cycle, being short during the night (when the prey are shallow) and deep during the day (when the prey are deep). At first glance, this appears to suggest that shallow night-time feeding would be preferable for an air-breather feeding within the SSL. However, in addition to the commuting cost, the optimum foraging strategy will also be dictated by the efficiency of prey capture once at the prey depth. For example, even if the prey are very shallow at night, a low commuting cost may translate into a poor rate of prey ingestion if it is too dark to locate and capture prey.

While studies of zooplankton DVM have been reported for a century or more, it is only relatively recently that technological advances have provided the tools to examine diel patterns in the diving performance of air-breathing vertebrates. For example, time-depth recorders (TDRs), which are data loggers that record ambient pressure (and hence depth) at intervals of a few seconds, allow dives to be recorded over periods of weeks or even months. An early description of the first widely used analogue TDR was provided by Gentry & Kooyman (1986), but nowadays miniature digital TDRs, weighing as little as 5 g, are commercially available from several manufacturers. As well as measuring the depth and duration of dives, additional sensor packages allow the swim speed, flipper movements, individual prey ingestion events and prey fields to be recorded (Wilson et al., 1993, 2002a,b; Hooker et al., 2002). TDRs may be interfaced with satellite transmitters which relay dive information from any location in the World via polar orbiting satellites that form part of the Argos tracking system (<http://www.argosinc.com/>), so that the study animal need not be recaptured for data acquisition to occur. Although the large amounts of data collected by TDRs (up to several Mb) cannot be relayed via the Argos system due to the limited bandwidth that is available (Fedak et al., 2002), onboard data analysis and compression allow dive profiles to be obtained remotely (Fig. 3). These types of technology have (and are currently) being used to explore the diving patterns of certain marine birds, marine mammals and marine reptiles that may feed on prey within the SSL.

Probably the best described interaction between air-breathing divers and vertically migrating prey concerns various species of penguin feeding on fish or euphausiids within the SSL (e.g. Wilson et al., 1993, 2002a; Cherel et al., 1999; Bost et al., 2002). For example, Wilson et al. (1993) recorded the diel

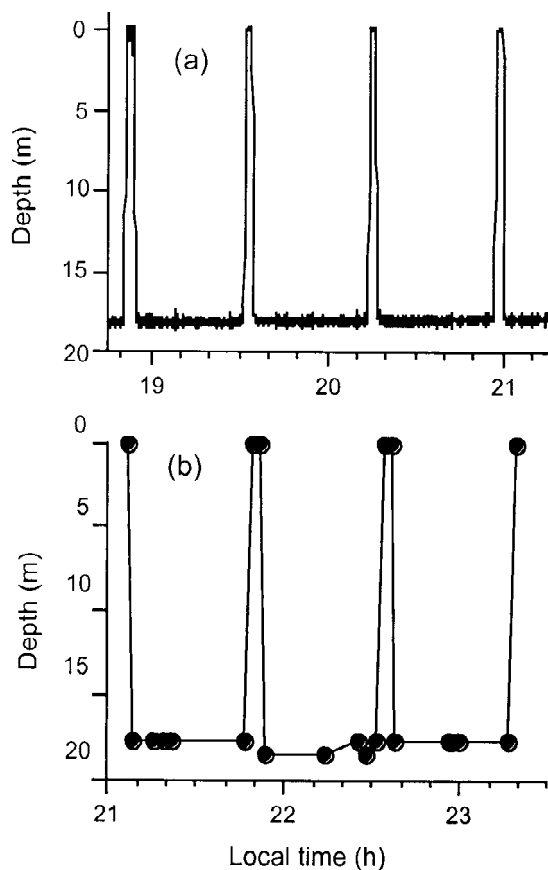


Figure 3. One of the most advanced satellite linked TDRs is the Satellite Relay Data Logger (SRDL) designed by the Sea Mammal Research Unit (SMRU) and originally described by McConnell et al. (1992). In order to allow dive profiles to be relayed via the limited bandwidth of the Argos system, depth is sampled every few seconds and then once a dive is completed there is on-board analysis of the dive profile and only the depth and time of the 5 most important points of inflection during the dive are transmitted, plus the time of the start and end of the dive. In this way the essential elements of the dive profile are transmitted in a most economical way. To illustrate this point, the figure shows the typical U-shaped dive profiles conducted by green turtles (*Chelonia mydas*) at Ascension Island obtained (a) with a time-depth recorder (TDR) sampling depth every 5 seconds during April 2002 and (b) with a SRDL in July 2001. In the latter case, the transmitted times and depths are shown by the symbols. See Hays et al. (2000) for details of this study site and field protocols. Since the dive profiles of planktivorous leatherback turtles and other air breathing planktivores are often very simple in shape (e.g. Southwood et al., 1999), obtaining accurate dive profiles remotely from free-living animals outside the breeding season is now possible.

dive patterns in king penguins (*Aptenodytes patagonicus*), African penguins (*Spheniscus demersus*), Ad-
elie penguins (*Pygoscelis adeliae*), gentoo penguins (*P. papua*) and chinstrap penguins (*P. antarctica*). While penguins tended to conduct shallow dives at

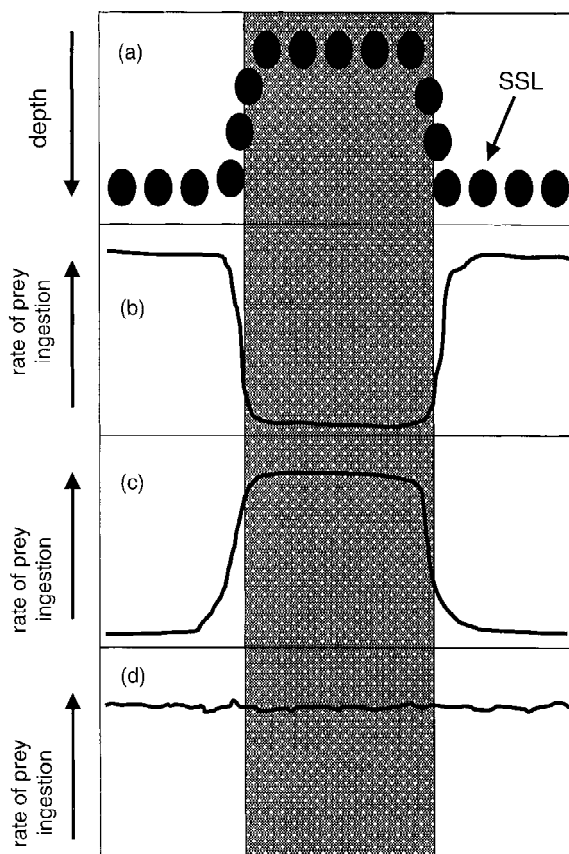


Figure 4. Schematic representation of how the rate of prey ingestion may vary over the diel cycle for various predators feeding within sound scattering layers (SSLs). Shaded area represents night. In (a) the black ovals represent the depth of a SSL. Empirical evidence suggests that penguins often feed best during the day when their prey are deep (b), while fur seals feed best at night when their prey are shallow and then stop diving during the day when the SSL has descended (c). The filter feeding megamouth shark has been shown to follow an isolume, presumably staying within a SSL so that they can feed both day and night (d).

night and deep dives during the day, there was a distinct diel pattern to prey capture with most prey being captured during daytime deep diving (Wilson et al., 1993). Presumably, this diel pattern is caused by the ambient light levels at prey depths being higher during the day than at night, even though the prey are located deeper during the day. Further support for this inference can be gauged by examining how isolumines approach the surface at dusk and descend at dawn (Fig. 2). Often an isolume will rise towards the surface at dusk, but then light levels everywhere near the surface will be less than this isolume during the middle of the night. This pattern is evident as the isolume 'disappearing' only to re-appear as the sun rises around

dawn. For animals in the SSL whose daytime depth is determined by such an isolume, this pattern will mean that despite the animals' vertical migration to the surface, ambient light levels will be lower at the animals' shallow night-time depths than their deep daytime depths.

Diel patterns in diving behaviour have been described for some marine mammals feeding within SSLs. In contrast to the diel pattern of feeding for penguins, deployments of TDRs on fur seals (*Arctocephalus* spp.) suggest that most prey are captured during shallow night-time diving, with individuals not diving during the day when their prey have descended (Croxall et al., 1985; Horning & Trillmich, 1999). During short-term deployments of TDRs on pilot whales (*Globicephala melas*) and pantropical spotted dolphins (*Stenella attenuata*), it was found that during the day individuals were always near the surface but then after dusk they started to dive, possibly in order to feed on animals within an ascending SSL (Baird et al., 2001, 2002). Presumably, differences in diel foraging patterns between different divers may reflect: (i) differences in ambient light levels at prey depths during the diel cycle, (ii) differences in the visual acuity of these different predators at low light levels, (iii) differences in the escape abilities of the different prey, so that ambient light levels are more important for the predator in one case than the other, and (iv) differences in the amplitude of DVM by different prey species so that the commuting costs in reaching the prey vary for these different divers.

In addition to marine mammals and birds, one species of marine reptile, the leatherback turtle (*Dermochelys coriacea*), feeds mainly on plankton and, more specifically, on gelatinous zooplankton such as scyphozoan jellyfish, siphonophores and pyrosomes. Often, these prey form part of the SSL. To date, relatively few records of leatherback diving performance have been obtained, with almost all records focussing on the interesting period when turtles are at their tropical and sub-tropical nesting areas. In some cases, leatherbacks dive to relatively shallow depths (rarely beyond 100 m) and, in these cases, their dives may be constrained by bathymetry and may not reflect their diving behaviour when they are in deep oceanic areas outside the nesting season (Southwood et al., 1999). However, for leatherbacks nesting at St Croix in the Caribbean, much deeper dives have been recorded in the interesting period, with a maximum measured depth of 475 m (Eckert et al., 1986); even deeper dives have been inferred when some dives were deeper

than the maximum range of the TDR (Eckert et al., 1989). Furthermore, a diel signal in diving behaviour was evident. At night, more time was spent diving and dives tended to be shallow, while, during the day, less time was spent diving but dives tended to be deeper. These diel patterns suggest an interaction between leatherback diving and vertical movements of SSLs but the details of this interaction remain unclear. It might be, for example, that leatherbacks are mainly shallow night-time feeders and their less frequent deep daytime dives reflect 'prospecting' to see whether the SSL is returning towards the surface. Alternatively, leatherbacks may feed day and night, and simply dive less during the day because deeper dives necessitate periods of recovery at the surface. Furthermore, the pattern of diving by leatherbacks outside the nesting season remains unknown, but the answer to this question is certainly attainable through the deployment of satellite-linked time-depth recorders.

Future studies

After more than a century of studies, there is probably little more to be gained by more simple descriptions of the day and night vertical distributions of zooplankton. However, some investigations of vertical migration are still in their infancy. Firstly, there has been relatively little consideration, particularly in marine environments, of the causes and consequences of individual differences in migration behaviour; for example, related to nutritional state. Secondly, the advent of equipment that allows various aspects of the free-living diving behaviour of vertebrates to be explored, often in remote locations and over time-scales of months, promises a new era of studies of the consequences of zooplankton vertical migration for higher trophic levels.

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