SYMPOSIUM

Hydrodynamic Constraints of Suction Feeding in Low Reynolds Numbers, and the Critical Period of Larval Fishes

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Synopsis Larval fishes suffer prodigious mortality rates, eliminating 99% of the cohort within a few days after their first feeding. Hjort (1914) famously attributed this "critical period" of low survival to larval inability to obtain sufficient food. We discuss recent experimental and modeling work, suggesting that the viscous hydrodynamic regime have marked effects on the mechanism of suction feeding in larval fish. As larvae grow, the size of the gape and associated volume of the mouth increase. At the same time, larvae swim faster and can generate faster suction flows, thus transiting to a hydrodynamic regime of higher Reynolds numbers. This hydrodynamic regime further leads to changes in the spatio-temporal patterns of flow in front of the mouth, and an increasing ability in larger larvae to exert suction forces on the prey. Simultaneously, the increase in swimming speed and the distance from which the prey is attacked result in higher rates of encountering prey by larger (older) larvae. In contrast, during the first few days after feeding commence the lower rates of encounter and success in feeding translate to low feeding rates. We conclude that young larvae experience "hydrodynamic starvation," in which low Reynolds numbers mechanically limit their feeding performance even under high densities of prey.

The "critical period" in larval fish

Most pelagic and benthic marine fishes reproduce by external fertilization of eggs which are then broadcast into the water column (Houde and Hoyt 1987; Houde 1989; Houde 2008). Larvae hatch from these pelagic eggs after several days (3–10), depending on temperature, oxygen saturation, and other environmental and intrinsic factors (Pauly and Pullin 1988). In general, the larva subsists on a yolk sac for several days until the mouth forms and the larva feeds for the first time (hereafter "first feeding"). The period immediately after larvae initiate feeding is characterized by mass mortality of young larvae, reaching over 90% mortality within the course of several days (Hjort 1914). Hereafter, we refer to larvae during the first few days after feeding commences as "early-stage larvae." Originally, starvation (stemming from inability of larvae to find sufficient prey) was suggested as the key agent of mortality during this "critical period" (Hjort 1914). For example, stocks of cod larvae only survive if fed six-fold the average food concentration available in the ocean (Tilseth 1984), indicating that starvation can result from larval inability to find highly dense patches of food. However, a "critical period" of larval mortality is commonly observed in mariculture facilities, with >70% mortality even under conditions of high concentrations of food (Shields 2001). Predation, advection to unsuitable habitats, and disease were also hypothesized to contribute to larval mortality during the critical period (Houde 2008), however, no consensus has yet emerged as to the relative contribution of these agents of mortality.

Although fish display dramatic variations in body size, the diameters of pelagic eggs are much less

variable, typically ∼1 mm and rarely above 3 mm (Pauly and Pullin 1988). The hatching larvae are only several mm in length, and possess a vastly different morphology to that of the adults (Houde and Hoyt 1987; Blaxter 1988; Osse and van den Boogaart 1999). In brief, at hatching and throughout the first weeks the bodies of larvae are not yet ossified, cranial features are cartilaginous, and the vertebral column has not yet formed (Fig. 1; but see [Kavanagh and Alford 2003] for benthic eggs). Other late-developing features are the gills, the swim bladder, and the fins. In many species, larvae hatch with a continuous, ribbon-like fin-fold that stretches from the dorsal part of the head to the ventral side. Specific areas of this anatomical feature degrade during larval development, in parallel with the appearance of fin rays to form the dorsal, caudal, and anal fins (Fig. 1). Two pectoral fins usually appear earlier, soon after hatching (Houde and Hoyt 1987; Blaxter 1988; Osse and van den Boogaart 1999). Note, however, that while these patterns reflect the major trends in larval teleosts, there is tremendous variation in their timing and magnitude across species. These differences and the developmental sequence of the larvae are described in detail elsewhere (Blaxter 1988).

Larval morphology has pronounced effects on various fitness-determining performances, such as swimming, feeding, and respiration (Houde and Hoyt 1987; Blaxter 1988; Osse and van den Boogaart 1999). For example, gas exchange in young larvae occurs mainly through the skin in the absence of functioning gills (Rombough 1988; Rombough 2007). The morphology of the fin and the absence of swim bladder in young larvae have strong effects on swimming ability and body kinematics (Muller et al. 2000; Muller and van Leeuwen 2004; Hale 2014). Sensing of the motion of water improves as surface neuromasts that degrade at hatching regenerate and the canal neuromasts gradually form (O'Connell 1981). Visual acuity improves as the density of sensory cells on the retina increases and the eye grows (Blaxter 1980; O'Connell 1981; Blaxter 1986). Concomitantly, ability to feed improves, especially throughout the early stage of larval development (Blaxter 1980; Blaxter 1986).

Fish use "suction feeding" to capture prey

The dominant mode of capturing prey by larval fishes (as well as by the majority of adults) is suction feeding, defined as the capture of prey by generating a flow of water into the mouth (Alexander 1970;

Lauder 1980b; Wainwright et al. 2007; Day et al. 2015). These flows are achieved through a rapid expansion of the buccal cavity, generating a gradient in pressure that induces water to flow into the buccal cavity (Lauder 1980b; Müller et al. 1982; Wainwright et al. 2007; Day et al. 2015). The flow external to the mouth exerts hydrodynamic forces on the prey that initially are located outside the mouth, drawing the prey inside and countering their ability to escape (Holzman et al. 2007; Wainwright and Day 2007; Wainwright et al. 2007). Furthermore, the suction flow improves capture of prey because it counters the propensity of the prey to be pushed away due to the water impacted by the advancing body of the predator (Dullemeijer 1994; Van Wassenbergh et al. 2010).

Because of its importance in governing the capture of prey by fishes, the kinematics and hydrodynamics of suction feeding have been the focus of multiple studies (e.g., [Weihs 1980; Lauder 1980b; Müller et al. 1982; Day et al. 2005; Van Wassenbergh et al. 2006; Holzman et al. 2008; Van Wassenbergh and Aerts 2009] reviewed by [Ferry-Graham and Lauder 2001; Westneat 2006; Day et al. 2015]). Several unifying principles have emerged from this body of literature. Suction feeding constitutes a rapid, ventral-to-dorsal expansion of the openings and cavities of the skull (Lauder 1980a; Sanford and Wainwright 2002; Gibb and Ferry-Graham 2005; Bishop et al. 2008). This pattern of expansion drives a unidirectional flow of water into the mouth, through the buccal cavity, and then externally via the gills (Lauder 1980b; Day et al. 2005). The suction flow in front of the mouth is an "unsteady" flow, characterized by strong spatial and temporal gradients (Day et al. 2005; Higham et al. 2006a; Day et al. 2007; Holzman et al. 2008). Spatially, flow is strongest at the center of the mouth's aperture, decreasing rapidly within a distance of ∼1 gape-diameter. In bluegill, for example, the speed of flow at the center of the mouth can exceed 1 m/s; 10 mm away from that point flow decreases by >90% (Day et al. 2005; Higham et al. 2006a; Day et al. 2007; Holzman et al. 2008). Suction flows also are characterized by sharp accelerations and decelerations, with flow at the mouth's center accelerating to >1 m/s in <6 milliseconds, and decelerating to zero flow ∼10 milliseconds later (Day et al. 2005; Higham et al. 2006a; Day et al. 2007; Holzman et al. 2008). Studies in which the flow in front of the mouth was visualized (hereafter "flow visualization") also reveal a general correspondence between the gape's cycle and the speed of flow at the center of the mouth: water begins to enter the mouth when the structure begins to open, with peak flow generally coinciding

Fig. 1 Larvae of *S. aurata* during early ontogeny. During early ontogeny, larvae undergo multiple morphological changes, including ossification of the skeleton and the fin rays. At the same time, larvae grow and transition into a regime of higher *Re*. Both processes have strong effects on fitness-determining performances such as swimming and feeding. Larvae are 13, 25, and 31 days post-hatching (DPH; top, middle, and bottom, respectively). Bone was stained using alizarin red, whereas cartilage was stained using alcian blue, following (Gavaia et al. 2000). Soft tissues, such as the dorsal and pectoral fins in 13 and 25 DPH are transparent and not visible in this protocol. (This figure is available in black and white in print and in color at *Integrative and Comparative Biology* online.)

with the time of peak opening of the mouth, and inward flow is maintained until the mouth is closed (Day et al. 2005; Higham et al. 2006a; Day et al. 2007; Holzman et al. 2008; Staab et al. 2012).

Larval fish experience a viscous flow-regime

The above-mentioned unifying principals derive from the fact that suction flows are governed by the expansion pattern of the buccal cavity and the dynamics of the mouth's aperture (gape). This understanding was also the basis for the hydrodynamic modeling of the mouth as an expanding cone and of the ensuing flows external to the mouth's orifice by Muller (Müller et al. 1982) and Weihs (Weihs 1980). Multiple predictions of these models have been experimentally verified, including the spatial distribution of flow speeds outside the mouth, the shape of the ingested volume, and the relationship between

the speed of expansion, peak pressure, and peak velocity of flow (Day et al. 2005; Higham et al. 2005; Higham et al. 2006b; Day et al. 2007; Holzman et al. 2008). A key assumption of the above models is that suction feeding in adult fishes is a hydrodynamic phenomenon in which viscous forces can be neglected. Due to viscosity, water that flows over a solid surface will experience a shearing force, similar to friction, which will act to slow down the particles nearest the stagnant surface (Vogel 1994). The fluid in turn exerts stresses on neighboring fluid, and a boundary layer develops, defined as the region of flow within which viscous forces have affected the motion of the fluid. The boundary layer develops gradually over time, and with the distance from the edge of the surface. In the context of the characteristically fast speeds and accelerations of flow observed in the suction flows of adult fishes, this boundary layer is considered negligible, and it is therefore valid to treat the flow as inviscid (Van Wassenbergh and Aerts 2009). This simplifying assumption allows analytical modeling of the flows that result from the expansion pattern of the buccal cavity and the dynamics of the mouth's aperture.

It is often useful to characterize the flow regime by the Reynolds number (Re), a non-dimensional parameter defined as: $Re = (\rho \cdot l \cdot u) / \mu$, where ρ is the density of the fluid (kg m3), l is the characteristic length of the flow field (m), u is flow speed (m·s^{-1}), and μ is dynamic viscosity (N·s·m^{-2}). When Re is low ($Re < 1$) viscous forces dominate, the flow is stable, and the above-mentioned boundary layer is relatively thicker. As Re increases, inertial forces become more important. Flow becomes less stable and turbulence is likely to develop when Re exceeds ~4000. The ''intermediate Re'' range ($1 < Re < 4000$) is a transition zone between these two flow regimes, where the flow can be partly laminar and partly turbulent. At the lower end of this transition range ($Re < 100$), viscous forces still dominate and the boundary layer is thick, although the flow is not always laminar (e.g., surface-attached vortices may appear) (Vogel 1994). Larval fish swim and feed at the lower end of this transition range, at Re values that are well below 100 (based on peak gape and maximum velocity of fluid [Muller and Videler 1996; Hernandez 2000; China and Holzman 2014]). In this lower Re regime, viscosity should have considerable effects on the dynamics of flow. Thus, the assumption that the effects of viscosity can be ignored is invalid in the case of larval fishes, and analytical models of suction flows are not well suited to studying the relation of suction flows to cranial kinematics and morphology in low Re.

Inherent difficulties in studying suction feeding in larval fish

Until recently, our understanding of suction flows and how they are related to feeding performance in larval fishes was limited. Inherently, there are two problems that pertain to the study of suction feeding by larval fishes. Visualization of feeding by larvae is challenging due to small body size and low survival of the larvae, short timescale, and rarity of feeding events. During early ontogeny, the body of a hatching larva can be only a few millimetres in length, and its mouth can be as small as 100 μm in diameter, especially in fish that broadcast fertilized eggs to the open water. The high-magnification optics required leads to a small depth-of-field and limits the field of view. Fast-cruising larvae remain in the visualized area for only a few seconds. A low feeding rate (especially during the first days after hatching) can result in a scarcity of feeding attempts in the visualized area (Drost 1987; Hernandez 2000; Krebs and Turingan 2003; China and Holzman 2014). As in adults, capture of prey by larvae takes a few tens of milliseconds (Drost 1987; Hernandez 2000; Westphal and O'Malley 2013; China and Holzman 2014), which can be easily overlooked using conventional videography or direct observation. While high-speed cameras are powerful tools for studying feeding kinematics of fishes (Wainwright et al. 2001; Ferry-Graham et al. 2002; Wainwright and Bellwood 2002; Wainwright et al. 2007; Oufiero et al. 2012; Westphal and O'Malley 2013), they are limited by the duration of the sequence that can be recorded (typically 1–10 s). These cameras are most effective if used when the events recorded are predictable in time and space. However, recent advances in high-speed video technology now permits continuous recording of high-speed videos (>300 fps) at a high resolution (>2 megapixels) for long periods of time (tens of minutes). Such systems (Fig. 2), therefore, provide the appropriate temporal and spatial resolution, while integrating over time to achieve large sample size. Furthermore, because the system is not triggered manually for each feeding event, there is no observer-bias in selecting which strikes are captured. Thus, high-speed continuous recording systems can be used to record strikes' kinematics, and also to quantify feeding success in response to various dependent variables.

A second problem has been the difficulty to tease apart the effects of ontogenetic changes on feeding performance from the effects of shifting hydrodynamic regime between early-stage larvae and their older conspecifics. Throughout ontogeny, larval
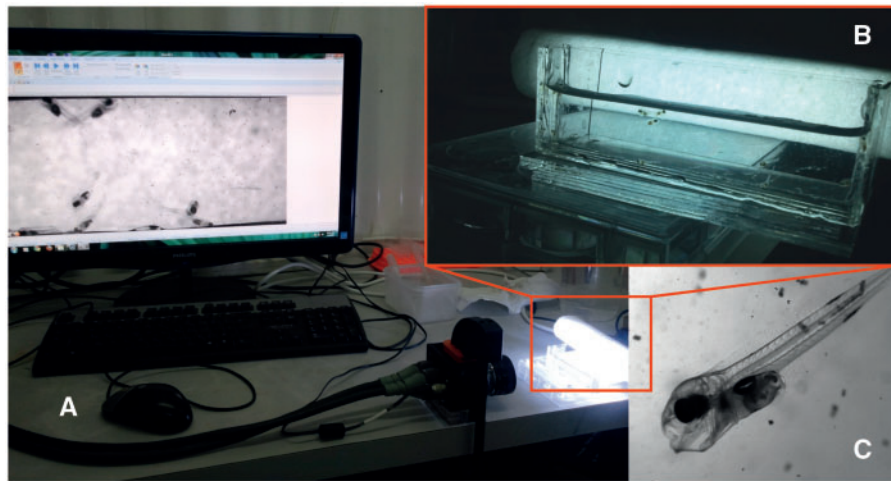
Fig. 2 High-speed continuous recording system for measuring feeding success and the kinematics of strikes by larval fishes. (**A**) The system consists of a high-speed camera (Vieworks VC-4MC-M/C-180) connected to a PC. This setup allows recording 22 min of high-speed, high-resolution videos (2048 × 1024 pixels at 300 frames per second). A macro lens provides a field of view of 15 × 28 × 3 mm (height, width, and depth, respectively) at $f = 5.6$. Backlit illumination is provided using an array of 16 white LEDs with a diffuser (∼280 lumen). Fish are housed in a small filming chamber (inset in **B**) and are allowed to freely feed while being filmed. The system produces high-resolution videos that enable tracking of food particles (black dots in **C**), and determining whether prey have entered and remained inside the mouth during the strike. The videos also allow detailed kinematic measurements, for example, time to peak mouth-opening, diameter of gape, and swimming speed of the larvae while feeding on cultured and field-collected prey. Images are for 19 DPH *S. aurata* larvae. (This figure is available in black and white in print and in color at *Integrative and Comparative Biology* online.)

fishes transition from a regime of low Re at first feeding ($Re \sim 30$) to a much higher Re (~ 150) at later ages (Muller and Videler 1996; Osse and van den Boogaart 1999). Concomitantly, larvae undergo morphological and developmental changes that could improve their ability to capture prey. For example, the skeleton ossifies, muscle mass increases, the eyes grow, and coordination improves with age. These trends in larval ontogeny were hypothesized to impede feeding at earlier stages of development (Blaxter 1986; Yúfera et al. 1993; Parra and Yúfera 2000; Yúfera and Darias 2007). Notably, an engineering technique termed "dynamic scaling" can be used to separate the effects of physical size (i.e., length) and other ontogenetic factors (e.g., visual acuity, skeletal ossification, coordination) (Bolton and Havenhand 1998; Bolton and Havenhand 2005; Danos and Lauder 2012). Experiments that use dynamic scaling are based on the hydrodynamic principle that, when comparing two scenarios of flow around a fully submerged body, the two regimes will be hydrodynamically identical if the non-dimensional parameters (e.g., Re) are identical (Vogel 1994); for example, the profile of the boundary layer over similarly-shaped bodies will be similar if they experience the same Re. It is thus possible to investigate the flow field generated by a body of small size by using a large-sized body while simultaneously increasing the viscosity (or decreasing speed

of flow) and keeping the non-dimensional parameters (Re) unchanged (Vogel 1994). For example, under conditions of a two-fold increase in fluid viscosity and constant flow speed, a 10-mm larva will experience the same hydrodynamic regime experienced by a 5-mm one, but will preserve all the morphological and cognitive features of its age group. Thus, experiments using dynamic scaling provide an experimental tool with which it is possible to tease apart the effects of hydrodynamics and ontogeny.

Experimental assessment of suction feeding in larval fishes

In the following sections, we detail key patterns of suction feeding in larval fish, focusing on patterns of suction-feeding kinematics, suction flows, feeding rates, and the mechanisms of success and failure. Our goal was not to provide a complete overview of the literature in this field, but rather to suggest a mechanistic framework that integrates the effects of cranial morphology, kinematics, and hydrodynamics on suction feeding in larval fishes. We also do not discuss the effects of other traits such as visual acuity, coordination, experience or swimming ability, which are discussed in other reviews (Houde and Hoyt 1987; Blaxter 1988; Muller and Videler 1996; Osse and van den Boogaart 1999).

In addition to examples from published studies, we also present original data, obtained for two species, *Sparus aurata* and *Denio rerio*. This is because much of the research on feeding kinematics and hydrodynamics in larval fish is focused on these species (Hernandez 2000; Westphal and O'Malley 2013; China and Holzman 2014; Yaniv et al. 2014). *Sparus aurata* is a marine fish of high commercial importance, commonly grown in fisheries, whereas *D. rerio* is a freshwater fish that has become an important model organism in evo-devo and genetic research. Both have life histories that are characteristic of pelagic and coastal fishes, and are therefore useful for studying general feeding behavior of larvae.

Original data presented here were obtained from prey-acquisition strikes identified for 8, 10, 13, 17, and 23 days post-hatching (DPH) for larvae of *S. aurata* ($n = 16, 23, 26, 32$, and 34, respectively) and 5–10 DPH for larvae of *D. rerio* ($n = 60$). Videos were obtained using the aforementioned recording system (Fig. 2), which captured 20-min-long, high-speed videos (300 frames per second for *S. aurata* and 400 frames per second for *D. rerio*). Prey-acquisition strikes were identified and analyzed following (China and Holzman 2014; Yaniv et al. 2014). Specifically, we extracted morphological (total length of the body and diameter of gape) and kinematic traits (swimming speed, time to peak gape, and the distance from which the prey is attacked) for each strike by digitizing landmarks on the fish's body (China and Holzman 2014; Yaniv et al. 2014). For each strike, we estimated flow speed at the mouth based on observed gape and the relationships between size of the mouth and flow speed presented by (Yaniv et al. 2014). *Re* for feeding was estimated, based on these flows and on size of gape. The legend of Fig. 3 and the text below detail which data are original and which are redrawn from published studies.

Feeding kinematics in larval fishes

The kinematics of mouth-expansion in larval fish are generally similar to those of adult fish (Hernandez 2000; Krebs and Turingan 2003; Beck and Turingan 2007; Yaniv et al. 2014). It typically occurs as a rapid anterior-to-posterior wave of expansion: opening of the mouth is first followed by depression of the hyoid, and then by the abduction of the opercular slits. Lateral movement seems to contribute to expansion of the buccal cavity, although quantitative data on lateral expansion are lacking. Unlike the condition in adults, the upper jaw does not protrude forward during opening of the mouth in early-stage

larval fishes. The time-scale of cranial kinematics is similar to that of adults ($\sim$10–100 ms), with a general increase in the speed of cranial events throughout the larval period in *D. rerio* (Hernandez 2000; Westphal and O'Malley 2013) but not in *S. aurata* (Yaniv et al. 2014). Prey-acquisition strikes are sometimes accompanied by a distinctive S-start manoeuvre (MacKenzie and Kiorboe, 1995). However, our observations using a continuous high-speed video indicate that >80% of the strikes are executed while coasting or burst-swimming, and that S-start manoeuvres often are performed regardless of feeding (our unpublished data). In larval *S. aurata*, swimming speed during the acquisition of prey is $\sim$2.5 body lengths/sec, indicating an increase of unscaled swimming speed (i.e., in units of distance per time) throughout ontogeny.

Suction flows in larval fishes

Empiric assessment of suction flow in fish has been limited to the adult and juvenile stages only in a few species. Published data are available for bluegill (Day et al. 2005; Higham et al. 2005; Holzman et al. 2008), largemouth bass (Higham et al. 2006a), goldfish (Staab et al. 2012), and zebrafish (Gemmell et al. 2013), ranging in size from 5 to 45 cm. These data were collected using flow-visualization techniques, namely Particle Image Velocimetry (PIV) and Particle Tracking Velocimetry (PTV). In brief, these techniques are based on tracking the movement of neutrally buoyant particles, which move at the speed of the water (Zachary et al. 2014). Tracing of particles is usually done using cameras, while illuminating the particles using a laser or other powerful illuminator. These demands add a further layer of difficulty to the inherent difficulties in filming the feeding behavior of larval fish. It is, therefore, not surprising that empiric data on suction flow of larval fishes are limited to quantifying the speed of the drifting prey (Drost 1987; Hernandez 2000; China and Holzman 2014).

Analytical models of the suction flow generated by the expanding mouth have played an instrumental role in the understanding of suction flow and their relation to cranial kinematics and morphology in fishes (Müller et al. 1982; Van Leeuwen and Muller 1984). Unfortunately, a major assumption of these analytical models is that the effects of viscosity can be ignored, whereas this assumption is clearly invalid in the case of larval fishes. This gap in modeling can be narrowed by using numerical models, namely Computational Fluid Dynamics models (CFD). In these models, the interaction of fluids (the water)
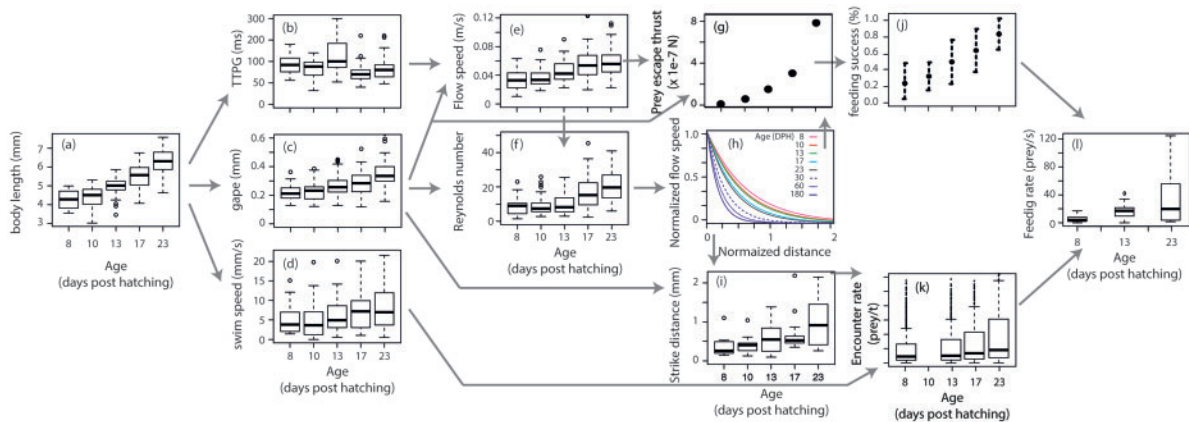
Fig. 3 Conceptual view of hydrodynamic effects on feeding rates of larvae, through their effects on rates of encounter and success in feeding in *S. aurata*. As larvae grow, total length (**A**), size of the gape, (**C**) and associated buccal volume increase, while mouth opening speed (TTPG; **B**) remains unchanged. Correspondingly, larvae swim faster (**D**) and can produce faster speeds of flow (**E**). The above changes in characteristic scales of length (*l*, gape diameter) and flow speeds (*v*, peak flow-speed at the mouth) increase the *Re* (**F**), which characterizes feeding (and swimming) by the larvae. Consequently, the spatial gradients in the suction flows become steeper as the larva transitions into an area of higher *Re* (**H**). Changes in these gradients, gape, and flow speed result in lower forces exerted on the prey of smaller larvae; these forces determine feeding success (the proportion of prey captured in relation to the number of strikes) (**I**) because when weak forces are exerted on the prey, weakly swimming prey can escape the strike (**G**). Simultaneously, changes in swimming speed and the distance at which prey can be captured result in lower rates of smaller larvae encountering prey (**J**). Together, encounter rates (**J**) and feeding success (**I**) determine feeding rates (**K**). Original data are presented in panels (**A–D**, **I**). Flow speed at the mouth is based on observed size of gape and the relationships between size of the mouth and flow speed presented by (Yaniv et al. 2014). *Re* for feeding was estimated based on these flows and on the size of the gape. Data in (**G, J, L**) are redrawn from (China and Holzman 2014). Panel (**H**) describes the decay of flow speed as a function of the distance from the mouth, based on data from (Yaniv et al. 2014); flow speed (*y*-axis) is normalized such that 1 is peak flow speed at the mouth; distance from the mouth is scaled to peak gape diameter; colours represent larvae from different ages (DPH). Prey escape thrust (panel **G**) is the minimal trust needed to escape the feeding larvae, estimated using numerical simulations that solve the forces exerted on the prey (SIFF; [Holzman et al. 2012; China and Holzman 2014; Yaniv et al. 2014]) Encounter rates are in arbitrary units. Within each panel, horizontal bold lines indicate the mean in each age group; the upper and lower margins of boxes enclosing the mean indicate the 1st and 3rd quartiles, respectively; while whiskers represent 1.5 inter-quartile distances. Gray arrows represent our inference regarding the directional effects of dependent variables on each other.

with surfaces (the body and mouth of the fish) can be simulated by numerically solving the governing equations of water motion (also known as the Navier-Stoke equations) across the computational domain (Van Wassenbergh and Aerts 2009). Because the Navier-Stoke equations account for the viscous forces, they are well suited to solving problems in low Reynolds flows (Miller et al. 2012). A two-dimensional (2D) CFD model, assuming that the mouth is composed of two infinitely wide parallel plates, was designed for suction-feeding carp larvae by Drost et al. (1988). The model simulated the two plates to separate by a distance of 0.256 mm within 8 ms, generating speeds of flow >0.6 m/s at the mouth's aperture (*Re* ≈ 150). This pioneering model also predicted that, under these conditions, about 40% of the energy spent on expansion of the mouth was lost to frictional forces, rather than to acceleration of water toward the mouth (Drost et al. 1988). They further reported that flow speed decayed rapidly as a function of the distance from

the mouth, consistent with the (inviscid) analytical model of Müller et al. (1982). Recently, this computational framework was extended by Yaniv et al. (2014) who constructed an axi-symmetric 3D model, simulating the mouth as a series of interconnecting truncated cones that expand radially. The study included different-sized models, simulating mouth-opening and the ensuing suction flows in *S. aurata* from first-feeding larvae to adults. Their results showed that larval fish produced suction flows that were ∼2 orders of magnitude slower than those of adults (Fig. 3E), while *Re* at the mouth was much lower than *Re* = 150 for models that represent *S. aurata* larvae during the critical period. Compared to adult fish, in which the velocity of flow decays steeply with distance in front of the mouth, flow speed decayed gradually in larval fish (Fig. 3H). Thus, viscous forces at low *Re* modify the spatial distribution of flow speed in front of the mouth. Moreover, they predicted that the combination of lower flow speed and its gradual decay in front of

the mouth would result in weaker pressure gradient forces exerted on the prey of larval fishes (Yaniv et al. 2014). Based on these hydrodynamic considerations, larval fish can be expected to suffer reduced performance when feeding on prey that employs an escape response (Fig. 3G).

Suction-feeding performance in larval fishes

What are the possible limitations on suction-feeding performance that can result in failure of prey-acquisition strikes? Drost et al. (1987) suggested that catch success was determined by the ratio of gape diameter and aiming inaccuracy, which increased throughout larval ontogeny. Taking a mechanistic approach, Yaniv et al. (2014) used flow fields derived from CFD modeling to calculate the forces exerted on prey in the suction flow field (Fig. 3G). In their model, adult fish with larger gapes (and faster suction flows) could capture prey that exert greater thrusts during escapes. Furthermore, such fish could still capture prey that had started their escape from a distance of up to 0.9 of the diameter of the peak gape. In contrast, the model indicated that larval fish with small mouths of peak-gape diameters of ≤ 0.5 mm could only capture weakly escaping prey, and from only a limited distance of >0.6 peak diameter of the mouth. This prediction was corroborated by analysis of prey-acquisition strikes on *S. aurata*. China and Holzman (2014) quantified the distance between larval *S. aurata* and their swimming prey at the time of mouth-opening. Their analysis showed that older larvae (22 DPH) were able to successfully capture prey at a distance of up to 1.2 of the peak diameter of the gape, whereas smaller larvae (13 DPH) were successful in capturing prey at a distance of up to 0.8 peak diameter. Coupled with their larger gapes, larger larvae therefore can capture prey from a greater absolute distance (Fig. 3I).

The hypothesis that smaller larvae would fail to capture weakly escaping prey at a moderate distance from the mouth, based on calculation of the force exerted on the prey, should be manifest in prey that are drawn toward the mouth but do not enter into it. To quantify the prevalence of this mechanism in larval fishes, we obtained and analyzed high-speed videos (Fig. 2) of feeding interactions of 8–11 DPH *S. aurata* and 5–10 DPH *D. rerio*. From these videos, we extracted and analyzed attempts to capture prey (hereafter "strikes") in which there was only a single mouth-opening cycle in each attempt. Larval *D. rerio* (5–10 DPH; $n = 60$ strikes) failed to capture the prey
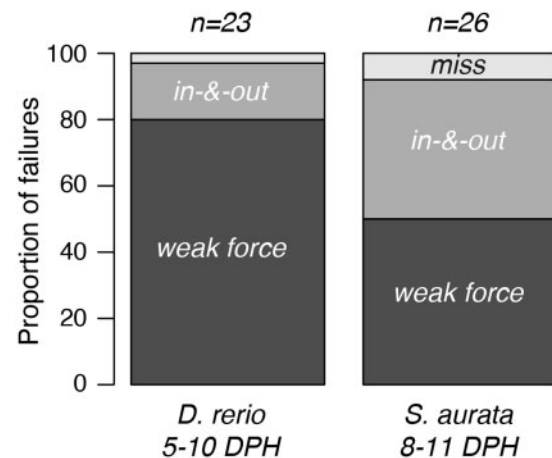
Fig. 4 Mechanisms of failure of strikes by early-stage larvae of *D. rerio* and *S. aurata*. Larval *D. rerio* ($n = 60$ attempts) failed to capture the prey (rotifers) in the first attempt in ~38% of strikes, while *S. aurata* larvae ($n = 40$ attempts) failed in ~65% of strikes. The dominant mechanism of failure for both species was weak suction force exerted on the prey, as indicated by prey that advanced toward the mouth but did not enter the buccal cavity ("weak force"). Failure to capture prey also occurred when prey entered the mouth but slipped outside again before the mouth closed (within the same cycle; "in-&-out"). A minority of failures was attributed to prey not moving during the strike ("miss").

(rotifers) at their first attempt in ~38% of the strikes. Eighty percent of the failures were cases in which the prey was drawn toward the mouth but did not enter it (hereafter "weak force"; Fig. 4). Larval *S. aurata* (8–11 DPH; $n = 40$ strikes) failed to capture the prey at the first attempt in ~65% of the strikes, and in 50% of these the prey was moved toward the mouth but did not pass through the gape (Fig. 4). Although younger larvae struck from a shorter (both absolute and scaled) distance, they still failed to draw the prey into the mouth. Consequently, we infer that the striking fish did not exert sufficient suction force on the prey.

Insufficient force, however, did not explain all the cases of failed strikes. Complete misses, in which the prey was not drawn forward at all during opening of the mouth, were rare for both species (2 and 1 cases for *S. aurata* and *D. rerio*, respectively). However, we observed multiple instances in which prey were drawn into the mouth, but then exited before the mouth closed, during the same gape cycle (usually during closure of the mouth). In 5–10 DPH larval *D. rerio* ~17% of the failures were cases in which the prey moved in and out of the mouth, whereas in 8–11 DPH *S. aurata* ~42% of the failures were cases in which the prey moved in and out of the mouth (Fig. 4). Because rotifers have a negligible escape response, we attribute this high prevalence of

in-and-out strikes to reversals of the suction flow. Therefore, we suggest that, unlike in adults, suction flows in larval fish are not always unidirectional. These reversals could be because the gills become a significant barrier to flow in low Re flows, or because the coordination of gape, hyoid, and opercular slits in young larvae is ineffective.

The importance of feeding to the survival and growth of larvae has triggered broad research and multiple attempts to quantify feeding rates (Blaxter 1986; Yúfera and Darias 2007). Most studies have used analysis of stomach contents (after sacrificing the larvae) to quantify prey items eaten within a given time-frame. The emerging conclusion was that feeding rate increases sharply with age (Fig. 3L), and that this increase is faster than that of body mass with age (Yúfera and Darias 2007; Parra and Yúfera 2000; Hamre et al. 2013; Rønnestad et al. 2013). As previously noted, it has been difficult to attribute the increase in overall performance with ontogeny to a single variable, because many performance-determining mechanisms change during the larval period. Using dynamic scaling experiments, it is possible to isolate the effect of size on the hydrodynamic regime experienced by the larvae. China and Holzman (2014) dynamically scaled three age classes of *S. aurata* larvae and measured their feeding rates. Their experiments indicated a strong effect of dynamically scaled length on feeding rate (based on stomach contents), with no significant effect of age. They noted that ~25% of the reduction in feeding rate with increasing viscosity was due to lower rates of encounter with prey (resulting from slower swimming by the prey), but that most of the decay was due to direct limitations on the suction-feeding mechanism at low Re. Interestingly, the reduction in encounter rates in smaller larvae are not attributed to swimming speed alone, but can also be attributed to a reduction in the distance from which prey can be captured. Because this distance is shorter in smaller larvae, it could be that the volume in which larvae can respond successfully to prey is reduced through the hydrodynamic effect of Re on the spatial distribution flow speeds in front of the mouth (Fig. 3H, I).

Implications for predator-prey interactions

If the force exerted on prey is important for determining the success of a strike, the prevalence of failed strikes is expected to increase when feeding on assemblages of wild plankton, which include highly evasive prey such as copepods. Using the filming system depicted in Fig. 2, we filmed 9–11 DPH *S. aurata* feeding on zooplankton that are typically encountered in the wild. Zooplankton were obtained by a swimmer hauling a 100 μm plankton net (4 m long, 0.6 m mouth diameter) for ~200 m in the sea (Gulf of Aqaba, Eilat, Israel). The net was washed and its contents sieved on a fractionation column. Prey retained between the 50 and 120 μm meshes (mainly copepods) were used for these experiments. When feeding on an assembly of natural zooplankton, all observed strikes of *S. aurata* larvae ($n = 15$) were directed at copepods. However, none of the strikes resulted in a capture, indicating that the rapid escape response of copepods significantly reduces the probability of larval fishes capturing prey, even compared to their already weak performance on rotifers (Chi square test comparing feeding success of 9–11 DPH *S. aurata* on rotifers and copepods; $\chi^2 = 5.54$, $P < 0.024$).

Can poor suction performance by early-stage larvae explain the composition of prey in the diet of larval fishes? In general, the diets of larval fish from many species include increasing proportions of evasive prey as the larvae grow, and this trend was widely observed in wild-caught larvae (Brodeur 1998; Schabetsberger et al. 2000; Tancioni et al. 2003; Llopiz and Cowen 2008; Llopiz and Cowen 2009). While this could be attributed to different rates of encounter rates with different types of prey, for example, higher rates with more mobile prey (MacKenzie and Kiorboe 1995), a similar pattern also emerges in laboratory experiments. Under laboratory conditions, it is possible to calculate the selectivity toward prey, defined as the proportion of each prey consumed relative to their relative density around the predator, or their encounter-rate (Chesson 1978; Chesson 1983). For example, laboratory experiments with *S. aurata* larvae showed that the proportion of live prey in the diet increased during the first 10 days after feeding commenced, while the proportion of inert particles decreased (Fernández-Díaz et al. 1994), despite an equal density of the two types of "prey." Similarly, young larval herring fed on poorly escaping mollusk veligers and copepod nauplii in proportions significantly greater than their relative density around the predator, but shifted to more evasive copepods and copepodites at later larval stages (Checkley 1982). Gulf menhaden fed in the laboratory on poorly-escaping tintinids, but later switched to copepod nauplii (Stoecker and Govoni 1984). Multiple traits of prey, such as pigmentation, size, and armor affect the selectivity of fish for the type of prey, and it could be that these are responsible for the observed

pattern. However, the generally lower success in capturing fast-escaping prey could merely reflect the reduced ability of smaller larvae to exert strong suction forces (China and Holzman 2014; Yaniv et al. 2014). Most of the experiments described above depend on stomach contents to establish selectivity, and it could be that young larvae fail to feed on highly evasive prey despite repeatedly trying (similar to our observations on *S. aurata* feeding on copepods).

Implications for the evolution of egg size

Experimental data on feeding ability, swimming, respiration, and metabolism of larval fishes suggests that overall performance of larval fishes improves dramatically as they transition to a regime of higher *Re* (Webb and Weihs 1986; Muller and Videler 1996; Osse and van den Boogaart 1999; Muller et al. 2008; China and Holzman 2014; Yaniv et al. 2014) Thus, selection for larger initial size would be expected because a larger body is capable of overcoming viscous forces. Paradoxically, however, virtually all species of fish that release fertilized eggs to the open ocean produce small eggs, which results in the hatching of relatively small larvae (Pauly and Pullin 1988). This could imply a strong stabilizing selection on the size of eggs and larvae. The agents of selection for small egg size likely include increased predation by species that rely on visual cues, limitations of diffusion in large eggs, environmental heterogeneity favoring more offspring at the cost of individual fitness, or fertilization-constraints on large eggs (Jørgensen et al. 2011). In fact, life-history models predict that conditions of low and stochastic survival favor the evolution of an *r*-selection strategy, with many small offspring and minimal parental care (Jørgensen et al. 2011). However, given the importance of hydrodynamics in governing the performance of larvae, the role of fluid dynamics in constraining the size of embryos should also be considered. Pelagic eggs drift in currents and are small enough to be unaffected by turbulence (Vogel 1994). Consequently, they are practically stagnant with respect to the surrounding water. Under these conditions, mass transfer of commodities (e.g oxygen) and waste products (e.g., ammonium) is governed by passive (molecular) diffusion (Rombough 1988; Vogel 1994). Importantly, the metabolic demand of the embryo and the rate of diffusion into the egg do not follow the same scaling. The rate of diffusion is limited by the surface area through which diffusion occurs, the gradient of the diffused substance, and its diffusion coefficient (Rombough 1988; Kranenbarg et al. 2000). In larger eggs housing larger embryos, the surface area of the egg scales by the square root of the volume, while the metabolic demand scales in proportion to the volume and can be, therefore, limited by diffusion (Rombough 1988; Kranenbarg et al. 2000). It is possible to increase the flux of commodities to the embryo by reducing the thickness of the diffusive boundary layer by generating flow around the egg. Thus, it could be that larger embryos cannot obtain the flux of oxygen needed to support their growth, unless they experience forced convection (i.e., flow relative to the egg). The idea of a maximal size of egg was suggested by Kranenbarg et al. (2000, 2001), but has received very little attention since, and experimental evidence for this idea is still lacking.

Conclusion

As larval fish grow, both total length, gape size, and associated volume of the mouth increase (Fig. 3A,C). Correspondingly, larvae swim faster (Fig. 3D) and can produce faster suction-flows (Fig. 3E), because a larger buccal volume is realized faster (or at least at the same speed) in older larvae (Fig. 3B). The above increases in characteristic scales of length (*l*, gape diameter) and flow speeds (*v*, peak flow speed at the mouth) during early ontogeny facilitate a transition into a hydrodynamic regime of higher *Re* (Fig. 3F), which characterize feeding by larvae (and their swimming). Consequently, the spatial gradients in the suction flows become steeper as the larvae transition into an area of higher *Re* (Fig. 3H). The combined effect of shallow gradients, small gape, and low speed of flow result in lower forces exerted on the prey of smaller larvae (Fig. 3G). These forces determine success in feeding (the proportion of prey captured in relation to the number of strikes [Fig. 3i]), because when weak forces are exerted on the prey, even weakly swimming prey can escape the strike (Figs. 3G and 4). Furthermore, lower swimming speed and the shorter distance from which prey is captured (resulting from smaller gape and shallower spatial gradients) result in smaller larvae having lower rates of encounter rates prey (Fig. 3J). Together, lower rates of encounter (Fig. 3J) and lower success in feeding (Fig. 3I) translate into lower feeding rates (Fig. 3K).

Mortality during the "critical period," identified by Hjort (1914), was originally attributed to the inability of the larvae to find food in sufficient quantities, leading to their starvation (Hjort 1914; Houde and Schekter 1980; Huwer et al. 2011; Meyer et al. 2012). Although alternative hypotheses have been suggested to explain the observed variability in the

survival and recruitment of larvae, starvation is still widely considered a major agent of mortality in larval fishes (Liem 1984; Cowen 2002; Huwer et al. 2011). The experimental and modeling work discussed here indicate pronounced effects of the hydrodynamic regime on feeding rates in larvae, revealing strong constraints on the ubiquitous "suction-feeding" mechanism of larval fishes under a low *Re* regime. Given the meager feeding success of early-stage larval fishes, it is not unlikely that these constraints limit feeding rates and induce starvation even when prey is abundant. This would be especially true in the ocean, when the majority of potential prey have the ability to perform escape maneuvers. However, that a "critical period" of larval mortality is commonly observed in mariculture facilities (Shields 2001) could indicate that starvation in early-stage larvae may occur even when encountering high densities of weakly escaping prey. Indeed, DNA/RNA ratios, an indicator of overall physiological condition, were indistinguishable between fed and starved larvae during the first few days after feeding commenced, and were similar to their levels in starved older larvae (Clemmesen 1994). We conclude that early-stage larvae experience "hydrodynamic starvation", in which low *Re* mechanistically limits their performance in feeding, even under high densities of prey.

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