## Contribution to the Themed Section: 'Larval Fish Conference'
## Food for Thought

# Can behavioural ecology unite hypotheses for fish recruitment?

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Since the classical works by Hjort linked the survival of early life stages of fish to year-class strength and recruitment, fisheries science has struggled to understand the fate of fish eggs and larvae. Here we discuss how food availability will influence growth and survival of larvae when foraging behaviour is flexible and involves predation risk. We use theory to show that small larval fish with a high risk of predation should nevertheless forage intensely and maintain high growth rates. The implication of this is that food availability is more important to recruitment success than is often assumed from studies of growth rate, since the main effect of low food availability appears as increased predation rates. As larvae develop and grow bigger, they are expected to tailor their behaviour to balance food intake and predation risk, which makes it more probable that environmental fluctuations will cause growth differences. A theoretical framework including larval behaviour thus illustrates how several existing hypotheses, i.e. "bigger is better", "stage duration", and "growth-selective predation", emphasize different aspects of larval success but can be understood more generally and coherently when interpreted in the light of behavioural trade-offs. This may lead to more consistent consideration of larval behaviour in biophysical models of fish recruitment.

Keywords: adaptations, larval fish behaviour, life history theory, recruitment success, trade-offs.

## Introduction

Many pelagic fish larvae hatch as vulnerable and almost immobile particles, but can quickly develop locomotory capabilities (Clark et al., 2005) and may eventually adopt schooling behaviours (Leis, 2007). The extraordinary high mortality experienced during their earliest life stages (McGurk, 1986) exerts strong selective pressures to fine-tune their behavioural strategies through Darwinian evolution. *A priori*, one would therefore expect them to have adapted behaviours such as activity level, depth positioning, and aggregation tendency to maximize survival, and that these strategies would be flexible with regards to their size, internal condition (e.g. hunger), and the anticipated risk of predation in their current environment (based on e.g. light levels or direct cues). Behavioural capacities are known to have profound effects on the interplay between environment, growth and survival (Lima and Dill, 1990); in this paper we assess the value of a behavioural perspective for understanding recruitment processes in fish larvae.

In Hjort's time, data was scarce, which had the side-effect of leaving ample room for speculation. A common contemporary belief was that all herring belonged to one inexhaustible population in the Arctic and that variable migratory routes explained why local fishing grounds were fluctuating (Sinclair and Solemdal, 1988). Using age reading from fish scales, Hjort and his co-workers were able to show how some strong year-classes swept through the population like a wave and could dominate for almost a decade (Hjort, 1914). At the same time, these strong year-classes could not be linked to a large parental population, so their formation seemed almost random or caused by some undetermined environmental factor. Attempting to provide a mechanistic link to the observed fluctuations, Hjort (1914) formulated the "critical period" hypothesis, stating that newly hatched larvae that "did not succeed in finding the very special food they wanted would die from hunger" (Hjort, 1926). This hypothesis was later explored in detail for Norwegian spring spawning herring (Dragesund, 1970), and refined to become

the more general match–mismatch hypothesis by Cushing (1973; 1990). The match–mismatch hypothesis proposed that larvae hatching near the peak abundance of their zooplankton prey would survive and recruit better, thus forming strong year-classes.

Hjort's (1914; 1926) concept of a "critical period" still dominates fisheries recruitment science a century later, although it has been complemented by more specific hypotheses that attempt to explain how food can be mechanistically and causally linked to recruitment success. The "bigger is better" hypothesis (Houde, 1987; Litvak and Leggett, 1992) is based on the observation that predation rates are high but decline rapidly with size in marine organisms in general (Peterson and Wroblewski, 1984) and for fish larvae in particular (McGurk, 1986; Houde, 1987). An implicit consequence is the closely related "stage duration" hypothesis. Rather than explicitly addressing size, it focuses on the time spent in the smaller and vulnerable size-classes; if growth increases, this period is shortened and survival is therefore higher (Shine, 1978; Houde, 1997). A third perspective is the "growth-selective predation" hypothesis, based on observations that slow-growing larvae were more likely to be eaten, presumably because too little food reduced performance and anti-predator behaviours (Takasuka *et al.*, 2003).

The common assumption made by the three hypotheses is that favourable food conditions will increase growth rate, which in turn has a positive effect on survival. In this paper we suggest that behavioural responses play a central role in this chain of causal mechanisms, based on developments made within behavioural ecology and life-history theory over recent decades. A core mechanism is that food abundance will increase survival through changes in behaviour, whereas there can be little or no concurrent change in growth (McNamara and Houston, 1987; Fiksen and Jørgensen, 2011). Our manuscript is structured as follows.

We first point to mechanisms and selection pressures that link growth rate to predation risk in larval fish. Our focus is on species from high latitudes with a pelagic larval phase, but many of the mechanisms and relationships are general and would apply to tropical regions as well. With reference to a detailed state-variable dynamic optimization model for growth and survival in fish larvae, we argue that a main role for adaptive larval behaviour is to maintain high growth rates across a wide range of food concentrations, but that survival can be compromised (Fiksen and Jørgensen, 2011). We highlight some key predictions from this model and use them to demonstrate links between behaviour, growth, and survival.

Whereas Hjort's (1926) starting point was that larval fish suffering mismatch "would die from hunger", the theory we present indicates that less food may alter foraging behaviour and cause larvae to take more risks, making predation rather than starvation the main cause of death. The distinction between these two views is discussed.

The above points indicate that evolved strategies and environmental variation are two sources of differences between individuals. These are compared and contrasted. We then illustrate how a focus on larval fish behaviour may help bring together the perspectives of the "bigger is better", "stage duration", and "growth-selective predation" hypotheses. Finally, we end the paper with a brief discussion of implications for biophysical models that explicitly consider the larval phase.

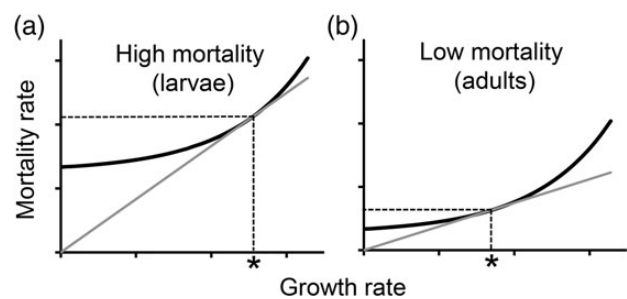## Trade-offs between growth and survival

What does theory have to say about how animal behaviour can modify growth and survival? Think of an animal with some foraging behaviour, for instance activity level or boldness during foraging. Pivotal to understanding the selection pressures on such behaviours is to identify the involved trade-offs, i.e. how an individual may need

to sacrifice ingestion to achieve survival, or the other way around. If predation rate is plotted as a function of growth rate, Gilliam's rule (Werner and Gilliam, 1984) can be applied to find the evolutionarily optimal growth rate. Graphically, this is done by drawing the tangent through the origin, and it will intersect the curve at the point where the ratio between mortality and growth is minimized, i.e. where growth is optimal (denoted with *) because a larger size is achieved with the lowest probability of predation (Figure 1).

The exact relationship between growth rate and predation rate is variable and depends on the type of predator, the type of prey, the environment, the individual's behaviour, and strategic life history trade-offs (Huse and Fiksen, 2010). The relationship is furthermore expected to change with development as larvae aquire increased capabilities of locomotion, sensing, escape, and defence. In herring larvae, it is for example observed that responsiveness to a predation cue increases with age, presumably due to development, but also with size (Skajaa *et al.*, 2004) in line with the expectation of more cautious behavioural strategies as size-dependent mortality declines. At the broad scale, growth rate is a trait that has evolved to an optimal level to maximize expected offspring production during a lifetime (Arendt, 1997). Many processes contribute to growth, some of which affect acquisition or foraging rates, and some that determine how growth is prioritized over other processes that compete for resources (Enberg *et al.*, 2012). A good starting point when thinking about all these processes can be to ask the two following questions about the benefits and costs.

### What can be achieved by increasing foraging activity?

Generally, growth will increase with increasing foraging activity, although there will typically be diminishing returns. Behaviour can cause this due to: (i) a functional response with handling time limitation, causing ingestion rate to approach a ceiling even though further foraging increases the encounter rate with prey (Holling, 1965), which is particularly relevant for species such as planktivorous fish that ingest single food particles that are small relative to body size; (ii) inclusion of less-preferred items in the diet, which may reduce the energy efficiency of foraging (Emlen, 1966); or (iii) first utilizing the hours of the day that are most efficient for foraging, typically at dusk and dawn, (Clark and Levy, 1988), then extending foraging to



**Figure 1.** A graphical illustration of optimal growth rates (*) under different mortality levels, given a behavioural trade-off between growth rate and survival. By drawing the tangent to the mortality curve through the origin, the point is found where the ratio between mortality and growth is minimized, analogous to Gilliam's rule (Werner and Gilliam, 1984). The optimal growth rate (*) is higher when mortality is high (**a**), compared with a situation where mortality is lower (**b**). Note that the figure shows growth rate on the *x*-axis and each panel assumes a constant size; the generally declining mortality rate with increasing size is visible in the contrast between panels (a) and (b).

times with less favourable conditions. One can also think of other mechanisms, as well as constraints e.g. from the processing capacity of the gut, but in general we expect growth to increase, but to approach an asymptote, with increasing foraging activity.

### What are the costs of increasing foraging activity?

Increased foraging may require a larger gut or better swimming muscles, which have energetic costs that will reduce the energetic efficiency of foraging or may incur elevated maintenance costs when running idle. Still, survival costs are probably most important, especially for small fish larvae that may encounter many potential predators while having limited abilities to escape. An overall finding is that an individual who follows a strategy of faster growth will suffer increased mortality risk because it takes more chances during foraging. More swimming generally makes the individual more easily detected by predators (Kiørboe, 2011). Some modes of predation have been modelled mechanistically. For example, if the foraging activity of a larval fish is swimming speed, and the main predators are ambush predators, then the rate of predation will be proportional to foraging activity (Visser and Kiørboe, 2006). An individual can also increase its ingestion rate by visiting more well-lit layers, but with a concomitant increase in predation rate (Iwasa, 1982). In an elegant series of experiments, it was shown that rapid digestion leaves less aerobic scope for escaping predation attempts (Billerbeck *et al.*, 2001; Lankford *et al.*, 2001; Arnott *et al.*, 2006). Fast growth may furthermore consume resources that become unavailable for other processes that may reduce mortality, such as cellular maintenance and repair, immune defence, or armoury (reviewed in Arendt, 1997; Enberg *et al.*, 2012).

Together, the benefits and costs of foraging typically scale in such a way that predation risk is an accelerating function of growth rate (Figure 1), and that the optimal growth rate is faster when the mortality rate is higher (Figure 1a vs. 1b).

This insight is particularly relevant for fish larvae because they suffer very high predation rates, particularly early in their ontogeny (McGurk, 1986). An important role for behaviour may then be to keep growth at high levels, by making sure that the digestive system has sufficient food to process at all times. Should the environment become worse, ingestion can be kept high by accepting more risk (Fiksen *et al.*, 2007). As development progresses, growth rates can be expected to fall as more cautious foraging behaviours become adaptive due to the general reduction of size-dependent predation mortality.

### Starvation or predation?

From an individual perspective, death by starvation is a dramatic and irreversible situation that individuals will go to great lengths to avoid. Theoretical studies have highlighted that one cannot infer from the frequency of starvation whether food is important, because individuals will increase their risk-taking long before starvation happens (McNamara and Houston, 1987; Krebs and Kacelnik, 1991). While Hjort (1914, 1926) was right when he linked food abundance to recruitment success, he may have jumped to conclusions when he reasoned that larvae who suffered mismatch "would die from hunger". It is more likely that they died from predation because hunger made their behaviour more risk-prone. There is also growing awareness of the distinction between prey abundance and prey availability, i.e. the former is only the numbers or biomass of prey, whereas the latter also includes other factors that make that potential prey more or less easy to capture and consume—such as light, turbulence, prey-size spectra (Sheldon *et al.*, 1972; Pope *et al.*, 1994), and ontogenetic development of the larva's sensory and locomotory capabilities.

Using a detailed state-variable optimization model for the foraging of and predation on larval fish, Fiksen and Jørgensen (2011) found optimal behavioural responses (vertical habitat selection and foraging activity) in a range of environmental settings (Figure 2). Optimality was defined as the behaviour that maximized the probability of survival to a given size (metamorphosis). The key assumptions linking behaviour to growth and predation risk were: (i) that more swimming activity led to higher encounters with both prey and ambush predators; and (ii) that more light increased both the detection of prey and the chance of being detected by a predatory fish. Behavioural strategies of activity and light-exposure therefore had consequences for both growth and survival, and the optimal strategy was found by state-dependent optimization (Clark and Mangel, 2000). When food levels were varied from very low to very high, there was a gradual increase in survival, but the optimal behavioural strategies maintained growth close to the maximum possible, except for in the very worst environments where starvation occurred (Figure 2). In the model, the high mortality that fish larvae experience makes it optimal for them to keep their physiological machinery running at maximum rates (even if this has survival costs), and behaviour is modified adaptively to ensure sufficient food is supplied. At higher food levels survival improves, as less risky behaviours are needed to maintain high growth rates. This model's predictions are consistent with several observations. A review of growth studies in Atlantic cod concluded that cod larvae grew at their temperature-dependent maximum rates under field conditions, whereas sub-maximal growth was often observed in laboratory studies, presumably because larvae cannot express their behaviour fully (Folkvord, 2005). Similarly, a large field study of Japanese anchovy larvae found no effect of prey density on growth rates (Takasuka and Aoki, 2006).

It should be noted that situations exist where food limitation appears to actually constrain growth rate (e.g. Huwer *et al.*, 2011). As individuals grow bigger, their feeding strategies are expected to become more cautious. In those situations, a perceived presence of predators can induce less foraging and more time spent in safety. This is often referred to as a non-consumptive effect of predation and is contrasted to the consumptive effect by which the prey is eaten by the predator (Peacor *et al.*, 2013). A trait change commonly has both consumptive and non-consumptive consequences.

### Two sources of individual variation

In a given population there may not be a single optimum or a single dominating strategy, but there is often between-individual variation in how much risk individuals accept (Biro *et al.*, 2006). Commonly, a strategy is only optimal under a narrow range of environmental conditions, and if the future environment is uncertain, patchy or variable, it can be adaptive for parents to hedge their bets by producing a clutch of offspring that follow strategies that differ from one another (Crean and Marshall, 2009). If these behavioural and growth traits are heritable, then the larvae with higher survival will be more likely to produce the descendants for the next generation, and in this way natural selection may fine-tune larval strategies for behaviour and growth. It may also be that heritable lines coexist in the same population because differences from year to year or area to area select for a range of strategies.

Another source of individual variation is short-term environmental variability that may influence individual state. Because two individuals who follow the same strategy may differ in the history of their environmental exposure, this can lead to differences first
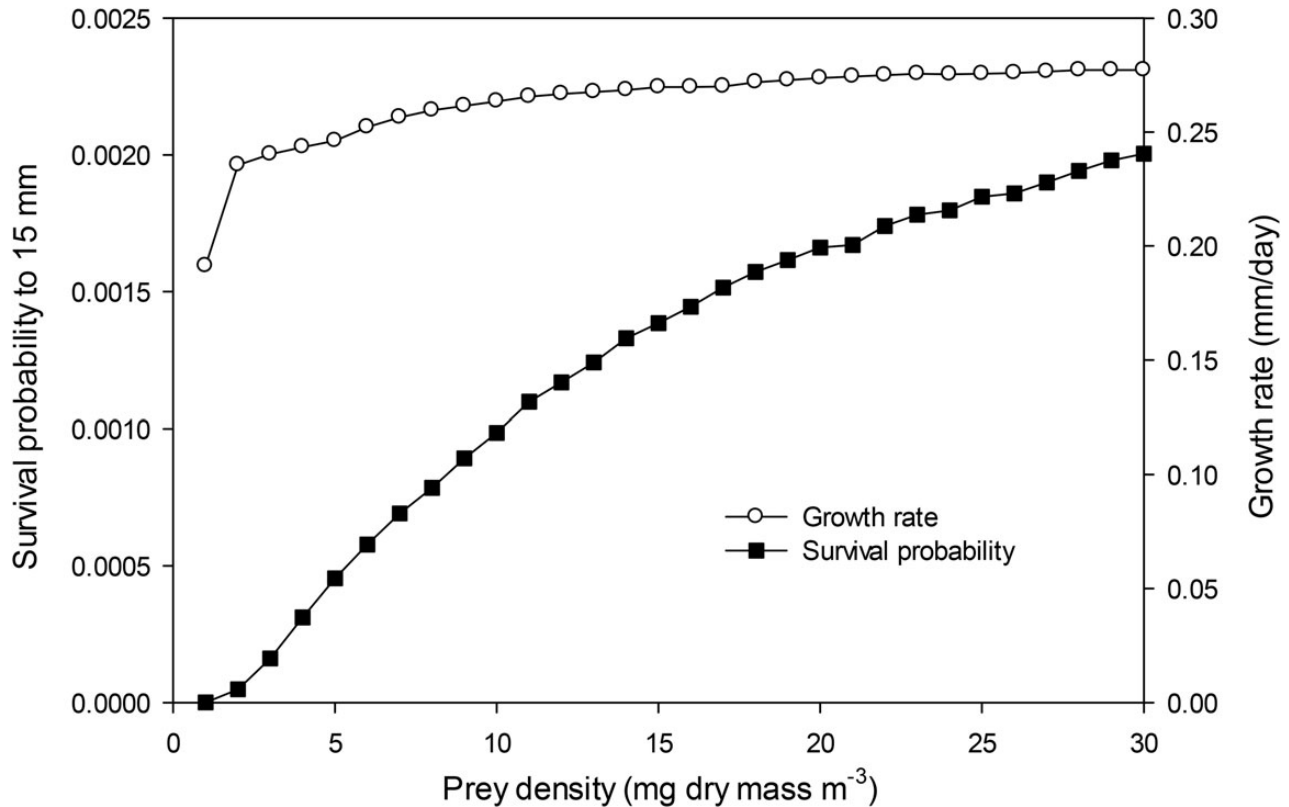
**Figure 2.** Predictions of optimal growth and resulting survival over a range of prey densities according to a detailed simulation model for state-dependent larval behaviour (Fiksen and Jørgensen, 2011). The model includes mechanistic behavioural trade-offs between growth and predation, and follows a larva hour by hour over day and night while it adjusts its behaviour adaptively to the prey availability. Larval survival was quantified as the probability of survival from 5 mm to a length of 15 mm, and the figure shows the corresponding average growth rate (open circles) and survival (solid squares) as a function of prey density in the water column.

in how much food their guts contain or how full their energy stores are, then over time this can cause growth differences and variation in size. Behavioural ecology has a rich tradition for studying how differences in state may affect behavioural decisions (Houston and McNamara, 1999; Clark and Mangel, 2000). Food is more valuable for a hungry larva than for one who is satiated, and in one experiment well-fed cod larvae spent more time in the safety of a group whereas hungry larvae foraged more solitarily (Skajaa et al., 2003). Initial size and condition during egg and early life stages can also influence survival. Jørgensen et al. (2011) show in a theoretical model how optimal offspring size in fish may depend on both environmental and parental conditions. Such state-dependent strategies illustrate how individual larvae, but also their parents, may influence larval risk-taking depending on their current state, which reflects recent history.

The combination of strategic and environmental effects on rates of growth and predation are shown in Figure 3. Because fish larvae suffer high mortality rates (Peterson and Wroblewski, 1984; McGurk, 1986), low food availability leads to minor reductions in growth but major increases in predation as individuals compensate behaviourally by taking more risk (Figure 3b and top-right end of Figure 3c). Thus, when behaviour can be fully expressed, fish larvae grow near their maximum rates, and the price of a bad environment becomes reduced survival.

As fish larvae develop, better sensory apparatus and improved locomotory capabilities make surviving a predator attack more likely, and mortality generally becomes lower. Larvae also form a larger visual image as they grow bigger, and therefore become more vulnerable to visual predators such as fish (Aksnes and Utne, 1997; Vikebø et al., 2007). Experiments have revealed that younger larvae do not respond to predators while older ones do (Fuiman, 1989; Skajaa et al., 2003). For instance, herring larvae develop bullae and a gas-filled lateral organ capable of hearing at ∼ 26 mm of length, and this implies a quantum leap in their ability to avoid predation attempts (Fuiman, 1989). In sum, reduced overall mortality, increased visibility to predators, and increased sensory and locomotory capabilities make it profitable, in evolutionary terms, for fish larvae to gradually become more risk-sensitive with age and ontogenetic development (exemplified in Figure 3a), and this will likely continue until adulthood (gradually moving towards the lower-left corner of Figure 3c).

### Recruitment hypotheses in fisheries science

If behaviour can modify growth and survival, what is the relevance for fisheries science and recruitment success? In Figure 4 we assume that mortality decreases with size, as observed and reflected in the "bigger is better" hypothesis, and contrast different views of how growth and mortality may vary over the early life stages of fish. A common assumption, derived from laboratory experiments, is that periods of reduced food availability will translate to periods of reduced growth (Figure 4a). Slower growth implies a longer larval phase. Because total mortality can be visualized as the area under the curve of mortality rate plotted over time, slower growth causes longer "stage duration" and a higher cumulative mortality.
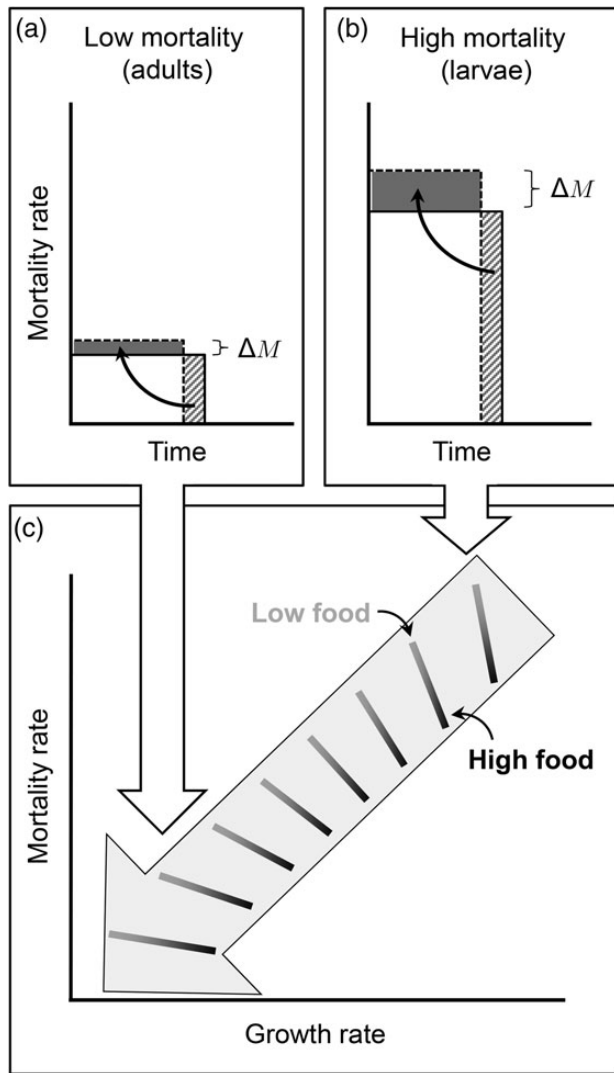
**Figure 3.** Schematic illustration of how adaptive growth and environmental effects of food variability influence growth and mortality through ontogeny. (**a**) In older individuals, the mortality rate is comparatively low, and due to trade-offs strategies that grow faster may shorten the duration of a given mortality rate (removing the mortality in the hatched area) but incur a higher mortality rate ($\Delta M$), which together influence the overall survival (faster growth increases fitness if the grey area is smaller than the hatched area). (**b**) For larval fish, the mortality rate is usually higher, and reducing the time one is exposed to that mortality has a large effect on survival. To attain that effect, fish larvae may evolve rapid growth strategies that accept higher instantaneous mortality, again being selected for as long as the grey area is smaller than the hatched area. (**c**) The difference in this trade-off between larval fish and older individuals suggests two broad patterns. First, larval fish will likely grow faster and take higher risks, this being at the upper-right corner of the graph. As they develop and the mortality rate declines, it becomes optimal to reduce risk level and grow slower, and through ontogeny one would therefore expect that they move towards the lower-left corner of the figure (indicated with wide grey arrow). At each ontogenetic stage, food variability can induce changes in growth and risk-taking. If food is abundant, mortality will be lower (the black end of each little line), but in larval fish it is expected that food variation will translate mostly to changes in survival (lines are almost vertical), whereas for older fish the extra risk may not be worth taking and food variation will have stronger effects on growth (lines are more horizontal).

This would be the case also if mortality was assumed to be independent of size. Under food-limited growth, a slowing down at early ages will have more pronounced effects because it prolongs development at a size where the mortality rate is higher.

An alternative mechanism, explained above, is that growth is a trait subject to trade-offs, and that behaviour plays the role of jointly determining risk exposure and growth rate. For example, herring larvae reduce their foraging behaviour in experimental tanks where they can see a potential predator (Skajaa *et al.*, 2003) but maintain their escape response (Skajaa and Browman, 2007), thus suggesting that behaviour can be environmentally conditioned. Given such trade-offs, reducing growth rate entails a more cautious behavioural strategy that will incur lower mortality rates but also lengthen the exposure to mortality because growth to a given size takes a longer time (Figure 4b). Note that here a longer "stage duration" is not necessarily linked to higher mortality; if growth is faster than optimal then slower growth and longer duration would decrease the overall mortality.

The two perspectives from panels 4a and 4b are combined in panel 4c, where it is assumed that behaviour is plastic and can change rapidly and according to local environmental variables. When food availability varies over time, these fish larvae may change their behaviour to accept more risk when food is scarce, thus maintaining rates of ingestion, digestion, and growth, albeit at costs in terms of survival (Fiksen and Jørgensen, 2011). This also describes a role for individual states, as lower food availability is likely to first reduce gut levels, then energy stores, and if behavioural changes are insufficient to bring ingestion back up, then finally growth.

From this behavioural perspective it is easier to see how the three recruitment hypotheses are related:

The "bigger is better" hypothesis cannot be used to infer that larvae should hatch bigger because evolution of egg size is determined by selection pressures on maternal investment (Smith and Fretwell, 1974; Jørgensen *et al.*, 2011), but it can guide our understanding of the role of behaviour. This hypothesis recognizes the overall pattern that mortality rate declines rapidly with size for fish eggs and larvae, which has a sound empirical (McGurk, 1986) and theoretical basis (Peterson and Wroblewski, 1984; Andersen and Beyer, 2006) related to development of e.g. locomotory capabilities, sensory systems, adaptive colouration, scales, and immune defence. The pattern of declining mortality with size leads to the prediction that behaviour should be more risk-taking for small larvae, and gradually become more cautious as the larvae grow bigger. The "bigger is better" hypothesis also emphasizes the importance of body size for larval ecology, for example how the growing larval body forms a larger visual image that behaviour can counteract by seeking darker surroundings, or by conferring advantages in terms of intraspecific competition (Reznick *et al.*, 2006) or surf-riding of size-spectra (Pope *et al.*, 1994).

Whether "stage duration" has a positive or negative effect on survival depends on the behavioural strategy. This hypothesis focuses on the time spent in vulnerable size-classes where longer stage duration is assumed to increase mortality, but taking behavioural trade-offs into account suggests that prolonged stage duration may be caused by a more cautious behavioural strategy, with slower growth and lower mortality rate. Whether the overall effect on survival is positive or negative depends on the area under the curve of mortality rate plotted over time, until a given size is reached. Thus, stage duration has no simple effect on survival or recruitment; it depends on the environment and behaviour.
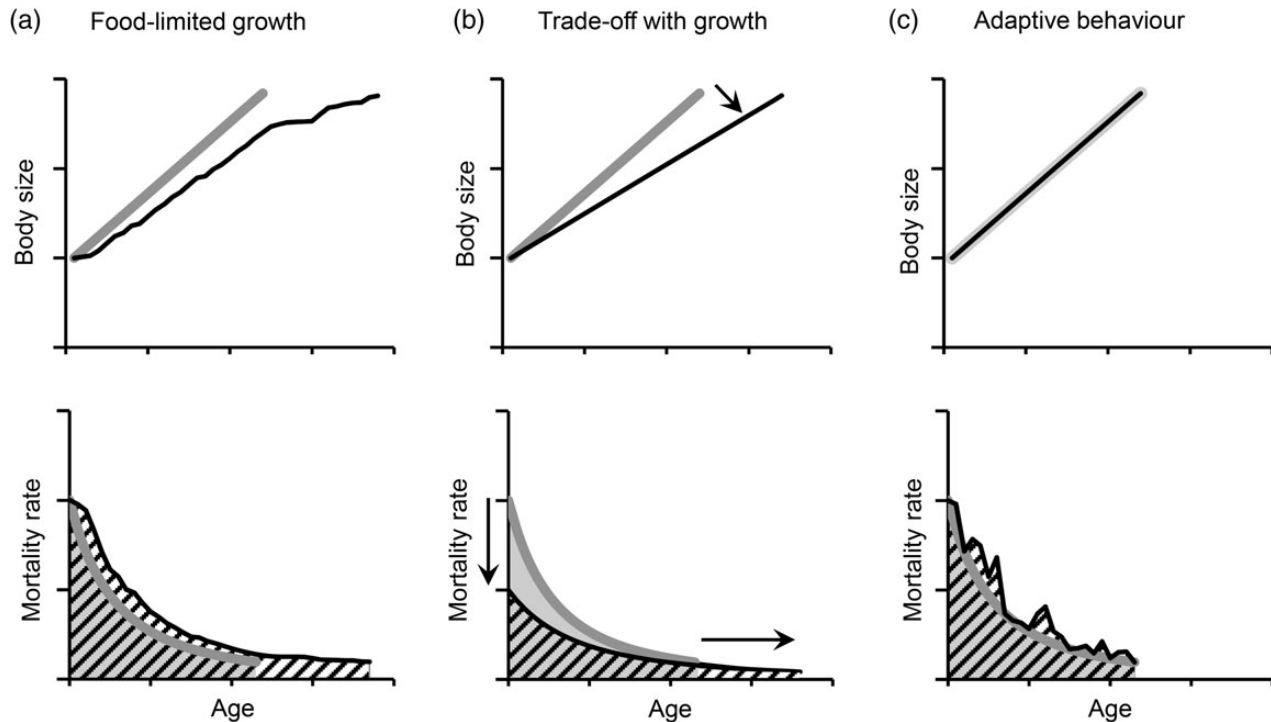
**Figure 4.** Schematic illustration comparing mechanisms that link growth and survival in larval fish. (**a**) Under food-dependent growth, periods of low food availability (black lines) will reduce growth below the physiological maximum (grey line in all panels) and thus prolong the developmental phase. Assuming mortality is size-dependent, it will be higher at any given age and last longer because development to metamorphosis takes more time. (**b**) Behavioural ecology focuses on trade-offs with growth, and how risk acceptance and growth rate are related. Growth rate could be reduced by following a more cautious strategy (black line), which would incur a lower mortality rate at any given size (indicated by vertical arrow next to the mortality axis) but a longer duration (horizontal arrow). The trajectory of age-dependent mortality with lowest area under the curve has the highest survival and will likely be favoured by natural selection. (**c**) Behaviour can change rapidly, and optimization models suggest that fish larvae increase their risk-taking during periods of low food availability to maintain high growth rates (Fiksen and Jørgensen, 2011). Environmental variation in food levels (black lines) would then not be visible in growth rates, but would reduce survival because mortality is elevated when food is low).

Behavioural trade-offs may also cause patterns of "growth-selective predation". Although Figure 2 emphasizes how the main effect of variation in food is to affect survival, it also shows a correlation between growth rate and survival rate. If the environment is sufficiently severe, larvae may grow more slowly and take higher levels of risk, thus reducing their survival, which could be observed as "growth-selective predation".

To some degree, it might therefore seem that the various hypotheses appearing in the oceanography literature have remained as catchy phrases that identify isolated parts of a larger puzzle. A more coherent perspective can be gained by adopting evolutionary thinking and concepts from behavioural ecology. As an example, consider how adaptive behaviour may explain the abovementioned observed relationships between food and survival: Beaugrand et al. (2003) showed that recruitment of North Sea cod over 42 years was correlated to a broadly composed plankton index, which seemingly contrasts the observation that cod larvae in the sea apparently grow close to their temperature-dependent capacity, independent of food density (Folkvord, 2005). To reconcile these observations, the key is to de-emphasize the link between food and growth: through adaptive behaviour, variation in food and match−mismatch can cause large variations in risk-taking, survival, and recruitment, but may not involve variation in growth. The optimality model referred to above (Fiksen and Jørgensen, 2011) suggests a role for food availability in influencing survival that extends far beyond the level where it becomes limiting for growth (Figure 2), which in fact strengthens the importance of prey availability for recruitment success. It should be borne in mind that all these factors may explain how efficient a given spawning stock biomass is at producing recruits; it does not challenge the very real effect of the size of the spawning stock on recruitment to fish stocks. Still, in a modelling study of developing fish larvae in a water column of observed environmental parameters, vertical migration increased survival from 6 to 18 mm by several thousand times compared to random behaviour (Kristiansen et al., 2009), suggesting that adequate larval behaviour can improve fitness by a magnitude that can rarely be achieved e.g. through increased maternal production of gonads.

We are also aware that not all species fit within this framework. In some species, larvae depend on benign environments to find ephemeral patches of food (Winemiller and Rose, 1993) or to drift into profitable nursery habitats (Siegel et al., 2008); for these species, variable strategies and bet-hedging may be more important for recruitment success than the growth-survival trade-offs on which we have focused. In other species, the bottleneck is not at the larval stage but later, and in those species detailing the early life stages will have little bearing on predictions of recruitment.

## Implications for biophysical models of fish larvae

To assess larval survival and recruitment success, modern fisheries science relies heavily on large-scale physically-coupled ecosystem models. In linking recruitment success to environmental conditions, the emphasis has been on how differences in temperature

and food availability lead to fluctuations in growth, survival and recruitment success. While mortality is usually parameterized as constant or size-dependent, the focus has been on how food variation may induce differences in growth, with consequences for survival (e.g. Peck and Hufnagl, 2012). This is natural, since these processes can be studied in the laboratory and used as input to biophysical models. Several experiments have quantified how well-fed larvae grow at different temperatures (Otterlei *et al.*, 1999; Houde, 1989), and how much larvae feed and grow when administered different food rations (Letcher and Bengtson, 1993). The loss due to mortality in the field is much more difficult to observe and quantify due to obvious logistic reasons.

The above arguments suggest that improved predictions for recruitment may require a focus on how adaptive behaviour can have strong effects on survival. A first and easy modification is to replace the current assumption that reduced food reduces growth with implications for survival, with the perspective suggested in this paper, whereby reduced food leads to reduced survival through adaptive behaviour, but with few implications for growth. A more explicit way to do it is to implement the trade-offs directly into the model, for instance by a suite of behavioural options (such as swimming speed and depth selection) which influence growth and mortality. The assumption that individuals instantly minimize the ratio between mortality and growth (Gilliam's Rule, see Figure 1) is a good approximation to fitness, and this will incorporate the direct survival-effect from increased food availability (see Vikebø *et al.*, 2007; Kristiansen *et al.*, 2009 for examples). These types of model mechanistically connect environmental conditions to larval survival (Vikebø *et al.*, 2007; Opdal *et al.*, 2008), allow incorporation of behavioural strategies that are responsive to individual state (Kristiansen *et al.*, 2009), and may link larval traits to parental reproductive strategies (Opdal *et al.*, 2011).

If prey is size-structured, then models need to specify which prey should be included in the diet, and a similar approach could be taken by use of optimal foraging theory, for which an algorithm has been developed for larval fish (Letcher *et al.*, 1996). A similar behavioural approach to diet breadth may also be useful in ecosystem models (Visser and Fiksen, 2013). The inclusion of flexible or adaptive behaviours in mass-balanced ecosystem models is currently a central theme in ecology, and marine ecosystem models with behaviourally responsive agents are emerging (Castellani *et al.*, 2013).

Finally, biophysical models would benefit from incorporating predation more mechanistically (Huse and Fiksen, 2010). This would require careful and detailed consideration of larval behaviour, predator–prey mechanics, and the proximate aspects of sensory systems, decision-making, and behaviour. This is definitely not an easy task and presupposes basic research in a range of disciplines, but may offer a route to more reliable models and better understanding of the role of ocean productivity in the formation of strong year-classes.

## Acknowledgements

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