Copeia

Sexual Dimorphism and Size-Related Changes in Body Shape in Tule Perch (Family: Embiotocidae), a Native California Live-Bearing Fish

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The Tule Perch, *Hysterocarpus traskii*, is a viviparous and externally monomorphic, internally fertilizing fish. Despite appearing monomorphic, males and females are expected to differ in body shape because the different reproductive roles occupied by the sexes should influence patterns of selection and, ultimately, lead to differences in morphology. The objectives of this study were to determine if the Sacramento–San Joaquin subspecies of Tule Perch (*H. t. traskii*) exhibit (1) sexual dimorphism in body shape, (2) size-related changes in body shape, and (3) sexual size dimorphism. Geometric morphometric analyses indicated that *H. t. traskii* exhibited significant sexual dimorphism of body shape and identified the mid-body and caudal peduncle regions as the most effective discriminators between the sexes. Females were narrower through the caudal peduncle and mid-body and had anal-fin origins that were more posteriorly located than males. Additionally, *H. t. traskii* exhibited significant size-related changes in body shape. Larger fish were deeper bodied with blunter snouts and wider caudal peduncles. The eyes of larger fish were relatively smaller and located higher on the body than those of smaller fish. *Hysterocarpus t. traskii* did not exhibit differences between the sexes in standard length, but males were significantly heavier than females.

SEXUAL dimorphism is prevalent in animal taxa and can result from a variety of factors including natural selection, sexual selection, and the sexes occupying dimorphic niches (Blanckenhorn, 2005; Kitano et al., 2007; Hassell et al., 2012). Sexual selection typically acts on males via female choice or intrasexual competition, while the dimorphic niche hypothesis usually applies to females due to reproductive constraints (Hedrick and Temeles, 1989; Herler et al., 2010). Fishes exhibit sexual dimorphism as variations in size, body proportions, fins, and/or color (Echeverria, 1986).

The Tule Perch, *Hysterocarpus traskii*, is the only freshwater member of the surfperch family Embiotocidae (Hopkirk, 1973). Endemic to California (Moyle, 2002), *H. traskii* is the only native, viviparous freshwater fish species in the state (Baltz and Moyle, 1981). Three subspecies of *H. traskii* are recognized in three drainage systems: Clear Lake (*H. t. lagunae*), Russian River (*H. t. pomo*), and Sacramento–San Joaquin (*H. t. traskii*; Baltz and Moyle, 1981; Baltz and Loudenslager, 1984).

Of the 23 surfperch species (Baltz, 1984), *H. traskii* is the only surfperch with permanent, non-sexual color dimorphism (Phelps, 1989). Additionally, in this otherwise relatively monomorphic species, the sexes only differ outwardly in appearance in the region of the anal fin. Males have semilunar depressions in the body surface above the anal fin and a fleshy, glandular enlargement at its base (Bundy, 1970; Bryant, 1977). Sexual size dimorphism is not well documented in *H. traskii*. It has been reported that males are significantly smaller than females (Phelps, 1989), but some data, including that presented in this paper, suggest otherwise (Bundy, 1970).

Despite appearing monomorphic, males and females are expected to differ in body shape because the different reproductive roles occupied by the sexes should influence patterns of selection and, ultimately, lead to differences in morphology (Casselman and Schulte-Hostedde, 2004). It is also expected that the body shape of *H. t. traskii* changes as it

matures, especially the abdomen shape as reproductive structures develop (Hassell et al., 2012).

The objectives of the present study were to determine if *H. t. traskii* exhibits (1) sexual dimorphism in body shape, (2) size-related changes in body shape, and (3) sexual size dimorphism. This study provides both valuable information regarding the most prevalent subspecies of *H. traskii* and contributes to the broader understanding of sexual dimorphism and morphology of viviparous fish species.

MATERIALS AND METHODS

A total of 275 *H. t. traskii* were collected from Baum Lake, Shasta County via an electrofishing boat on 30 July 2014. Located in the Pit River subprovince at an elevation of approximately 3000 feet, Baum Lake represents the northernmost end of the range for *H. t. traskii* (Moyle, 2002). It is important to note that the fish were collected in the middle of breeding season. Fish were preserved via freezing because it causes less change in specimen length and weight than other preservation methods (DiStefano et al., 1994). Additionally, the freezing and thawing process does not cause significant shrinkage or swelling that would affect geometric morphometric analyses (Cadrin and Silva, 2005). Samples of *H. t. traskii* were deposited in the CSUS Fish Collection (accession numbers SSU BP1–BP275).

The weight, standard length, and sex of each thawed fish were recorded for use in sexual size dimorphism analyses. Fish bent during the storage and/or the preservation process were not included in the analyses if they could not be manually straightened without distorting the lateral body shape. A total of 269 *H. t. traskii* were included in analyses.

Morphometric information was acquired from a lateral image of the left side of each fish (Fig. 1A). Landmarks were selected using criteria supplied by Zelditch et al. (2012). The following 18 biologically homologous landmarks were identified: (1) anterior tip of snout, (2) most anterior point of eye outline, (3) most posterior point of eye outline, (4)
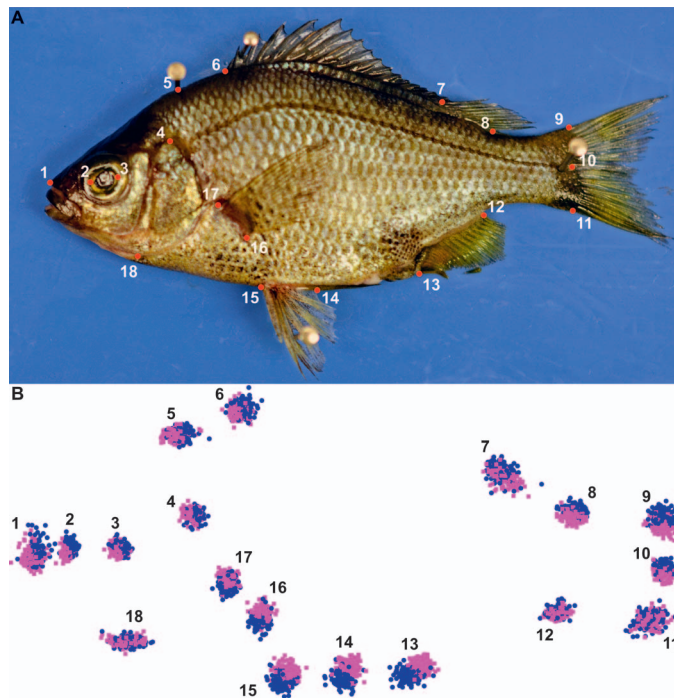
Fig. 1. (A) Landmarks used for geometric morphometric shape analysis of *H. t. traskii*: (1) anterior tip of snout, (2) most anterior point of eye outline, (3) most posterior point of eye outline, (4) dorsal origin of the operculum, (5) posterior boundary of the supraoccipital bone, (6) dorsal-fin origin, (7) soft dorsal origin, (8) dorsal-fin insertion, (9) dorsal insertion of caudal fin, (10) lateral line at caudal fin, (11) ventral insertion of caudal fin, (12) anal-fin insertion, (13) anal-fin origin, (14) pelvic-fin insertion, (15) pelvic-fin origin, (16) pectoral-fin insertion, (17) pectoral-fin origin, and (18) ventral origin of the operculum. (B) Generalized Procrustes Analysis (GPA) of 130 male (blue) and 139 female (pink) *H. t. traskii*. GPA mathematically removes non-shape variation due to size, scale, and position.

dorsal origin of the operculum, (5) posterior boundary of the supraoccipital bone, (6) dorsal-fin origin, (7) soft dorsal origin, (8) dorsal-fin insertion, (9) dorsal insertion of caudal fin, (10) lateral line at caudal fin, (11) ventral insertion of caudal fin, (12) anal-fin insertion, (13) anal-fin origin, (14) pelvic-fin insertion, (15) pelvic-fin origin, (16) pectoral-fin insertion, (17) pectoral-fin origin, and (18) ventral origin of the operculum (Fig. 1A). Pins were inserted on each specimen at landmarks 4, 5, and 10 prior to taking photographs to ensure the accuracy of landmark location during digitization. Landmarks were digitized using tpsDig2 software. All geometric morphometric software used for this study is publicly available at https://life.bio.sunysb.edu/morph/index.html.

Shape coordinates were calculated from the landmark data provided by tpsDig2 for analyses. Using CoordGen8, a Generalized Procrustes Analysis was performed to remove all non-shape variation due to position, orientation, and scale of the specimen (Zelditch et al., 2012; Fig. 1B). To test for sexual dimorphism, a single factor permutation Multivariate Analysis of Variation (MANOVA) was performed using the software CVAGen8 (Zelditch et al., 2012). Additionally, a Canonical Variates Analysis was performed in CVAGen8 to describe the differences in body shape between male and female *H. t. traskii* with regard to variation within each sex. Differences between the sexes were visualized using deformation grids generated in CVAGen8.
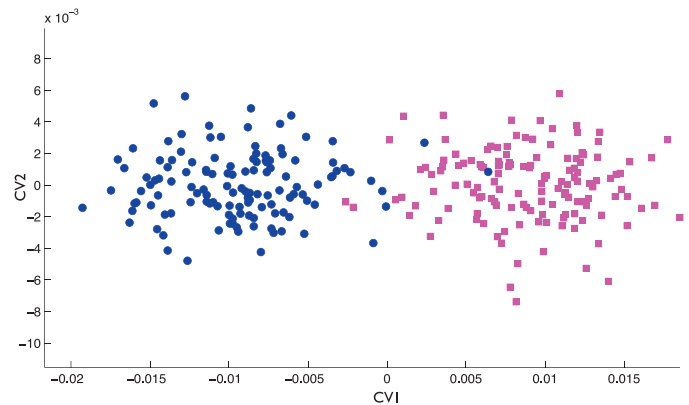

Fig. 2. Canonical Variates Analysis of the sexes. Results demonstrate that one dominant canonical variate axis described significant differences between male (blue circles) and female (pink squares) *H. t. traskii*.

To test for body shape change with respect to centroid size, a multivariate regression was performed using Regress8. Centroid size is calculated as the square root of the summed squared distances of all the landmarks from the centroid of the landmark configuration. Centroid size is the preferred size measurement in geometric morphometrics because it is uncorrelated with shape in the absence of allometry (Zelditch et al., 2012). Differences in body shape with respect to centroid size were visualized using deformation grids generated in Regress8.

To test for sexual size dimorphism with regard to standard length, a two-sample t-test was performed. The assumption of normality was tested by plotting the data on a normal probability plot. The assumption of equal variances was tested using an F-test. These procedures were repeated to test for sexual size dimorphism with regard to weight. All analyses investigating sexual size dimorphism were performed using PAST Version 3.11.

RESULTS

Sexual dimorphism of body shape.—There was a significant difference in body shape between males and females ($F = 59.17$, df $= 268$, $P < 0.001$). The first canonical variate (CV1) was the only unique axis (Wilk's $\Lambda = 0.1782$, $X^2 = 432.98$, df $= 32$, $P < 0.001$) and accounted for 96.7% of the variance (Fig. 2). A jackknife test of group assignments resulted in 258 correct assignments and 11 incorrect assignments (Table 1). Given the group sizes, the expected random rate of correct assignments was 50.2% and the observed rate of correct assignments was 95.9%.

The deformation grid associated with CV1 illustrated that the most effective discriminators between the sexes were

Table 1. Results of the jackknife analysis demonstrate that 95.9% of Tule Perch were assigned to the correct group (sex) based on body shape.

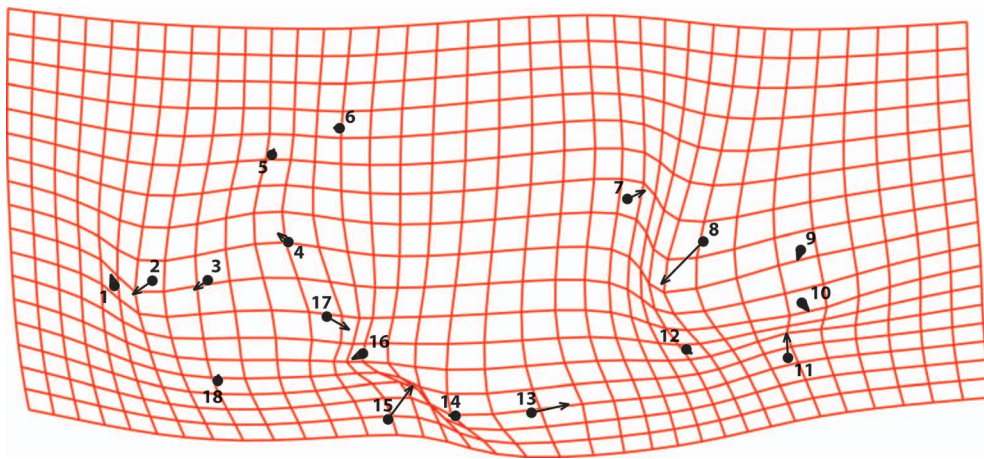|	*a posteriori* assignment	
a priori assignment	Female	Male
Female	135	4
Male	7	123

Fig. 3. Deformation grid of the first canonical variate (CV1). This deformation grid depicts the shape transformation associated with the CV1 axis, which represents the variables that maximally discriminate between the sexes. Circles on the grid represent the reference body shape for male *H. t. traskii* and the vectors demonstrate the direction and relative magnitude of local shape change to the reference body shape of female *H. t. traskii*.

landmarks 8, 13, and 15 (Fig. 3). Females were narrower through the caudal peduncle and mid-body and had anal-fin origins that were more posteriorly located than males. Additionally, the deformation grid associated with the regression of CV1 illustrated females had steeper foreheads, as well as lower, more anteriorly located eyes and more dorsally-located pectoral fins than males.

Size-related changes in body shape.—In females, variation in shape was related to centroid size ($F = 8.924$, df1 = 32, df2 = 4384, $P < 0.01$). The deformation grid obtained from the regression of shape on size illustrated that larger females were deeper through the mid-body, more blunt through the snout, slightly wider through the caudal area, and had steeper foreheads than smaller females (Fig. 4A). Additionally, the anal-fin origin was posteriorly shifted in larger females. The pectoral fin in larger females was shifted ventrally compared to its placement in smaller females. Finally, the eyes of larger females were relatively smaller and located more dorsally on the body than those of smaller females.

In males, variation in shape was related to centroid size ($F = 13.41$, df1 = 32, df2 = 4096, $P < 0.01$). The deformation grid obtained from the regression of shape on size illustrated that larger males were deeper through the mid-body, more blunt through the snout, wider through the caudal region, and rounder through the posterior edge of the caudal peduncle than smaller males (Fig. 4B). The pectoral fin in larger males was shifted ventrally compared to its placement in smaller males. Finally, the eyes of larger males were relatively smaller and located higher on the body than those of smaller males.

Sexual size dimorphism.—There was no significant difference between males and females with regard to standard length (Table 2). The variance of male and female standard lengths did not differ significantly ($F = 1.14$, df = 270, $P = 0.46$) and each standard length dataset was normally distributed (female correlation coefficient = 0.98; male correlation coefficient = 0.99).

Males were significantly heavier than females ($t = -3.51$, df = 270, $P < 0.001$; Table 2). The variance of male and female weights did not differ significantly ($F = 1.04$, df = 270, $P = 0.82$). A log transformation was applied to both weight datasets prior to analyses because they did not exhibit a normal distribution. After transformation, the datasets were normally distributed (female correlation coefficient = 0.99; male correlation coefficient = 0.98).

DISCUSSION

Sexual dimorphism of body shape.—*Hysterocarpus t. traskii* collected in the present study exhibited sexual dimorphism with regard to body shape. The most effective morphological discriminators between the sexes occurred along the ventral edge of the body and in the caudal region.

The finding that females were narrower through the mid-body than males is not only inconsistent with expectations based on the respective reproductive roles of each sex, but also with previous research in both oviparous and viviparous species (e.g., Hood and Heins, 2000; Cadrin and Silva, 2005; Hassell et al., 2012; Unito-Ceniza et al., 2012). One possible explanation for this discrepancy may be elucidated by the finding that the anal-fin origin was more posteriorly placed in females than in males. While males had a deeper ventral outline, the posterior shift of the anal fin, and by association the anus, in females may indicate the availability of additional volume in the body cavity for ovary development. Another possible explanation may be due to the asynchronous enlargement of the gonads in the sexes. The *H. t. traskii* used in this study were collected in the middle of breeding season. During this time, male gonad size is maximized, while female gonad size is minimized (Bryant, 1977). Gonad size in females is highest in the spring, just before parturition (Bryant, 1977). Further investigation comparing body shape of each sex during peak and quiescent gonad development periods would be necessary for clarification.

Table 2. Tule Perch standard length and weight averages. Males were significantly heavier than females ($t = -3.51$, df = 270, $P < 0.001$).

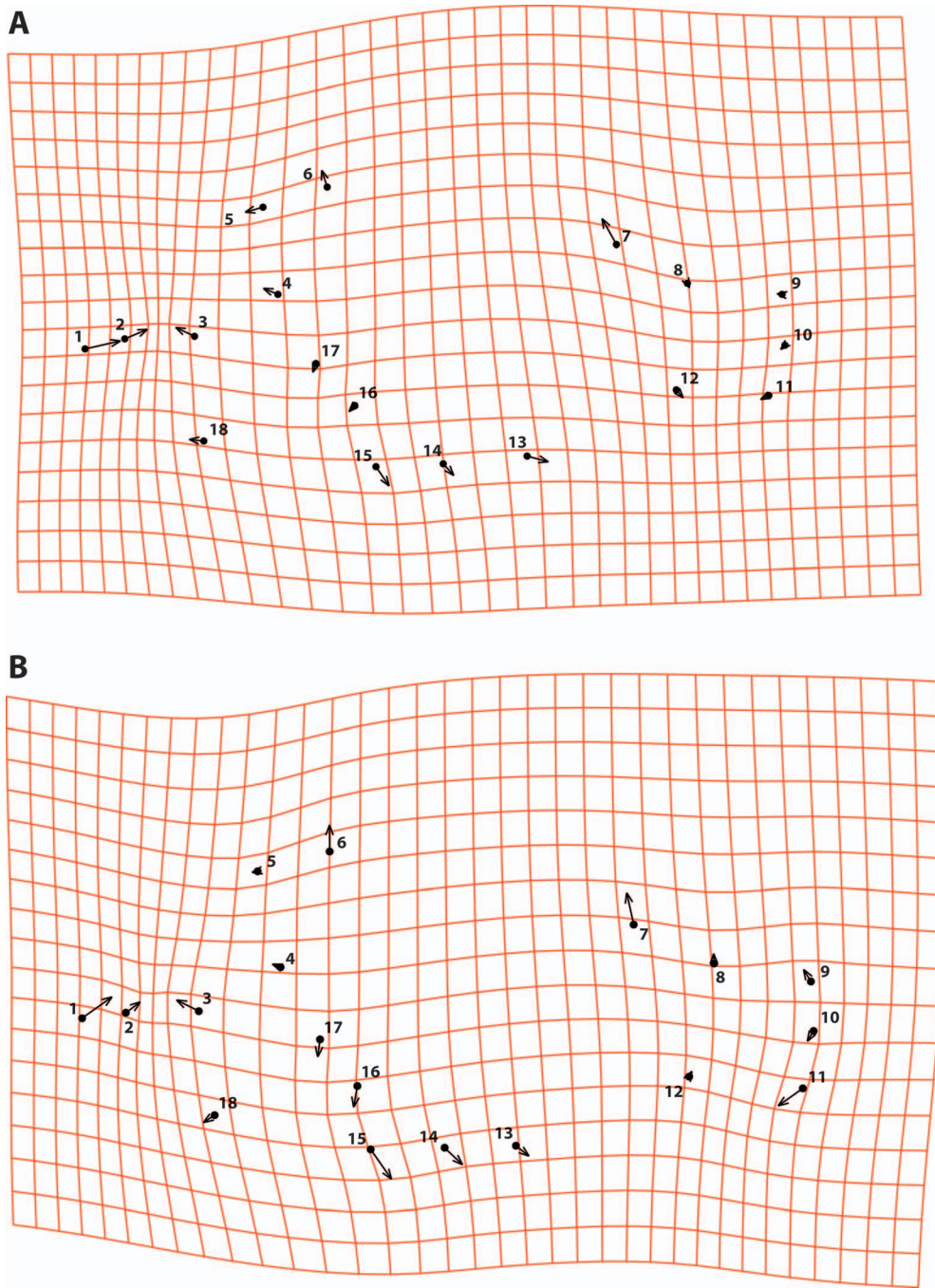|	Average standard length ± SD (mm)	Standard length range (mm)	Average weight ± SD (g)	Weight range (g)
Male ($n = 132$)	87.1±15.0	42.8–126.2	23.0±13.6	1.4–70.2
Female ($n = 140$)	84.5±16.0	40.6–131.5	18.0±12.0	1.7–67.4

Fig. 4. Deformation grids of regression of *H. t. traskii*. These deformation grids depict the shape transformation associated with the regression of shape on centroid size for female (A) and male (B) *H. t. traskii*. Circles on the grid represent the reference body shape for smaller *H. t. traskii* and the vectors demonstrate the direction and relative magnitude of local shape change to the reference body shape of larger *H. t. traskii*.

As previously mentioned, the anal-fin origin was posteriorly shifted in females. In addition to the implication of this finding regarding the placement of the anus in females, it also illustrates that males had a longer anal-fin base. This finding is consistent with studies in oviparous fishes (e.g., Japanese Medaka [*Oryzias latipes*], Koseki et al., 2000; Spotted Barb [*Puntius binotatus*], Dorado et al., 2012; Longnose Gar [*Lepisosteus osseus*], McGrath and Hilton, 2012; Blackstripe Topminnow [*Fundulus notatus*], Welsh et al., 2013; Alligator Gar [*Atractosteus spatula*], McDonald et al., 2013) and has only been documented in one viviparous fish species, Honeycomb Rockfish (*Sebastes umbrosus*; Chen, 1971).

As observed by Phelps (1989), *H. t. traskii* are lek-type breeders. Males hold small display territories, which are defended by posturing, biting, and chasing away other males.

It has been suggested that a longer anal-fin base could increase the success in these activities as a larger fin base increases the surface area displayed to an opponent during antagonistic interactions (Oliveira and Almada, 1995; McGrath and Hilton, 2012). An additional possibility is that a larger anal fin aids in swimming stability and maneuverability (Eklöv and Jonsson, 2007) and could facilitate optimal male–female placement during breeding to maximize fertilization success (Casselman and Schulte-Hostedde, 2004). Because *H. traskii* are internal fertilizers, male positioning during mating is critical to fertilization and reproductive success.

Although it has yet to be documented in a viviparous fish species, the finding that males were wider through the caudal peduncle is consistent with studies on oviparous fishes

(Hood and Heins, 2000; Cadrin and Silva, 2005; McDonald et al., 2013). Based on work completed in *A. spatula*, the authors suggested that a larger caudal peduncle may be beneficial for a competitive male during spawning because it may (1) enhance the ability of a male to distribute milt over egg batches and (2) afford an advantage in accessing eggs during spawning events (McDonald et al., 2013). Although the former benefit may not apply to *H. traskii* given their viviparity, the latter may translate as males compete for access to females during mating events.

Size-related changes in body shape.—In addition to exhibiting sexual dimorphism in body shape, *H. t. traskii* in this study exhibited different body shapes with regard to size. Universal differences included deeper mid-bodies, blunter snouts, and wider caudal peduncles in larger fish. Furthermore, the eyes of smaller fish were much larger relative to their body size than those of larger fish. These findings are consistent with previously documented patterns of ontogenetic change in a variety of fish species (e.g., Reis et al., 1998; Hood and Heins, 2000; Cadrin and Silva, 2005; Hassell et al., 2012). This pattern has been interpreted as a juvenile morphology that emphasizes sensory abilities and feeding systems manifested into a shape determined by the reproductive requirements of adults (Hassell et al., 2012).

Besides allowing room for reproductive structures, deeper bodies also provide a shape more suitable for swimming manueuverability (Webb, 1984). The importance of this with regard to mating has been previously discussed. Additionally, deeper bodies and blunter snouts may increase the chance of escape from predation by piscivorous fishes. Generally, piscivores swallow their prey head first and are limited by prey body depth relative to their mouth width (Eklöv and Jonsson, 2007). Nilsson and Brönmark (2000) found that piscivorous pike preferred more shallow-bodied fishes because deep-bodied prey are more difficult, and require more handling time, to swallow. Furthermore, Eklöv and Jonsson (2007) found juvenile perch that were grown in environments with a pike predator presence had deeper bodies than juveniles in a pike-free environment.

Although age was not investigated in this study, Bryant (1977) demonstrated a well-fit, positive linear relationship between age group and mean standard length in *H. t. traskii*. The work completed by Bryant (1977) and the consistency of the findings in this study with previously completed ontogenetic studies suggest that the documented shape differences may be ontogenetic rather than simply size-related.

Sexual size dimorphism.—*Hysterocarpus t. traskii* in the present study did not exhibit sexual size dimorphism with regard to standard length. This was similar to findings in studies on other internally fertilizing, viviparous fishes (e.g., Bisazza, 1997; Froeschke et al., 2007). For example, Redtail Splitfin (*Xenotoca eiseni*) only exhibit a slight sexual size dimorphism with the average male standard length equaling 91% that of females (Bisazza, 1997). Bisazza (1997) determined that male *X. eiseni* preferred similarly sized mates and that significantly more copulations were successful between similarly sized pairs than mismatched pairs. Additionally, the author noted that in instances where the female was much larger than the male, the male struggled to place his anal fin in the correct position and was too far forward to copulate. It has been

suggested that it is beneficial for males to be similarly sized to their potential mates given the difficulty of achieving internal fertilization underwater (Bisazza, 1997).

Finally, *H. t. traskii* did exhibit sexual size dimorphism with regard to weight; specifically, males were heavier than females. However, this finding may be due to the aforementioned discrepancy in breeding status at the time of collection. Bundy (1970) and Bryant (1977) found testicular enlargement to be the highest during the summer months. Furthermore, a study in another surfperch species, *Micrometrus minimus*, documented that testes actively produce sperm during the mating season, but are inactive during the remainder of the year. During breeding season, gonads comprised an average of 9.4% of a male's body weight, a relatively high gonad weight for vertebrates (Warner and Harlan, 1982). Although this specific metric has not been documented in *H. traskii*, given the phylogenetic relationship (Bernardi and Bucciarelli, 1999) and similar seasonal reproductive cycles between *H. traskii* and *M. minimus*, it is possible that the difference in average weight between male and female *H. traskii* in this study may be partially attributed to the enlarged gonads in males during breeding season.

The findings of sexual size dimorphism presented here conflict with the only other investigation of sexual size dimorphism in *H. traskii*. Phelps (1989) documented that the standard lengths and weights of male *H. t. traskii* were significantly less than those of female *H. t. traskii* and suggested earlier investment in reproduction by males than females was the cause. However, Phelps' (1989) sample was heavily female-biased (75 and 25%) and approximately 90% of the females were pregnant. Additionally, of the 44 males that were included in the analyses, 28 were young-of-the-year that were lab-raised for two months prior to being measured. It is clear that using a sample which ultimately compares heavily pregnant females to young-of-the-year males would produce misleading results of sexual size dimorphism with regard to weight. Additionally, given Bryant (1977) demonstrated a well-fit, positive linear relationship between age group and mean standard length in *H. t. traskii*, it is likely that the sample composition would also produce misleading results of sexual size dimorphism with regard to standard length. Unlike the sample analyzed in this study, the sample analyzed by Phelps (1989) is likely an inaccurate representation of the sizes and/or age classes present in the population of Sacramento–San Joaquin *H. traskii* that was sampled.

Finally, it is important to note that through traditional morphometric analyses, Baltz and Moyle (1981) determined that *H. traskii* differed phenotypically among and, to a lesser extent, within the Sacramento–San Joaquin, Clear Lake, and Russian River drainages. Although there is little genetic divergence among these subspecies, there are significant differences at individual loci that reinforce observations of differences in color frequency and gill-raker morphology (Baltz and Loudenslager, 1984). *Hysterocarpus traskii* vary morphologically, ecologically, and in life history among and within the drainages they inhabit due to selective pressures associated with habitat and prey types and environmental predictability (Baltz and Moyle, 1981, 1982). Given the wide range of variability within the species, further investigation is necessary to determine if this study's specific findings of sexual dimorphism and size-related changes in body shape and sexual size dimorphism are present in the Clear Lake (*H.*

t. lagunae) and Russian River (*H. t. pomo*) subspecies of Tule Perch. However, as viviparity and ontogenesis are universal characteristics of *H. traskii*, it is expected that the broad findings of sexual dimorphism and size-related changes in body shape documented in this study will likely be present in the other subspecies.

This study demonstrates that *H. t. traskii* exhibit differences in body shape with regard to sex and size, despite their monomorphic appearance. *Hysterocarpus t. traskii* in this study did not exhibit sexual size dimorphism in standard length, but did exhibit sexual size dimorphism in weight. This study contributes to the very limited knowledge of a California native fish species and augments the collected works of geometric morphometric studies in viviparous fishes. Although additional investigation of sex-related body shape during peak and quiescent gonad development periods would be necessary for clarification, these findings provide opportunities for future research, which will increase the knowledgebase regarding the influence of ontogeny on the onset and development of dimorphic changes in fishes, as well as the evolutionary biology leading to these differences.

ACKNOWLEDGMENTS

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