

predation risk from visual predators is low at depth and varies diurnally at the surface. Consequently, many zooplankters undertake diurnal vertical migration, such that they always reside at a depth where the ratio of gain to risk, or some other measure of fitness, is maximized. Vertical migration is well documented and is a classical example of how individual behaviours dictate the distribution of the population. Several authors have elaborated on the general idea of fitness optimization with respect to vertical distribution in zooplankton attempting to predict vertical distributions from behaviour (e.g. Aksnes and Giske 1990; Ohman 1990; De Robertis 2002). The study by Titelman and Fiksen (2004) is particularly illuminating in the present context as it combines detailed mechanistic descriptions of predator encounter risk from visual (fish) and tactile (zooplankton) predators as functions of individual prey behaviours, individual predator avoidance capability, and temperature-dependent growth rates in a habitat optimization model to predict the ontogenetic vertical distribution pattern of various copepods. The general prediction from this exercise is that nauplii and small copepods will reside near the surface, while later developmental stages and larger copepods should reside deeper, consistent with observations (Fig. 6.8).

Similar considerations of the trade-off between feeding opportunities and predation risk would predict that zooplankters should reside shallower in the water column when feeding conditions are poor and deeper when they are better. Such variation in feeding opportunity may be a simple function of food concentration, but may also be mediated by variation in small-scale turbulence. If turbulence enhances the predator-prey contact rate, as suggested by some laboratory studies (see above) elevated levels of turbulence during wind events should lead to a deeper optimal zooplankton residence depth. Although other hypotheses lead to a similar prediction (Pringle 2007), observations of vertical distributions of copepods (Mackas *et al.* 1993; Lagadeuc *et al.* 1997; Incze *et al.* 2001; Visser *et al.* 2001) and fish larvae (Heath *et al.* 1988; Reiss *et al.* 2002) consistently show that these zooplankters reside deeper in the water column during wind events than during calm weather. This prediction is robust, because even in cases where turbulence has a negative effect on feeding,

deeper residence should be preferred in turbulent environments because turbulent intensities typically decline with depth.

6.5.2.2 Motility and mortality

Most zooplankters move, either by passive sinking or active swimming, and/or they produce feeding currents. There are gains and risks associated with moving. Specifically, moving enhances the chance of encountering food and mates, but moving also elevates the risk of meeting predators and has energetic costs. The optimal motility is that which maximizes gains over risks, in whatever units are relevant for the situation considered. Here we examine the case of mortalities in mate-searching pelagic copepods. Because it is typically the male that has to find the female, rather than vice versa, males often swim faster and with more directional persistence than females. This implies a higher mortality in males than in females and leads to female-biased adult sex ratios in field populations. The male should swim at the speed which optimizes the number of females he will encounter during his adult life. That speed may depend on the feeding strategy of the male. Some adult males do not feed at all (common among calanoid copepods), others cruise through the water while feeding and thus may feed and search for females simultaneously (most copepods of the superfamily Centropagoidea), while others again are ambush feeders and, thus at any point in time *either* feed *or* search for females (common among Oithonid copepods). Analytical predictions of the swimming velocity that optimizes the trade-offs between mate encounters, predation mortality, and energetics as well as empirical evidence suggest that the optimal swimming velocities of males with these different feeding strategies are dramatically different: ambush feeders swim at very high velocities when they swim, and at orders of magnitude faster than the females; non-feeding and cruise-feeding males swim quite slowly and at speeds that are within a factor of 2 of those of the females (Kjørboe 2008; Table 6.3). Simple models allow one to estimate the ratio of male to female mortalities (or average longevities) from differences in energetics (feeding or not) and swimming speed and, in turn, to predict adult sex ratios in field populations (Kjørboe 2008). The correspondence between observed and