

A Development Series of the
Soft Sculpin
Psychrolutes sigalutes

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Abstract

The development of larval fishes is a chronically understudied, critically important field, which offers broad insight into a defining period in the life history of fishes. Examinations of development shed light on the behavior and ecology of fishes at a stage wherein they are difficult to observe directly. We cleared and stained 36 specimens of the soft sculpin, *Psychrolutes sigalutes*, in an effort to link morphological development to preexisting studies on their behavioral shifts with growth. Rapid development of feeding structures suggests a fish that quickly grows into a highly capable hunter, well-suited to its lengthy transitional feeding period in the plankton. Given the intense focus of development on hunting, we believe that transforming *P. sigalutes* may be the apex predators in their habitat, possibly responsible for the top-down control of local ichthyoplankton.

Introduction

The early life history of fishes transitions them from a relatively simple, soft-bodied organism to a fully-ossified body capable of powerful swimming and effective feeding. Born with many systems incomplete, larval fishes often bear little resemblance to their adult form. Formless and relatively helpless, the vast majority perish (Dahlberg, 1979). Those that survive undergo a rapid transformation from a tiny pelagic juvenile to a capable, highly-specialized adult. The size of larval fishes makes tracking them as they grow difficult, but such studies offer major insights into one of the most defining stages in the life history of fishes.

On the sub-10mm scale, movement of larval fishes is largely governed by the viscosity of water, as opposed to the inertial forces that are the primary controller of propulsion in larger organisms (Muller et al., 1996 & 2000; Osse et al., 2000). Osse (1990) noted that larval carp initially utilize anguilliform locomotion, wherein the entire body is flexed in a sinusoidal motion to provide forward thrust. Prolonged swimming in larval fishes is rare, with most movement accomplished in short bursts (Hale, 1999; McHenry & Lauder, 2006). Such locomotion is necessary in lieu of a caudal fin and rigid skeleton. Larvae undergo a process called flexion, wherein the tip of the notochord flexes upwards, coinciding with the development of the hypural plate—the base of the caudal fin. (NOAA, 2014). As flexion progresses, fish shift to carangiform locomotion, in which the front end

of the body is held stiff, with propulsion accomplished by prolonged, powerful strokes of the tail (Mauguit et al., 2010).

As preflexion larvae have no tails to speak of, they utilize a medial finfold to maximize the volume of water shifted during propulsive motions (Muller et al., 2012; Van Den Boogaart & Osse, 2012). In most species, this finfold is later resorbed and replaced with distinct caudal, dorsal, and anal fins; a transition concurrent with the move to a carangiform-type swimming style (Mauguit et al., 2010). This transition does not always take place at a time optimal for propulsion. McHenry et al. (2012) noted that zebrafish undergoing the shift from anguilliform locomotion to utilization of adult fins suffer a temporary reduction in swimming performance. The generally allometric nature of fish development (Osse et al., 1995 & 1997) suggests that a biological trade-off takes place wherein the fish sacrifices locomotive prowess for another function, such as moving from pectoral-fin assisted ventilation to respiration through developed gills (Osse & Van Den Boogaart, 1999; Hale et al., 2012). These trade-offs suggest that fish developmental pathways are distinctly prioritized to optimize survivability.

Most larval fishes hatch initially incapable of consuming prey, instead relying on sustenance from an external yolk sac. Development of the jaw structures necessary for feeding corresponds with a transitional stage in which larvae begin hunting. Initially, most larvae lack the capability of premaxillary protrusion, and rely predominantly on ram feeding (Sanderson & Kupferberg, 1999). The frenetic nature of preflexion larval locomotion adds considerable yaw (and inaccuracy) to early lunges at prey (Osse et al., 1990). As the notochord stiffens and jaws develop, this feeding behavior gives way to a forward lunge with improved suction. Suction capabilities and success rate increase markedly with growth (Hunter et al., 1980, Drost et al., 1987).

Sanderson & Kepferberg (1999) noted the paucity of research on the development of the skeletal system of fishes, especially concerning the connections between functional groups of bones. Prior research into the formation of the adult skeletal system has focused primarily on the time to complete ossification, (e.g. Kuzir et al., 2009; Zouiten et al., 2011). Research focused on functional groups of bones has largely been confined to the model organism *Danio rerio* (e.g. Cabbage et al., 1996) or on fishes with novel morphology, (e.g. Britz et al., 2005 & 2012; Johnson et al., 2005, Zhang et al. 2011). Few species have had their skeletal development well-studied. The objective of this study is to describe the skeletal development of a larval teleost as it undergoes transformation, the period in which larval fish develop an adult skeletons and behavior shifts from larval to adult. Our primary focus is the relative progress of functional groups throughout the skeleton.

We used the soft sculpin, *Psychrolutes sigalutes*, for our research. *P. sigalutes* is a benthic hunter reaching 8.3 cm in length. It inhabits subtidal and deep shelf rock crevices, and is rarely seen as an adult. Members of the genus *Psychrolutes* are relatively understudied; only *Psychrolutes paradoxus* is easily collected once mature. Contributions to knowledge of an enigmatic group notwithstanding, what little research has been done on *P. sigalutes* suggests it has excellent characteristics for a study of development. Marliave (1975) documented, at length, the behavioral transitions of *P. sigalutes*, (Then *Gilbertidia sigalutes*) from hatching to settlement. With background study on behavioral shifts already present, we have the opportunity to expand on this information with a look at the changing morphology of the fish over the same period.

Unlike most larval fishes, which transform quickly and settle immediately thereafter, *P. sigalutes* has a novel, protracted transitional period. Once transformation has begun, *P. sigalutes* attempts settlement many times, choosing increasingly suitable locations as development progresses. Rather than searching along the benthos for a suitable rock crevice, unsuccessful juveniles lie still on the bottom

until dusk. As night falls, they rejoin the plankton, gorging themselves on zooplankton to fuel their next effort. In general, juvenile *P. sigalutes* will not engage prey from the bottom until properly settled. Marliave noted that even subadult *P. sigalutes* had often not yet settled, and made regular vertical migrations. The unconventional, extended nature of the transitional period makes *P. sigalutes* an especially interesting candidate for a study of morphological development, given both the lengthy growth period and well-documented behavioral regime. We attempted to link our morphological data with the previously studied and behavioral shifts during the development of *P. sigalutes*, offering broad implications for the biology and ecology of the species.

Materials and Methods

Fish were collected from the docks at the University of Washington's Friday Harbor Laboratories over the summer of 2014. A total of 61 specimens of *P. sigalutes* were collected.

After initial fixation in non-buffered formalin, the fish were measured, numbered, and sorted by size. They were then cleared and stained, using the procedure outlined in Dingerkus & Uhler (1977). Specimens damaged during sample preparation and/or showing significant loss of mineralization from prolonged non-buffered formalin exposure were not used. The final subsample consisted of 36 *P. sigalutes*, ranging in size from 6.1mm to 41.0mm SL. Specimens were then examined under a Zeiss Discovery V20 stereo microscope, and photographed with an integrated Zeiss Axiocam.

Results

All fish below 7mm display no significant mineralization or notochord flexion (Fig 1) Structures in specimens of this size are cartilaginous. By 11.8mm, the notochord is flexed to approximately 40 degrees. The beginnings of the hypural plate are clearly visible, along with all of

the simple fin rays and a single procurrent ray. The medial finfold is receding, with dorsal and anal fin rays clearly visible. Notochord flexion is complete by 13.8mm, and most procurrent rays are fully formed. A far denser matrix of cartilage is present on the hypural plate. By 15.8mm SL, transformation is fully underway. The hypural has begun to mineralize, along with all fin rays. Traces of the medial finfold remain visible near the caudal peduncle. (Fig 1). The hypural plate continues to ossify through 26.7mm, at which point the notochord tip has nearly fused to it. We observe complete fusion at 29.0mm.

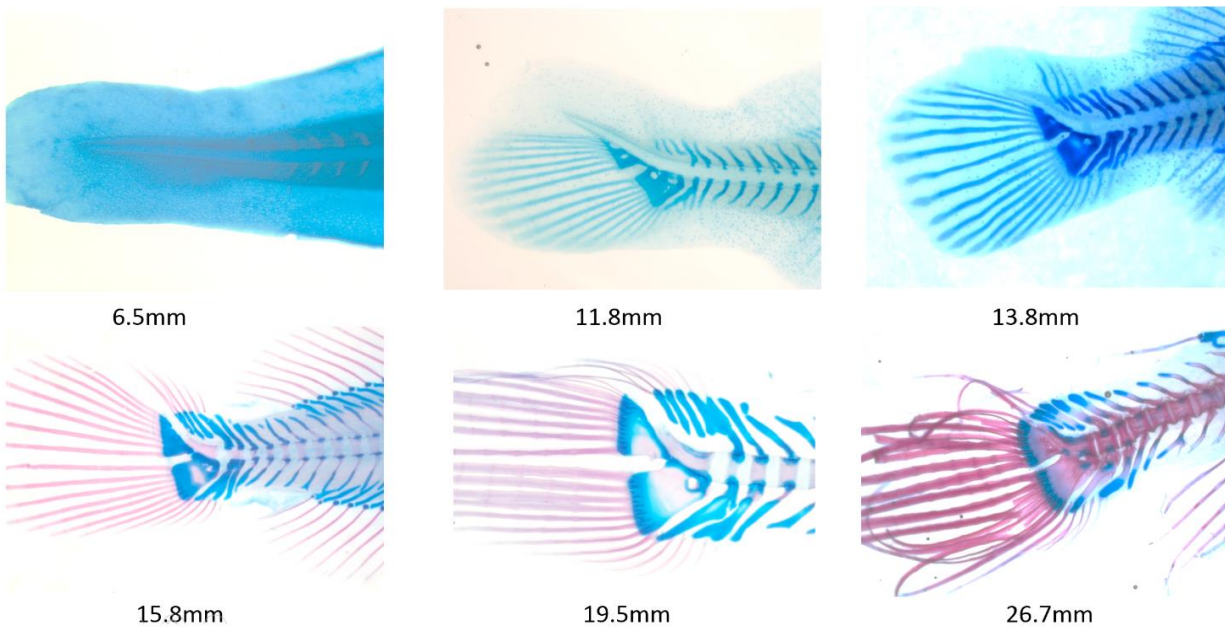


Figure 1: Development of the caudal complex. Note flexion and eventual fusion of the notochord tip.

In preflexion larvae, no spinal column is visible, though the cartilaginous beginnings of neural and haemal arches are present. Their cartilage grows denser as flexion progresses, with mineralization present on the first transforming specimen (Fig 2). The ribcage, invisible in the 13.8mm specimen, has fully formed and mineralized in the 15.8mm fish. The pores of the lateral line are both visible and chondrified at this point. The vertebrae have also begun to develop and harden, though the vertebral column has not yet articulated. This process is complete by 20.0mm SL.

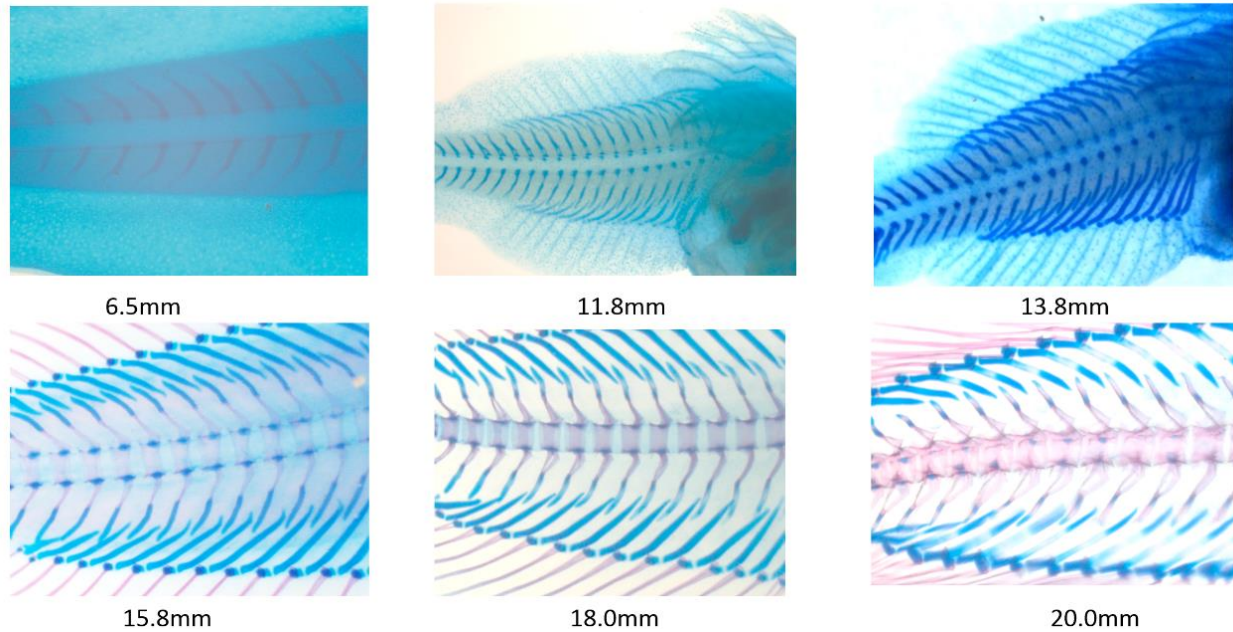


Figure 2: Development and articulation of the vertebral column.

By 6.5mm SL, the mouth is visible on preflexion larvae. As flexion progresses, structures on the head, especially the various mouth parts, grow better defined, with heavier matrices of cartilage. The premaxilla and mandible are the first structures to harden on the entire body, mineralizing at 13.8mm SL. This is immediately followed by the mineralization of the maxilla, preoperculum, operculum, cleithrum, and subsections of the pectoral girdle. (Fig 3). The dentary is well-developed in early transformation. By 18.0mm SL, ossification has progressed to the gill arches and scapula, with initial mineralization of the hyoid beginning by 18.5mm. By 20.0mm, bone is present on the ethmoid, parasphenoid, and frontal elements of the skull. (Fig 4). Between 20.0mm and 26.7mm, the hyomandibula and supraoccipital mineralize, with no further bone development visible until 32.3mm, at which point ossification is observed on the pelvis and neurocranium. Not all elements of the skeleton have mineralized by the end of the sequence. The last bone we observe hardening, the parietal, ossifies at 37.3mm SL. We constructed a table (table 1) to track the progress of skeletal development and articulation through specimens.

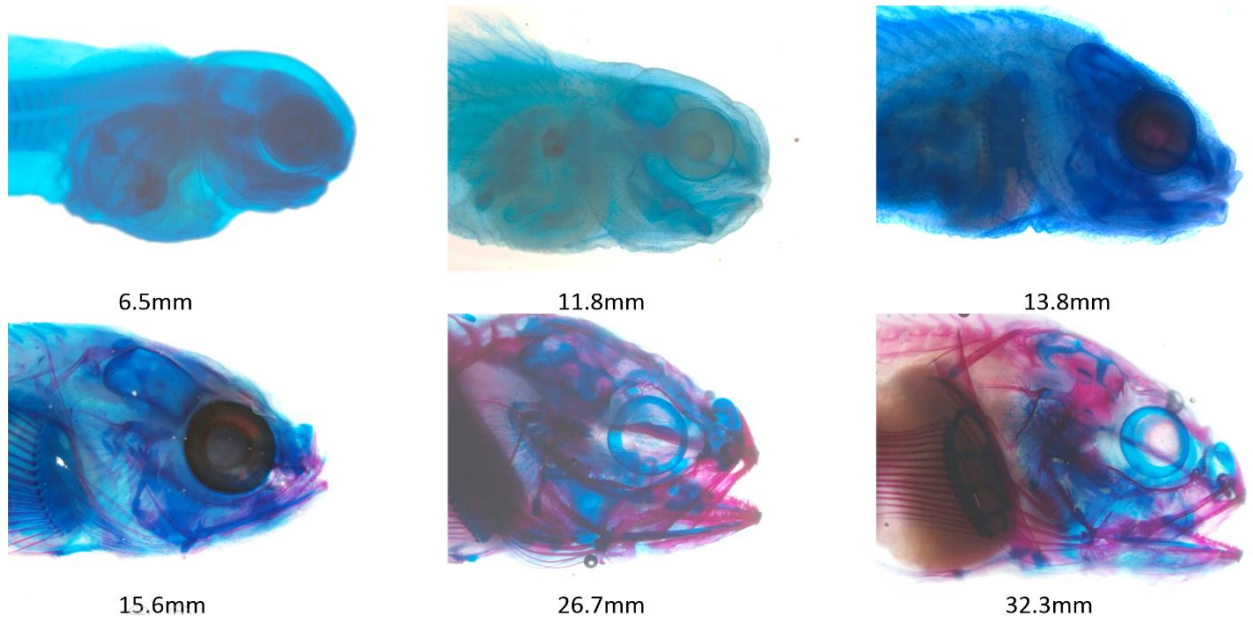


Figure 3: Side view of skull development from Preflexion larva to late-stage transition.

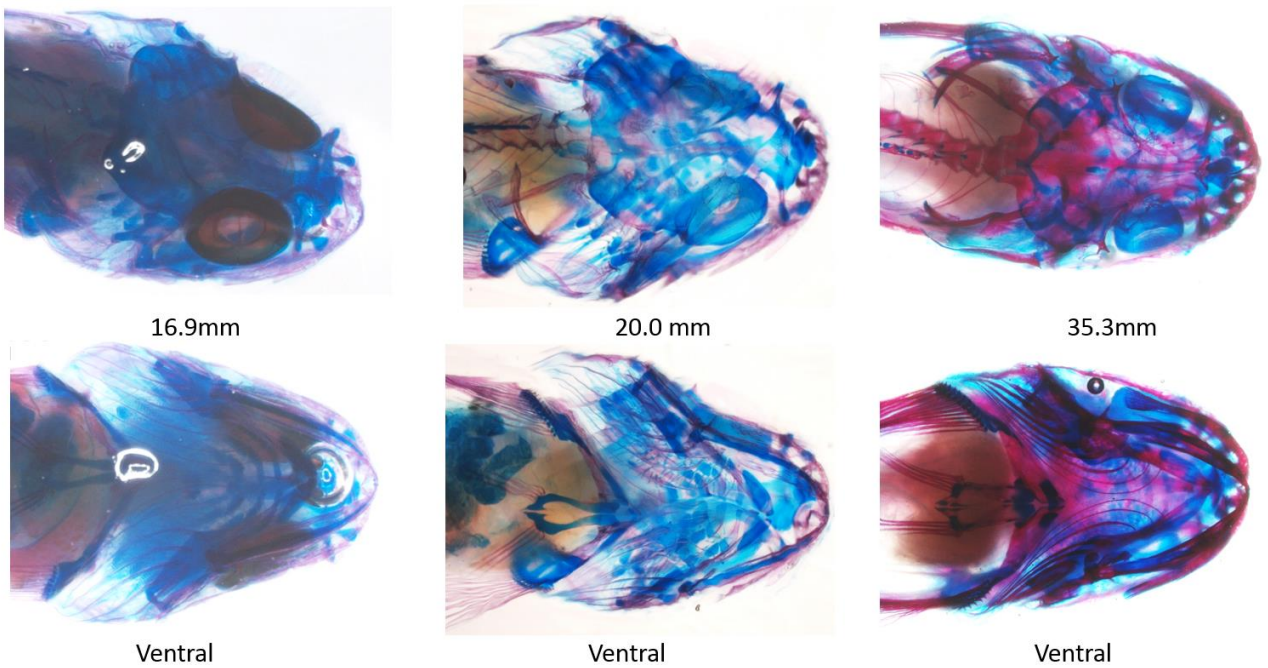


Figure 4: Top and bottom views of mineralization in skull structures.

Table 1: Mineralization on structures through size range of *P. sigalutes* with bone development. X denotes the presence of mineralization. Shaded boxes indicate complete articulation of a given structure.

SL(MM)	13.8	15.8	16.9	17.6	18.0	18.5	18.6	19.5	20.0	26.7	28.1	28.5	29.0	29.6	32.0	32.3	32.8	33.3	34.5	34.6	34.7	35.1	35.3	36.4	37.3	37.5	38.0	41.0
Premaxilla	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Mandible	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Ribcage	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Maxilla	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Preoperculum	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Vertebral column	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Hypural	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Fin rays	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Brancheostegals	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Neural/Haemal	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Spines	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Cleithrum	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Pectoral girdle	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Operculum	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Quadrates	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Gill Arches	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Scapula	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Hyoid	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Ethmoid	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Parasphenoid	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Frontal	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Supraoccipital	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Hyomandibula	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Pelvis	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Neurocranium	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Parietal	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X

Discussion

Specimen degradation from formalin made it unclear when bones finished hardening. As such, it is difficult to disentangle the order in which skeletal elements complete. However, the order in which elements *begin* to ossify was preserved, allowing us to comment on the meaning behind the sequence of bone development.

The protracted nature of the settlement period is reflected in the morphology of developing *P. sigalutes*. In general, we find that development is consistent with the behaviors documented by Marliave (1975). With structural bones such as the pelvis and neurocranium developing comparatively late (table 1), far more emphasis is devoted to the early growth of elements that rapidly transition juveniles to highly effective predators.

Although no mineralization is present on flexion larvae between 11.8mm and 12.0mm, the heavy cartilage matrix on developing caudal elements suggests a more powerful subcarangiform style of swimming (Fig 1). Osse (1990) discussed the importance of subcarangiform locomotion in successful capture of prey. The reduction in head yaw provided by caudal propulsion lends greater accuracy to the lunge. Mouth elements are well-defined (Fig. C), indicating that even pre-transformation, *P. sigalutes* quickly transitions from the ram feeding described by Sanderson & Kupferberg (1999) to a targeted suction. The pelvic fins are all but invisible at this stage of life—to be expected, considering the pelagic lifestyle of fish before transition.

Once a hypural has formed, and subcarangiform locomotion established, development turns to feeding elements. As these bones stiffen, the buccal cavity can expand faster, yielding greater suction power. The head has begun to streamline as the fish enters its transitional period, but it is still purely a diurnal, pelagic hunter. No structures from the acoustico-lateralis are yet visible, and the pelvic fins remain underdeveloped. Marliave documented feeding by pretransitional *P. sigalutes* as being vision-based, with greater reliance on the lateral line as the fish progressed in size. The development of the acoustico-lateralis coincides with increasingly nocturnal hunting.

Although dorsal and anal fin rays are visible, the medial finfold has not yet receded, suggesting that *P. sigalutes* is not yet capable of precision maneuvering at this stage. However, at this size, it would be well-suited to hunting smaller prey, which would be incapable of escaping its powerful forward lunge and suction.

With a considerable amount of bone already present, it would appear that transformation has been underway for a significant period by 15.8mm SL. The presence of a hardened ribcage means that the front portion of the body is stiff. Head yaw would be minimal at this stage; locomotion almost fully carangiform. Despite residual medial finfold ahead of the caudal peduncle, all adult fin rays are present and mineralized, suggesting a fish capable of fairly powerful and precise swimming. The most striking developments, however, are to the litany of elements utilized in suction feeding (Table 1). Of the 12 new bones we observed mineralizing, eight have direct roles in suction feeding, with the remaining four critical to propulsion. At this stage, prey capture appears to be the singular focus of developing fish. During early transformation, the teeth are especially large in proportion to body size (Fig 3). We believe that this is compensation for any deficiency in suction as the fish develops. With long teeth, juvenile *P. sigalutes* would be more than capable of holding onto any prey that they fail to engulf in a single gulp.

The late articulation of the vertebral column relative to the mineralization of feeding structures (Table 1) suggests that although *P. sigalutes* is a capable pelagic swimmer in early transition, chasing down prey is not a particularly significant challenge. Without a fully articulated spinal column, the power of swimming strokes is somewhat limited. However, considering that *P. sigalutes* is still feeding in the plankton, the majority of prey items would be limited in speed by their mass, and consequentially low Reynolds number. Unable to move effectively against the viscosity of water, planktonic prey would have difficulty escaping *P. sigalutes*. Smaller prey would be forced to make repeated stop-start motions, while the mass (and inertia) of the much larger *P. sigalutes* would allow for consistent speed throughout pursuit. With a large, stiff caudal fin, *P. sigalutes* is capable of quickly accelerating to speeds that zooplankton cannot hope to match over any distance. Observations corroborate the ease with which growing *P. sigalutes* capture prey—pelagic juveniles collected by Marliave had near-universally full stomachs.

Additionally, we observe a full arsenal of lateral line pores in our first transforming specimen, with internal structures chondrified. Though Marliave notes that these structures only become visible in “late transformation,” such a timeframe isn’t well-specified. Additionally, Marliave documented the pores initially appear on the head and develop towards the tail, but we observed a completed network of pores throughout the body by this point. As Marliave had both captive-bred and wild-caught fish, as well as a far larger sample size, it is possible that our 15.8mm specimen represents a comparatively “late transformation” animal, but clarification is necessary. In any case, it

would appear that by 15.8mm, *P. sigalutes* would be an effective hunter in darkness. Prior research on *Myoxocephalus scorpius* showed that before the acoustico-lateralis develops, juvenile shorthorn sculpin have difficulty detecting predators, even in daylight. (Killen et al., 2007). It is unclear if the main focus of lateral line development in *P. sigalutes* is prey detection or predator avoidance. However, the lack of mineralization in protective elements such as the neurocranium at small sizes (Table 1) presents a stronger case for the former. It is possible that juvenile *P. sigalutes* are the apex predators of their planktonic feeding grounds, and have few predators to worry about. Alternatively, selective pressure may favor fish overwhelmingly focused on prey capture.

Marliave documented that *P. sigalutes* exhibits low fecundity and minimal horizontal migration. Adult populations are limited by the presence of habitat on which to settle. With pelvic fin rays fully ossified at 15.8mm SL, the fish may make first attempts at settlement, but the soft pelvis would be ineffective at bearing the animal's weight. *P. sigalutes* is negatively buoyant, so the inability of the pelvis to hold the fish off the substrate would inhibit settlement on hard bottoms. Adult *P. sigalutes* settle exclusively among rocks in the lower subtidal and deep shelves, a difficult proposition for small fish that cannot easily keep themselves fixed off the bottom. Marliave noted that smaller juveniles typically attempted settlement on soft, open bottoms; habitat far from adults. Lab experiments showed that fish less than half of adult size will settle in more appropriate habitat when adults are not present, but refrain from settling contested territory to avoid being cannibalized. It is possible that the late development of the pelvis keeps juveniles from attempting premature settlement in possibly occupied territory. Larger fish would be at considerably less risk of cannibalization.

With the pelvis stiff, fish would be capable of more competent settlement in adult habitat for the first time, but this capability does not prompt immediate settlement. Marliave noted a simultaneous catch of 16 unsettled *P. Sigalutes* averaging 41.9mm SL. It seems *P. sigalutes* will not permanently settle until suitable habitat is found, irrespective of size. Without a rock crevice to inhabit, these fish will continue their nighttime migrations, possibly to full adult size. In any case, the full stomachs Marliave observed seem to indicate that *P. sigalutes* does not have any pressing need to settle prematurely, given the abundance of food.

If *P. sigalutes* does represent the apex predator of the planktonic environment, it is possible that the rapid development of these precocious hunters forces the prompt settlement of other ichthyoplankton. Marliave documented that growing *P. sigalutes* prefer other larval fishes out of all

available prey. It would appear prudent for other larvae to quickly exit the water column, faced with contending with a much larger, well-developed hunter in *P. sigalutes*. Perhaps, *P. sigalutes* is responsible for the top-down control of other ichthyoplankton species? It would be interesting to compare the development sequences of *P. sigalutes* with the various species cohabiting the water column as it grows. If all other species settle earlier, it may provide some evidence that *P. sigalutes* exerts top-down control. Given its limited horizontal migration, it may also be possible to remove a patch of *P. sigalutes* and compare the abundance and development of ichthyoplankton in the sample area. However the migratory nature of most larval fishes makes the former option a more attractive study.

The major limitation of our study was the lack of flexion larvae, and fishes at early transitional stages. Though we have a broad sense of the developmental priorities of these fish, small sample size inhibits more precise results. With more specimens between 8mm and 15mm, it would be possible to further disentangle the order in which skeletal elements develop. Captive breeding is an attractive option for the acquisition of more data in the future.

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