

## **The Importance of Functional Morphology for Fishery Conservation and Management: Applications to Hawaiian Amphidromous Fishes**

HEIKO L. SCHOENFUSS

*Department of Biological Sciences, St. Cloud State University,  
St. Cloud, Minnesota 56301, USA; email: hschoenfuss@stcloudstate.edu*

RICHARD W. BLOB

*Department of Biological Sciences, Clemson University,  
Clemson, South Carolina 29634, USA; email: rblob@clemson.edu*

### **Abstract**

The functional capabilities of species can have a strong effect on their ability to maintain sustainable populations in anthropogenically altered environments. This is especially true among species comprising freshwater ichthyofaunas on small oceanic islands, where fishes frequently traverse boundaries between different ecosystems. Many aspects of functional performance in fishes relate directly to morphological features and limitations. In this review, we use the ichthyofauna of the Hawaiian Islands as an example to demonstrate how the habits, habitat, and in-stream distribution of five amphidromous fish species relate to the functional morphology of locomotion and feeding. Furthermore, we evaluate how performance limitations related to functional morphology might affect each species under changing environmental conditions. Based on this analysis we make four key recommendations. (1) Hawaiian stream management plans need to be tailored to island-specific conditions. (2) Estuaries need to be studied as a critical habitat because of the interface between fishes and human populations in these areas. (3) New recruits of *Sicyopterus stimpsoni* might serve as a key indicator species to monitor long-term health of Hawaiian estuaries. (4) The broad use of the Index of Biological Integrity (IBI) to assess Hawaiian stream health needs to be critically evaluated.

### **Introduction**

Successful conservation and management of ichthyofaunas relies on the integration of ecological, economic, political, and sociocultural information as plans of action are developed (Krueger & Decker, 1993; Wolter, 2001; Arlinghaus *et al.*, 2002). The ecological context for management and conservation decisions includes both abiotic and biotic components. Measurement and analysis of many of these factors, such as flow rates, sediment loads, nutrient state, and fish density, can be performed by natural resource managers based on field data or laboratory chemical techniques. However, an additional, critical biotic component of the ecological context for ichthyological conservation and management that can require distinctly different analytical methods is the functional morphology of fish species. Studies of functional morphology, the functional analysis of structural features (i.e., anatomy) of animals (Schwenk, 2000), can provide tremendous insight into how fishes perform the behaviors that allow them to survive, and how the performance of a species might be impeded when environmental parameters are altered. Morphology can be one of the most critical factors affecting the performance of an individual, which in turn can determine its survival and fitness (Arnold, 1983, 2003; Irschick, 2003). Because constraints on function related to species morphology have the potential to result in dramatic performance failure of a species, especially after anthropogenic alterations to the environment (Holland, 1986; Wolter, 2001; Wolter & Arlinghaus, 2003), it is critical to consider the functional morphology of fish species as an important biotic factor during the process of making conservation and management decisions.

The performance of a wide range of behaviors can be considered in studies of functional morphology, but two that are generally considered among the most critical for fishes are locomotion and

feeding (Webb, 1984; Wainwright *et al.*, 2002; Walker, 2000; Fulton *et al.*, 2001; Domenici, 2003; Ferry-Graham & Wainwright, 2003; Westneat, 2004). Locomotion is critical for fishes because they must move to obtain the food they need as well as other resources, such as mates and shelter; feeding is critical because of the need to obtain nutrients to survive. A lack of knowledge about the functional morphology of either of these behaviors could impede management efforts and lead to erroneous conclusions about the quality of a stream habitat when fish diversity is used as part of an Index of Biological Integrity (IBI) (Novotny *et al.*, 2005). Such gaps in knowledge are a particular concern for ichthyological systems that span multiple habitats. Many fish species inhabit a range of different habitats, either seasonally or during ontogeny (Azevedo & Simas, 2000; Keith, 2003), and such species could be at risk from anthropogenic habitat changes in any of the environments they inhabit or traverse. The multi-habitat amphidromous fishes of the Hawaiian Islands provide an excellent example of how knowledge of fish functional morphology can provide informed decisions in stream management. This paper will provide a critical review of the application of functional morphological data to the conservation and management of Hawaiian stream fishes.

Only five indigenous species of fishes live as adults in Hawaiian streams (McDowall, 2003, 2004). This low species diversity is likely a result of the geographic isolation of these islands and their recent volcanic origin (far away from continental shelves that possess diverse and abundant fish communities). All five species belong to the mostly oceanic Gobiidae or Eleotridae. All undergo an extended oceanic larval phase (3–6 months) before undertaking amphidromic migrations into adult stream habitats (Radtke *et al.*, 1988; Radtke & Kinzie, 1991), and three of the five species climb waterfalls during instream migrations to adult habitats and spawning grounds (Nishimoto & Fitzsimons, 1999; Schoenfuss & Blob, 2003). Despite the intensive physiological and energetic demands of vertical climbing over long distances, fishes with similar lifestyles and locomotory abilities have been described from other Pacific islands such as Guam (Fitzsimons *et al.*, 2002), Pohnpei and Palau (Nelson *et al.*, 1997), Reunion (Voegtli *et al.*, 2002), and Japan (Fukui, 1979). Moreover, Hawaiian streams are similar in many respects to streams on other volcanic islands. These similarities include abiotic factors, such as small watersheds with brief retention times that are fed by periodic rain-storms with subsequent cyclic patterns of extremely high and low velocity flows (Juvik & Juvik, 1998; Fitzsimons *et al.*, 2002). Common biotic features of streams on volcanic islands include limited species diversity when compared to continental streams of comparable latitude, low nutrient loads, and a fish fauna comprised largely of migratory species that spend part of their life cycle in the oceanic or near-shore environment (Nelson *et al.*, 1997; Fitzsimons *et al.*, 2002). As a result, applications of functional morphology in the conservation and management of Hawaiian taxa might serve as an example for fisheries managers on many oceanic islands. Thus, in addition to highlighting the importance of functional morphological data for the management and conservation of Hawaiian stream fishes, a broader goal of this review is to provide a model for the application of functional morphology as a tool in stream fish management on other volcanic island systems.

In this review, we will examine functional morphology across life history stages for all five native Hawaiian freshwater fishes by synthesizing published information, as well as new data, to identify critical aspects of functional performance for each species. We will then describe how knowledge of functional morphology might influence the decision making process in managing Hawaii's ichthyofauna. Finally, we will outline future research needs with respect to the Hawaiian freshwater and estuarine ichthyofauna.

### **Functional morphology and natural history of Hawaiian stream fishes: Background for species management**

#### **General Observations**

All five species of native Hawaiian stream fishes belong to the superfamily Gobiodea (Pezold, 1993) and fall within two distinct, broadly recognized groups: the family Eleotridae, which contains *Eleotris sandwicensis*, and the subfamily Sicydiinae (Pezold, 1993) or *Sicydium* group (Birdsong *et*

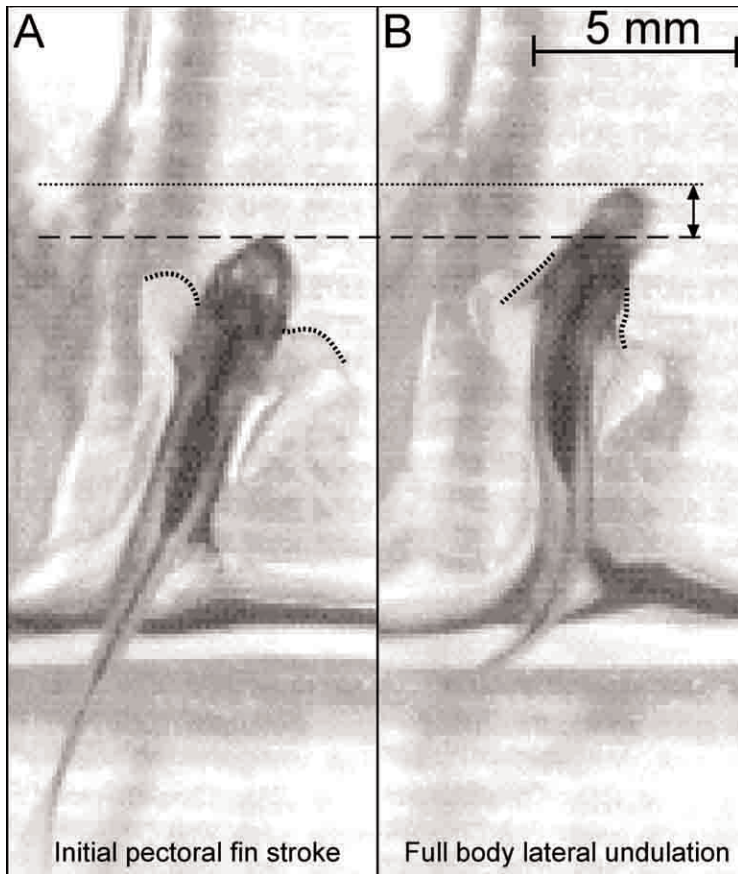
**Table 1. Comparison of life history traits of five amphidromous Hawaiian gobies.**

|                  | <i>Eleotris sandwicensis</i> | <i>Stenogobius hawaiiensis</i> | <i>Awaous guamensis</i>      | <i>Sicyopterus stimpsoni</i> | <i>Lentipes concolor</i> |
|------------------|------------------------------|--------------------------------|------------------------------|------------------------------|--------------------------|
| Oceanic phase    | 3–5 months                   | 3–5 months                     | 3–5 months                   | 6 months                     | 3–5 months               |
| Larval diet      | planktivore                  | planktivore                    | planktivore                  | planktivore                  | planktivore              |
| Recruit size*    | 13.5 mm                      | 14.1 mm                        | 16 mm                        | 23.6 mm                      | 14.5 mm                  |
| Adult diet       | carnivore                    | detritus feeder                | omnivore                     | herbivore                    | algivore & insectivore   |
| Adult size*      | 130 mm                       | 40–50 mm                       | 140 mm                       | 75 mm                        | 67 mm                    |
| Climbing ability | none                         | none                           | weak                         | good                         | excellent                |
| Station holding  | weak                         | weak                           | larvae: good<br>adults: weak | good                         | excellent                |
| Adult habitat    | estuary                      | estuary                        | low/mid-stream               | mid-stream                   | upper-stream             |

\*Mean standard length.

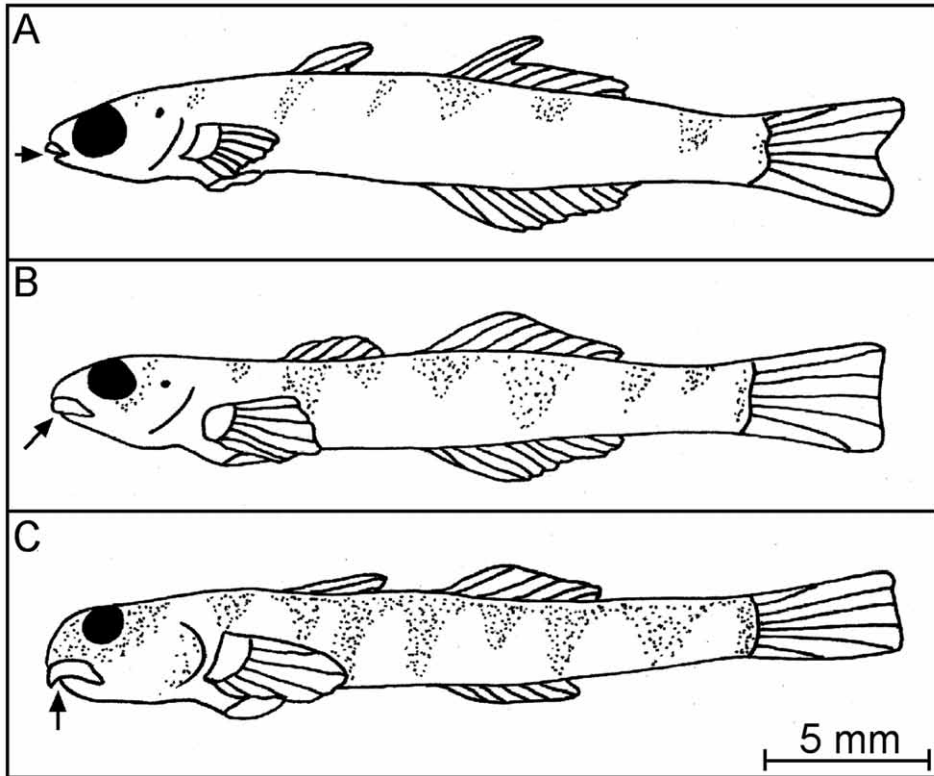
**Table 2. Climbing speed (cm/sec; mean ± standard error) for larvae of *Awaous guamensis* and *Lentipes concolor* on three substrates of increasing coarseness (modified after Blob *et al.*, 2006).**

| Substrate      | <i>Awaous guamensis</i> |                | <i>Lentipes concolor</i> |                |
|----------------|-------------------------|----------------|--------------------------|----------------|
|                | n                       | climbing speed | n                        | climbing speed |
| Smooth         | 12                      | 0.068 ± 0.0041 | 8                        | 0.59 ± 0.024   |
| Fine grained   | 12                      | 0.21 ± 0.028   | 17                       | 0.82 ± 0.084   |
| Coarse grained | 12                      | 0.71 ± 0.22    | 10                       | 1.2 ± 0.27     |



**Figure 1.** “Powerburst” climbing style common to juvenile *Awaous guamensis* and *Lentipes concolor* as recorded on a nearly vertical sheet of Plexiglas. **A:** Fish attached to the substrate via the pelvic suction disc. Pectoral fins (accentuated by dotted line) are outstretched in advance of a rapid adduction that begins the locomotory bout. **B:** The fish advances through rapid axial undulations of the entire body after rapid pectoral fin adduction. Arrow indicates the total advancement a fish makes during one climbing cycle. Adapted from Schoenfuss & Blob (2003).

*al.*, 1988) which contains the remaining four species (*Stenogobius hawaiiensis*, *Awaous guamensis*, *Sicyopterus stimpsoni*, and *Lentipes concolor*). The close relationship of these four species has been confirmed in several recent studies using both molecular (Thacker, 2002) and morphological analyses of phylogeny (Parenti & Thomas, 1998). All 5 species share an amphidromous life cycle that includes a larval oceanic period of approximately 6 months for *S. stimpsoni* and approximately 3–5 months for the remaining four species (Table 1) (Radtke *et al.*, 1988; Radtke & Kinzie, 1991). All five species are likely pelagic during their oceanic phase, and the terminal position of the mouth in the oceanic larvae of these species indicates their reliance on a planktonic diet. A pelagic larval phase is also consistent with the ontogeny of related oceanic gobioid species (Privitera, 2002; Keith, 2003). Although several studies have suggested that larvae from a single source can be distributed among multiple streams (Schoenfuss *et al.*, 2004) and even multiple islands (Zink, 1991; Zink *et al.*, 1996; Chubb *et al.*, 1998), most larvae likely remain close to the stream from which they were washed out shortly after hatching (Keith, 2003; Taylor & Hellberg, 2003). For at least one Hawaiian species, *S. stimpsoni*, the gut contents of larvae entering stream mouths indicate a near-shore food source dur-



**Figure 2.** Anatomical changes in larval *Sicyopterus stimpsoni* entering the freshwater system (arrow in each drawing indicates mouth position). **A:** Incoming recruit captured at the stream mouth; **B:** Larvae in fresh water for 16 h; **C:** Juvenile *Sicyopterus stimpsoni* 36 hours after entering freshwater and now able to climb small vertical barriers.

ing the days prior to their arrival in the stream (Julius *et al.*, 2005). There is little evidence from the available literature, or personal observations, that the larval oceanic development of the five Hawaiian species differs from that of most other near-shore oceanic gobies (Azevedo & Simas, 2000; Munday *et al.*, 2002; Privitera, 2002; Keith, 2003). However, the in-stream development of these five species is quite distinctive among gobioid fishes.

#### *Eleotris sandwicensis* ('o'opu 'akupa)

The only piscivore among native Hawaiian amphidromous fishes, *E. sandwicensis* lack fused pelvic fins and are unable to climb vertical obstacles in Hawaiian freshwater streams (Nishimoto & Kuamo'o, 1997). The poor station holding ability of these fish (Fitzsimons *et al.*, 1997) and their tendency to hide on pebbled portions of the stream bottom as an ambush predator also limit their range to stream estuaries. *Eleotris sandwicensis* appear to be poor continuous swimmers, with larvae relying on tides and wave action to be moved into the stream (Tate, 1997), and adults largely limited to short bursts of swimming to capture prey. Gut contents of *E. sandwicensis* include a mixture of animal and plant material (Kido, 1996b), but much of the plant material might enter the digestive tract as "by-catch" with the captured larvae of other Hawaiian amphidromous fishes. Although this species grows to a substantial size that is only rivaled by *A. guamensis* in the Hawaiian freshwater system, its station holding ability does not seem to change throughout its life and is the lowest among all native Hawaiian stream fishes (Table 1) (Fitzsimons *et al.*, 1997).

***Stenogobius hawaiiensis* ('o'opu naniha)**

Although *S. hawaiiensis* share an amphidromous life cycle with the three species of Hawaiian climbing gobies, a weak pelvic suction disc precludes them from climbing and effectively limits their range to the estuaries (Nishimoto & Kuamo'o, 1997). In addition, the limited station holding ability of *S. hawaiiensis* (Table 1) (Fitzsimons *et al.*, 1997) likely prevents movement into swifter upstream currents even in those Hawaiian streams not obstructed by waterfalls. These fish use their fused row of teeth in the upper jaw and conical teeth in the lower jaw to acquire small quantities of sand and mud from the stream bottom (see review: Kido, 1996b). Digestible items then are filtered out of ingested sediment by the well-developed gill-arch sieve (Kido, 1996b). The anatomy of this species appears to approximate the generalized gobioid "bauplan" described by Birdsong (1975), but its biology has generally received less study than that of other Hawaiian stream fishes.

***Awaous guamensis* ('o'opu nākea)**

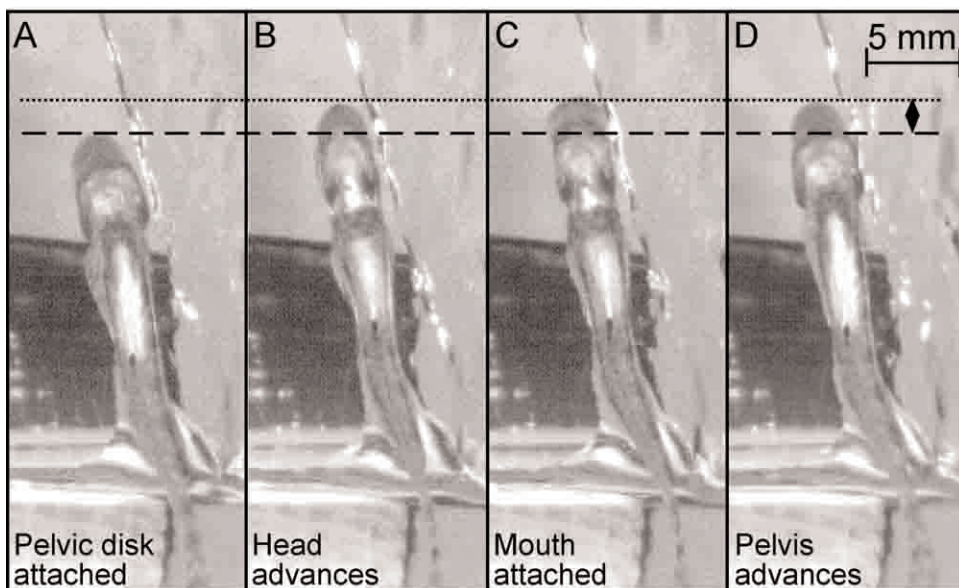
*Awaous guamensis* is the only nonendemic Hawaiian freshwater fish and has been found across Micronesia (Fitzsimons *et al.*, 2002). In contrast to *E. sandwicensis* and *S. hawaiiensis*, *A. guamensis* is able to climb obstacles during its return migration from the ocean into freshwater habitats (Nishimoto & Fitzsimons, 1999; Schoenfuss & Blob, 2003). However, in comparison to other climbing species of Hawaiian gobies (*S. stimpsoni* and *L. concolor*), *A. guamensis* has the poorest station holding ability (Fitzsimons *et al.*, 1997) and its upstream range usually falls short of that of either of the other climbing species (Fitzsimons & Nishimoto, 1991). The larval development of *A. guamensis* mirrors that of *L. concolor*, and migrating larvae of the former are usually only slightly larger than those of the latter (Table 1) (Nishimoto & Kuamo'o, 1997).

To climb obstacles in streams, juvenile *A. guamensis* employ a technique known as "powerburst" climbing (a strategy that is also used by larval *L. concolor*) (Schoenfuss & Blob, 2003). While attached to a vertical substrate, *Awaous guamensis* begin bouts of powerburst climbing with a single, rapid adduction of the outstretched pectoral fins (Fig. 1A). However, most of the climbing bout is powered by undulating the entire long axis of the body to propel the fish against the falling water of a waterfall (Fig. 1B). Because this locomotory style is quite rapid, it is likely powered mainly by fast-twitch (white) muscle fibers. This climbing style may be energetically expensive, but it allows immediate mobility of the larvae out of the predator-rich estuaries (Schoenfuss & Blob, 2003). However, *A. guamensis* consistently performed below the levels of the other powerburst climber, *L. concolor*, when climbing performance was measured over approximately 20 body lengths on an artificial waterfall (Table 2) (Blob *et al.*, 2006).

Among the five species of native Hawaiian stream fishes, *A. guamensis* undergo the most significant change in body shape during juvenile growth (*S. stimpsoni* undergo a substantial metamorphosis, but this occurs at the end of the larval period and is not associated with an overall change in body shape). During growth, *A. guamensis* become significantly larger than either of the other two species of climbing Hawaiian gobies, and their shape becomes considerably more plump and robust. As a result, fluid dynamic drag is likely to increase substantially (Vogel, 1994) and probably contributes to the dramatic decrease in the ability of *A. guamensis* to hold station as they grow larger than approximately 50 mm (Fitzsimons *et al.*, 1997). Both juveniles and adults of *A. guamensis* remain in lower stream reaches and adults do not appear to climb (Blob *et al.*, in press). Adults and juveniles both feed primarily on filamentous algae harvested together with its epiphytes through a biting action of the jaws (Steinmann, 1996; Schoenfuss, pers. observ.).

***Sicyopterus stimpsoni* ('o'opu nōpili)**

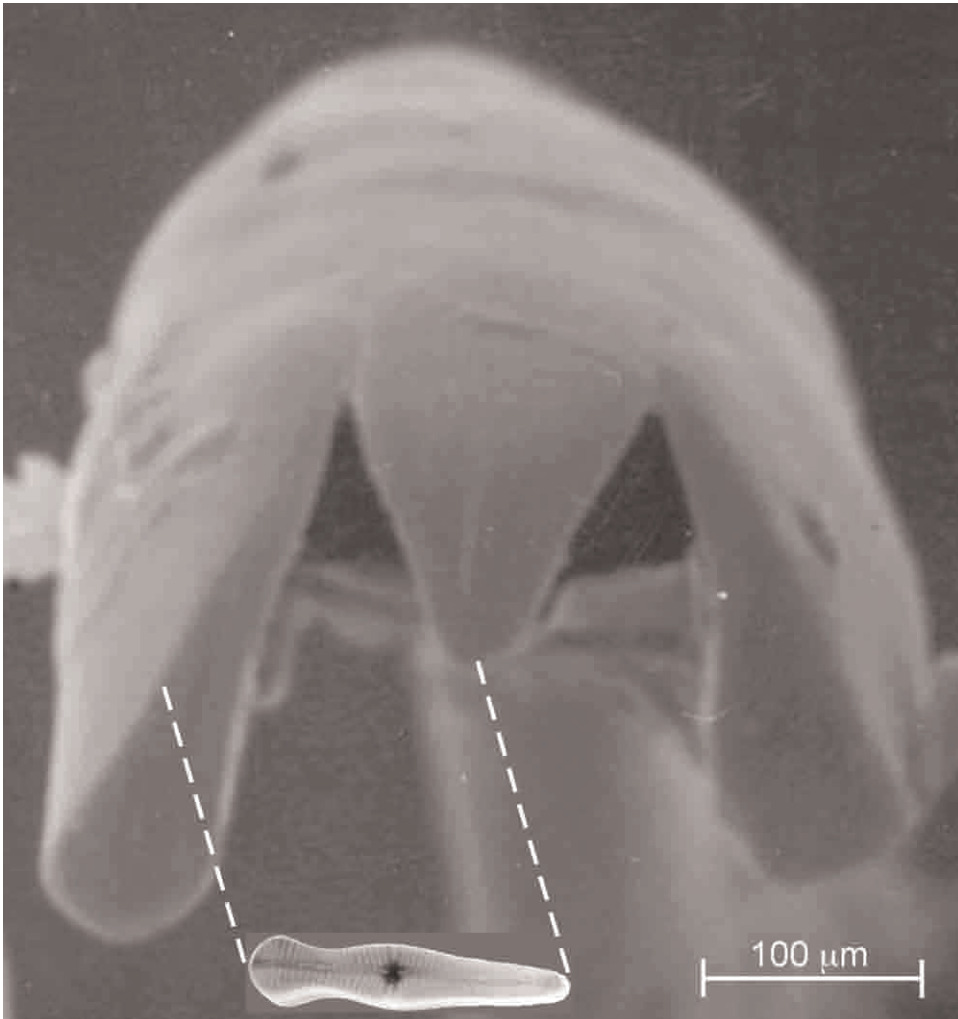
*Sicyopterus stimpsoni* is unique among Hawaiian amphidromous fishes in that it undergoes a dramatic metamorphic transformation prior to gaining the ability to climb and reach its adult mid-stream habitats. The early development and larval anatomy of *S. stimpsoni* mirror that of the other Hawaiian stream fishes and, indeed, most gobioid fishes (Fig. 2A). However, oceanic larval development lasts up to 180 days for *S. stimpsoni* (Radtko *et al.*, 1988; Radtko & Kinzie, 1991), substantially longer than for the other species of Hawaiian amphidromous fishes. As a consequence, recruits



**Figure 3.** “Inching-up” climbing style of *Sicyopterus stimpsoni* as recorded on a nearly vertical sheet of Plexiglas. **A:** fish attached to the substrate via the pelvic suction disc; **B:** the head of the fish advances and the mouth makes contact with the surface; **C:** the mouth of the fish seals against the substrate to anchor the animal; **D:** the pelvic and post-pelvic structures advance. Diamond in Figure 3D indicates the total advancement a fish makes during one climbing cycle. Adapted from Schoenfuss & Blob (2003).

of *S. stimpsoni* returning into the stream system (Fig. 2B) are about 1.5 times the length and 2–3 times the weight of the other four species (Nishimoto & Kuamo’o, 1997; Schoenfuss & Blob, 2003); moreover, *S. stimpsoni* recruits are able to actively swim through the stream mouth even with its high currents (Tate, 1997). Once in fresh water, larvae of *S. stimpsoni* are initially confined to the estuaries as their larval anatomy precludes climbing. While confined to the estuary, *S. stimpsoni* larvae are exposed to significant predatory pressure from estuarine species like *E. sandwicensis* as well as marine fish species that frequently invade the estuary (e.g., *Kuhlia xenura*). However, within 36–48 h of entering the freshwater environment, *S. stimpsoni* larvae undergo a dramatic metamorphosis during which the mouth shifts from its larval, terminal position to its adult sub-ventral position as the upper lip greatly increases in size (Schoenfuss *et al.*, 1997). After this metamorphosis (Fig. 2C), *S. stimpsoni* juveniles are able to climb waterfalls up to 100 m tall and will quickly move upstream into their adult habitats. This shift and re-structuring of the cranium of *S. stimpsoni* comprises one of the most dramatic rapid metamorphic events among all vertebrates. However, the metamorphosis is also an extremely expensive process energetically: *S. stimpsoni* larvae lose approximately 15% body weight during its 36–48-h progression (Schoenfuss *et al.*, 1997). The demands of the metamorphic transformation, as well as the energy-depleted state of the animal following the transformation, make *S. stimpsoni* particularly vulnerable to adverse environmental effects.

Waterfall climbing in *S. stimpsoni* differs markedly in style from *L. concolor* and *A. guamensis*. The changes in mouth structure during metamorphosis allow *S. stimpsoni* juveniles to use their mouth as a second suction disc during climbing. *Sicyopterus stimpsoni* climb by using an “inching-up” climbing technique where they alternately attach themselves to the rock surface with the mouth or their pelvic suction disc (Fig. 3A–D) (Schoenfuss & Blob, 2003). By using this climbing style, fish remain constantly attached to the surface of the waterfall and avoid the need for energetically costly bursts of swimming against falling water. In addition, the slow speed of motion during inch-



**Figure 4.** Scanning electron micrograph of a tri-cuspid tooth of *Sicyopterus stimpsoni* and of the diatom *Gomphonema truncatum* commonly found in the digestive tract of *Sicyopterus stimpsoni*. The diatom is illustrated at the same magnification as the fish tooth and positioned to demonstrate the similarity in diatom width and distance between the cusps of the tooth shown.

ing climbing suggests that it may be possible for *S. stimpsoni* to power climb by primarily using slow oxidative (red) muscle fibers and aerobic metabolism, preventing fatigue (Schoenfuss & Blob, 2003). The evolution of this distinctive juvenile climbing style in *S. stimpsoni* [and potentially other species of *Sicyopterus*, e.g., *S. japonicus*—Fukui (1979)] may have been correlated with the increased energetic cost associated with moving against falling water in juveniles with a greater body mass than that of other species of climbing gobies (e.g., Hawaiian *A. guamensis* and *L. concolor*). Because post-metamorphosed *S. stimpsoni* have already greatly depleted energy reserves prior to climbing (Schoenfuss *et al.*, 1997), aerobic “inching-up” might be the only energetically feasible mode of climbing that juvenile *S. stimpsoni* can use to overcome in-stream obstacles like waterfalls (Schoenfuss & Blob, 2003).



The metamorphosis of *S. stimpsoni* also signals a change in diet for this species. The sub-ventral mouth position of *S. stimpsoni* allows feeding on short-stalk diatoms. With the streamlined body of *S. stimpsoni* oriented parallel to flow, it is possible for these fish to feed even in high velocity currents. Diatoms are scraped off rock surfaces by cyclically raking rows of tricuspid premaxillary (upper jaw) teeth over the substrate (Schoenfuss, 1997). The two lateral cusps of the upper-jaw teeth in *S. stimpsoni* are slightly longer than the median cusp (Kido, 1996b) and all three cusps form an anterior semi-circle around the hollow crown of each tooth (Fig. 4). The distance between the central and each lateral cusp closely matches the size of the diatoms that comprise the main dietary resource for *S. stimpsoni* [Fig. 4; see also Julius *et al.* (2005)]. These teeth are continuously replaced from several rows of teeth located superior to the active row (T. Maie, pers. comm.). The unique feeding apparatus of *S. stimpsoni* allows this species to monopolize short-stalk diatoms as a high quality food source that is unavailable to other Hawaiian freshwater fishes in which jaw morphology seems to impede close contact between the teeth and the surfaces of feeding rocks. The unusual jaw structure of *S. stimpsoni* may also be related to an unusual behavior in this species: the guarding and “gardening” of feeding rocks by adult fishes (Fitzsimons *et al.*, 2003). The repeated grazing of feeding rocks as well as the location of feeding rocks in the highest stream currents will delay the growth of longer-stalked and filamentous algae that can block access to the low stalked diatoms that comprise most of the diet of *S. stimpsoni* (Julius *et al.*, 2005). These longer-stalked and filamentous algae grow over a 4- to 6-week period following high flow events on most rock surfaces in Hawaiian streams (Julius *et al.*, 2005). It is noteworthy that peak in-stream migration of oceanic larvae into Hawaiian freshwater streams occurs after storms (Nishimoto & Kuamo’o, 1997) that result in increased stream flow and a removal of filamentous algae from potential feeding surfaces (Julius *et al.*, in review). These events may expand the available surfaces for growth of short-stalked diatoms to non-guarded small rocks and pebbles in lower current areas of the stream, as well as provide areas for migrating juveniles to feed.

Once in its adult lower- to mid-stream habitats, *S. stimpsoni* maintain their exclusively herbivorous diet, retain a highly convoluted gut, and continuously replace worn teeth in the upper jaw (Kido, 1996b). Adult *S. stimpsoni* will readily climb to avoid perceived danger (Schoenfuss, pers. obs.). Adult *S. stimpsoni* climb by using the inching mechanism employed by juveniles, though studies of high speed video footage suggest that adults also incorporate pectoral fin adduction into each climbing cycle to increase propulsive thrust (Blob *et al.*, in press.).

#### ***Lentipes concolor* (‘o‘opu ‘alamo‘o)**

*Lentipes concolor* inhabit the highest reaches of Hawaiian freshwater streams (Englund & Filbert, 1997; Nishimoto & Fitzsimons, 1999) and frequently are the sole vertebrate inhabitants of these stream reaches. This species also exhibits the greatest station-holding ability among Hawaiian freshwater fishes (Table 1) (Fitzsimons *et al.*, 1997). Similar to the other two species of climbing Hawaiian amphidromous gobies, the life cycle of *L. concolor* is marked by amphidromous migrations before reaching maturity. *Lentipes concolor* return into streams after an oceanic larval period that is likely similar in duration (Radtke *et al.*, 1988) to that of the closely related *A. guamensis* (Parenti & Thomas, 1998). Significantly smaller than *S. stimpsoni*, migrating larvae of *L. concolor* rely on wave action and high tides to be swept into the estuaries of Hawaiian streams (Tate, 1997). Larvae traverse estuaries quickly and immediately climb if they encounter waterfalls or other vertical in-stream barriers. Like *A. guamensis*, *L. concolor* rely on the “powerburst” style of climbing to scale in-stream barriers (Schoenfuss & Blob, 2003). Little is known about the up-stream migration of *L. concolor* except that juveniles of different size classes are sometimes encountered climbing waterfalls along the way to known adult habitats (Yamamoto & Tagawa, 2000). Size distribution of *L. concolor* within adult habitats ranges from newly arrived fish weighing little more than 1g to adults large enough to suggest residence for several years (Fitzsimons & Nishimoto, 1990).

*Lentipes concolor* retain a torpedo-shaped body throughout life and will climb if threatened or displaced. However, *L. concolor*, which are powerburst climbers as juveniles, appear to dramatical-

ly alter their locomotory mechanics to climb as adults. High-speed footage indicates that climbing adult *L. concolor* greatly reduce axial undulation compared to juveniles, propelling themselves with pectoral fin adduction during each climbing cycle and producing climbing kinematics that strongly resemble those of adult *S. stimpsoni* (Blob *et al.*, in press.; Yamamoto & Tagawa, 2000).

Unlike *S. stimpsoni*, adult *L. concolor* exhibit significant dietary breadth. A large portion of the gut contents of *L. concolor* consists of insects, and the teeth in the upper jaw of *L. concolor* are conical (Kido, 1996b), similar to those of insectivorous fish species. However, other components of gut contents in *L. concolor* consist of a variety of items that are picked out of the water column as they float by in the stream. To catch floating food, *L. concolor* rises from a resting location on the bottom of a pool and quickly engulfs the food item. Rapid capture of floating food appears to be facilitated by the lever mechanics of the jaw skeleton in this species. A preliminary sample of measurements of jaw mechanical advantage (ratio of the lever arm for jaw adductor A2 to the distance from the jaw joint to the jaw tip: Westneat, 2003) indicates that the jaws of *L. concolor* have the lowest mechanical advantage of any Hawaiian goby and, thus, have the best advantage for rapid (as opposed to forceful) closing (Maie *et al.*, in prep.).

### **Discussion: How Functional Morphology Can Inform Efforts to Manage and Conserve Hawaiian Streams**

As noted in the Introduction, functional morphological analyses can provide valuable information for species conservation and management efforts. Our discussion in reference to Hawaiian stream fishes will focus on the functional performance of two major categories of behavior, locomotion and feeding.

#### **Locomotion**

Many studies in fishery research have examined the swimming performance of fishes as it relates to species management (e.g., under varying flow regimes or differing exposure to environmental contaminants: see Hammer, 1995; Wolter & Arlinghaus, 2003 and references therein). Very little is known about the swimming performance of Hawaiian stream fishes (or other closely related species: e.g., Todd, 1975; Bell & Brown, 1995), and this aspect of functional morphology represents an important area for future investigation. However, the importance of climbing locomotion in the life history of some Hawaiian stream fishes (as well as several stream fishes on other oceanic islands) is well known and has received recent study (Schoenfuss & Blob, 2003; Blob *et al.*, 2006). The significance of climbing as an aspect of locomotory functional morphology introduces a variety of factors that must be considered for effective management and conservation of these species.

Differences in locomotory performance among fish species, particularly in their ability to scale vertical barriers, can strongly affect the diversity of fishes found throughout a stream. Vertical barriers, both natural and man-made, are found in many Hawaiian freshwater streams; because of differences in climbing ability among species, such barriers limit the upstream diversity of fishes in a predictable fashion. Modest barriers of only a few feet are sufficient to preclude non-climbing species (*E. sandwicensis* and *S. hawaiiensis*) from stream reaches upstream from a barrier. If a barrier (a waterfall or man-made structure) exceeds several meters in height, it typically will also exclude *A. guamensis* from upstream reaches for two reasons. First, juvenile *A. guamensis* use energetically demanding powerburst climbing (Schoenfuss & Blob, 2003) but climb more slowly than the other powerburst climbing species, *L. concolor* (Table 2) (Blob *et al.*, 2006). This may limit the height of barriers that this species can scale and, thereby, limit its penetration into upstream habitats. Second, *A. guamensis* have the lowest ability to hold station among Hawaiian climbing gobies (Fitzsimons *et al.*, 1997) and do not appear capable of climbing vertical barriers as adults (Blob *et al.*, in press). Thus, in contrast to *S. stimpsoni* and *L. concolor*, which retain the ability to climb as adults (Blob *et al.*, in press), adult *A. guamensis* appear to be the climbing species most likely to be swept downstream and the least able to re-penetrate habitats above barriers. Because of the function-

al limitations that barriers place on the distribution of fish species in Hawaiian streams, stream surveys need to consider the potential influence of barriers when evaluating ichthyofaunal diversity. The increased use of Indices of Biological Integrity (IBI) in stream quality assessment, for example, might erroneously reduce the value of a stream where physical barriers exclude fish species as described above.

Differences in locomotory functional morphology among Hawaiian amphidromous species also can be correlated with differences in the ability of these species to climb barriers with specific physical characteristics. Our work has shown that the roughness of a barrier surface affects the climbing performance of juvenile powerburst climbers, but not the performance of the juvenile inching climber *S. stimpsoni* (Table 2) (Blob *et al.*, 2006). Over the range of surface textures that we tested (smooth to coarse sand, up to an average grain size of 1206  $\mu\text{m}$ ), increases in surface roughness did not affect climbing speed in juvenile *S. stimpsoni*, but significantly improved the climbing speed of powerburst climbing species. We believe that this pattern of performance occurs because rougher surfaces allow juvenile powerburst climbers to gain better purchase on the substrate with their pectoral fins and, thus, prevent slippage (and loss of propulsive force) during the initial rapid fin adduction at the onset of climbing bouts (Blob *et al.*, 2006). In contrast, juvenile inching climbers do not experience such effects because they do not use their pectoral fins during climbing (Schoenfuss & Blob, 2003). Surface textures of obstacles could be selected to facilitate or improve the likelihood of climbing success among powerburst climbing juveniles. Decisions about construction materials for in-stream structures should be made with an awareness of such potential long-term effects on the locomotory performance and recruitment of stream fishes.

Available data on the functional morphology of locomotion in juvenile Hawaiian stream fishes suggest several possible effects of in-stream barriers on these species, but barriers also have the potential to affect adult fishes in Hawaiian streams. Although adult locomotion has received less study than that of juveniles, our work suggests that in-stream barriers might become insurmountable as fish grow in size (Maie *et al.*, in press). For example, *A. guamensis* appear to lose the ability to climb as adults (Blob *et al.*, in press), potentially because their great increase in mass and shift to a plumper body shape during growth leads to an increase in fluid dynamic drag (Vogel, 1994) that powerburst climbing mechanisms cannot overcome. This possibility is further suggested by observations indicating that neither Hawaiian fish species that retains climbing ability into adulthood appears to use juvenile powerburst climbing mechanisms (Blob *et al.*, in press). Adult *S. stimpsoni* climb using the inching mechanism employed by juveniles, though adults may also incorporate pectoral fin adduction into each climbing cycle and add propulsive thrust (Blob *et al.*, in press). In addition, our data indicate that *L. concolor*, which is a powerburst climber as a juvenile, dramatically alters climbing as an adult by reducing axial undulation in comparison to juveniles, adding pectoral fin adduction during each climbing cycle, and producing climbing kinematics that resemble those of adult *S. stimpsoni* (Blob *et al.*, in press). The incorporation of pectoral fin adduction into adult climbing by both *S. stimpsoni* and *L. concolor* indicates that the surface roughness of stream barriers could affect climbing success in adults of both of these species, much as it does in juvenile powerburst climbers that use the pectoral fins to initiate climbing bouts (Blob *et al.*, 2006).

The functional morphology of locomotion in Hawaiian stream fishes is relevant not only to how these species respond to stream structures that might present barriers to climbing, but also to how they are likely to respond to changes in stream flow patterns. Hawaiian streams exhibit considerable natural variation in flow: sudden, violent rains and flash floods can quickly and dramatically increase flow rates, volume, and turbidity (Fitzsimons & Nishimoto, 1995). However, flow patterns can also be altered anthropogenically, as stream water diversion for agriculture or development can drastically reduce flow volumes. The three climbing species of Hawaiian gobies show excellent ability to hold station against high velocity flows of 70 cm/sec or more (Fitzsimons *et al.*, 1997). Such flows remove parasite-bearing exotic species, which are often introduced into streams but, without pelvic sucking discs, cannot withstand intense stream flow (Fitzsimons *et al.*, 1997). As a result, allowance for periodic high velocity flows appears to be a critical issue for stream management in order to remove exotic sources of parasites and promote the health of native Hawaiian stream fishes. In addi-

tion, high flow regimes and frequent flash floods limit the instream range of the piscivores *E. sandwicensis* and *Kuhlia xenura* in streams without vertical obstacles. As a result, patterns of stream flow and frequency of flash floods should affect amphidromous fishes differently on islands with frequent vertical barriers (i.e., Hawai'i) than on islands with larger river systems (i.e., Kaua'i).

### Feeding

The dramatic performance of several Hawaiian stream fishes makes the importance of locomotory functional morphology readily apparent for conservation efforts. However, recent data have shown that the functional morphology of feeding also can exert considerable influence on the in-stream distribution of Hawaiian stream fishes and, thus, should be considered as management and conservation strategies are developed for these species.

One of the most direct ways in which the significance of feeding functional morphology is evident in Hawaiian stream fishes involves predation on the four species of larval gobies. The estuaries of Hawaiian freshwater streams are frequented by several piscivorous predators, including the marine *āholehole* *K. xenura* and the amphidromous eleotrid *E. sandwicensis*. Data from Tate (1997) suggest that *E. sandwicensis* in particular are highly effective predators that have the potential to exert substantial selective pressure on migrating larvae. On the Island of Hawai'i, where estuaries are short before waterfalls exclude predaceous *E. sandwicensis* from upstream habitats, *A. guamensis* and *L. concolor* might not experience substantial selection due to predation as these powerburst climbing species typically climb out of the estuary very quickly (Tate, 1997). On the other hand, larval *S. stimpsoni* are unable to escape the estuary until after metamorphosis, when morphological changes make it possible for the juveniles to climb (Schoenfuss, 1997). *Sicyopterus stimpsoni* are likely exposed to higher predation pressure on Hawai'i than powerburst climbers despite short stream estuaries. However, these interactions may differ on islands in which streams have different physical characteristics. For example, estuaries of streams on Kaua'i are much longer than those on Hawai'i, and they allow predatory *E. sandwicensis* to penetrate further upstream (Schoenfuss & Blob, unpubl. data) where the larvae of the three climbing species are likely exposed to more extensive predation pressure. Predatory effects of *E. sandwicensis* on *S. hawaiiensis* are unknown on both Hawai'i and Kaua'i, though the fact that these species are found in close proximity in streams at all life stages suggests that predation by *E. sandwicensis* does not affect the sustainability of *S. hawaiiensis* populations. Nonetheless, the interactions of Hawaiian stream fishes as predators and prey illustrate two important points. First, they demonstrate the potential for interactions between the functional morphology of feeding (predation) and the functional morphology of locomotion (escape) to affect selection on populations. Second, they demonstrate that differences in the physical features of streams (e.g., long or short estuaries) can influence the importance of particular aspects of functional morphology across populations. This suggests that efforts at stream management and conservation will require a degree of specific tailoring to local conditions.

Feeding habits may also contribute to structuring interactions among age classes of Hawaiian stream fishes. For example, although juvenile and adult *A. guamensis* appear to eat similar material (Julius *et al.*, in prep.), high stream flows may reduce competition for food between juveniles and adults because station holding ability decreases as *A. guamensis* increases in size (Fitzsimons *et al.*, 1997). Feeding performance may also be important in determining habitat use among different size classes of *S. stimpsoni*. The feeding habits of *S. stimpsoni* are distinctive due to its ventral mouth position and its tendency to scrape its upper jaw over rocks in order to graze on short-stalked algae and diatoms. The growth of filamentous algae can impede access to shorter stalked food items, particularly for juvenile fishes (Julius *et al.*, 2005). However, high stream flows delay the growth of long algal strands, and periodic flash floods can "reset the clock" of algal growth by cleaning rocks of filamentous taxa (Julius *et al.*, 2005). Adult *S. stimpsoni* appear able to withstand longer periods of low flows as they actively remove filamentous algae from their feeding rocks (a behavior termed "gardening": Fitzsimons *et al.*, 2003). Adults defend large feeding rocks against incursions from other individuals, including juvenile *S. stimpsoni* (Fitzsimons *et al.*, 2003), which are forced to feed off smaller rocks and pebbles. Moreover, juvenile *S. stimpsoni* do not appear able to remove filamen-

tous algae from feeding rocks (Fitzsimons *et al.*, 2003). Thus, to successfully migrate upstream, juvenile *S. stimpsoni* may depend substantially on frequent (3- to 5-week intervals) flash floods to clean filamentous algae from small feeding rocks and pebbles (Julius *et al.*, 2005). Water management efforts should take this cycle into account, as failure of this cycle could contribute to poor recruitment of migrating juveniles into adult stream reaches and reduce the diversity of fish age classes in streams.

Differences in the functional morphology of feeding between species of Hawaiian gobies may also play a strong role in determining the stream habitats that these species exploit. For example, there appears to be dietary overlap between *A. guamensis* and *L. concolor* (Kido, 1996b; Julius, this issue). However, *A. guamensis* feeds in slower flowing water near the streambed, whereas *L. concolor* rises in the water column to pick food items out of the water (Schoenfuss, pers. observ.). Previously noted differences in jaw lever mechanics between these species may contribute to the differences in their feeding habits, as the jaws of *L. concolor* appear better suited than those of *A. guamensis* for the rapid movements required to snatch floating prey out of fast flowing water (T. Maie, in prep.). In addition, feeding requirements and abilities may sometimes exclude particular species of Hawaiian gobies from populating otherwise high quality freshwater habitats. A dramatic example of such exclusion was examined by Schoenfuss *et al.* (2004) in a unique freshwater habitat on the southeastern aspect of the Island of Hawai'i. Here, a fracture in the lava shield contains a spring-fed freshwater environment that is host only to *S. stimpsoni* despite excellent water quality. *Eleotris sandwicensis* and *S. hawaiiensis* may be unable to subsist in this habitat due to a lack of gravel and sand in the stream-bed that could provide food (for *S. hawaiiensis*) or cover for predatory strikes (for *E. sandwicensis*). Long-stalked algae are lacking in this habitat because of its restricted light regime (tall volcanic rocks flank the freshwater stream), precluding *A. guamensis*, which feeds heavily on these taxa (Kido, 1996b; Julius, this issue). Finally, insects and other floating food items are largely absent in this habitat and preclude *L. concolor*. Thus, despite excellent water quality, feeding restrictions appear to limit colonization of this locality to *S. stimpsoni*, which grazes on abundant low stalked algae and thrives at a population density considerably greater than that in other Hawaiian streams. Although the low diversity of fish species in this locality might suggest that it represents low quality habitat, this example illustrates how knowledge of functional morphology (in this case for feeding) provides alternative explanations for patterns of presence or absence of species in stream systems.

### Conclusions and Recommendations

The above discussion demonstrates that several aspects of functional morphology affect the distribution and sustainability of all five species of Hawaiian freshwater fishes. These factors are related in principle to locomotory limitations and dietary restrictions among Hawaiian freshwater fishes. Based on the published literature and our observations, we recognize several key findings. (1) Stream flow rates and frequency of maximum flow events are crucial to sustaining a healthy Hawaiian ichthyofauna. (2) The marine/freshwater interface and the estuarine environment are of critical importance to all five species of Hawaiian freshwater fishes. (3) Limitations in fish diversity within Hawaiian freshwater streams might be a result of locomotory or dietary constraints that are not attributable to environmental degradation.

These key findings lead us to recommend several avenues of future research to ensure the health not only of the Hawaiian freshwater ichthyofauna, but also for other organisms in the near-shore environment. (1) The Hawaiian Islands vary dramatically in geological morphology, leading to distinct, island-specific flow regimes and cycles of maximum flow events. Stream management plans need to be tailored to these local conditions. One freshwater management plan will not be applicable to all islands, and future research should carefully examine how environmental differences between the islands relate to population distribution in fish species. (2) Estuaries are a critical habitat for Hawaiian freshwater fishes and sustain several marine species as well. Estuaries are also

a common interface between Hawaiian streams and the local human population. These interactions need to be studied in greater detail to develop management plans that maximize public access while minimizing impact for the native ichthyofauna. (3) *Sicyopterus stimpsoni* might serve as a key indicator species to monitor the long-term health of Hawaiian estuaries, as its migrants spend the greatest amount of time in this habitat among species that traverse it. In addition, the metamorphosis of this species results in an especially energy depleted and vulnerable life stage in the estuarine habitat, making it the most vulnerable of the species that pass through it. Finally, this species has been studied extensively in the past 15 years, and future efforts could be focused on its interactions within the estuarine ecosystem. (4) The broad use of the Index of Biological Integrity (IBI) to assess Hawaiian stream health needs to be critically evaluated and possibly amended to reflect the uniqueness of the Hawaiian fish fauna.

#### Acknowledgments

We thank the organizers of this conference for inviting our participation, and the State of Hawaii for funding our previous research and this conference. We also thank the Stearns Manufacturing Company for additional support of our research along with faculty research grants from St. Cloud State University and Clemson University. For advice and logistical support during fieldwork we thank R. Nishimoto, M. Fitzsimons, D. Kuamo'o, B. Kaya, L. Nishimura, T. Sakihara, T. Shimoda, and T. Shindo. We also thank M. Julius and R. Rai (St. Cloud State University) and T. Maie, C. Mims, and M. Wright (Clemson University) for their contributions to data collection and analysis. The manuscript was improved through helpful suggestions by two anonymous reviewers.

#### Literature Cited

- Arlinghaus, R., T. Mehner & I.G. Cowx.** 2002. Reconciling traditional inland fisheries management and sustainability in industrialized countries, with emphasis on Europe. *Fish & Fisheries* **3**: 261–316.
- Arnold, S.J.** 1983. Morphology, performance, and fitness. *American Zoologist* **23**: 347–361.
- . 2003. Performance surfaces and adaptive landscapes. *Integrative & Comparative Biology* **43**: 367–375.
- Azevedo, J.M.N. & A.M.V. Simas.** 2000. Age and growth, reproduction and diet of a sublittoral population of the rock goby *Gobius paganellus* (Teleostei, Gobiidae). *Hydrobiologia* **440**: 129–135.
- Bell, K.N.I. & J.A. Brown.** 1995. Active salinity choice and enhanced swimming endurance in 0 to 8-d-old larvae of diadromous gobies, including *Sicydium punctatum* (Pisces), in Dominica, West Indies. *Marine Biology* **121**: 409–417.
- Birdsong, R.S.** 1975. The osteology of *Microgobius signatus* Poey (Pisces: Gobiidae), with comments on other gobiid fishes. *Bulletin of the Florida State Museum Biological Sciences* **19**: 136–186.
- , **E.O. Murdy & F.L. Pezold.** 1988. A study of the vertebral column and median fin osteology in gobioid fishes with comments on gobioid relationships. *Bulletin of Marine Science* **42**: 174–214.
- Blob, R.W., R. Rai, M.L. Julius & H.L. Schoenfuss.** 2006. Functional diversity in extreme environments: effects of locomotor style and substrate texture on the waterfall climbing performance of Hawaiian gobiid fishes. *Journal of Zoology* **268**: 315–324.
- , **K.M. Wright, M. Becker, T. Maie, T.J. Iverson, M.L. Julius & H.L. Schoenfuss.** In press. Ontogenetic change in novel functions: waterfall climbing in adult Hawaiian gobiid fishes. *Journal of Zoology*
- Chubb, A.L., R.M. Zink & J.M. Fitzsimons.** 1998. Patterns of mtDNA variation in Hawaiian freshwater fishes: the phylogeographic consequences of amphidromy. *Journal of Heredity* **89**: 8–16.

- Domenici, P.** 2003. Habitat, body design, and the swimming performance of fish, p. 137–160. *In*: Bells, V.L., J.-P. Gasc & A. Casinos (eds.), *Vertebrate biomechanics and evolution*. BIOS Scientific Publishers Ltd, Oxford.
- Englund, R. & R. Filbert.** 1997. Discovery of the native stream goby, *Lentipes concolor*, above Hawaii's highest waterfall, Hi'ilawe Falls. *Bishop Museum Occasional Papers* **49**: 62–64.
- Ferry-Graham, L.A. & P.C. Wainwright.** 2003. Evaluating suction feeding performance in fishes: implications for evolutionary diversification, p. 101–115. *In*: Bells, V.L., J.-P. Gasc, & A. Casinos (eds.), *Vertebrate biomechanics and evolution*. BIOS Scientific Publishers Ltd., Oxford.
- Fitzsimons, J.M., M.G. McRae, H.L. Schoenfuss & R.T. Nishimoto.** 2003. Gardening behavior in amphidromous Hawaiian fish *Sicyopterus stimpsoni* (Osteichthyes: Gobiidae). *Ichthyological Exploration of Freshwaters* **14**: 185–191.
- . & **R.T. Nishimoto.** 1990. Territories and site tenacity in males of the Hawaiian stream goby *Lentipes concolor* (Pisces: Gobiidae). *Ichthyological Exploration of Freshwaters* **1**: 185–189.
- . & **R.T. Nishimoto.** 1991. Behavior of gobioid fishes from Hawaiian fresh waters, p. 106–124. *In*: Devick, W.S. (ed.), *New directions in research, management, and conservation of Hawaiian freshwater stream ecosystems*. State of Hawaii, Honolulu.
- . & **R.T. Nishimoto.** 1995. Use of fish behavior in assessing the effects of Hurricane Iniki on the Hawaiian island of Kaua'i. *Environmental Biology of Fishes* **43**: 39–50.
- , **J.E. Parham & R.T. Nishimoto.** 2002. Similarities in behavioral ecology among amphidromous and catadromous fishes on the oceanic islands of Hawai'i and Guam. *Environmental Biology of Fishes* **65**: 123–129.
- , **H.L. Schoenfuss & T.C. Schoenfuss.** 1997. Significance of unimpeded flows in limiting the transmission of parasites from exotics to Hawaiian stream fishes. *Micronesica* **30**: 117–125.
- Fukui, S.** 1979. On the rock-climbing behavior of the goby, *Sicyopterus japonicus*. *Japanese Journal of Ichthyology* **26**: 84–88.
- Fulton, C.J., D.R. Bellwood & P.C. Wainwright.** 2001. The relationship between swimming ability and habitat use in wrasses (Labridae). *Marine Biology* **139**: 25–33.
- Hammer, C.** 1995. Fatigue and exercise tests with fish. *Comparative Biochemistry & Physiology* **112A**: 1–20.
- Holland, L.E.** 1986. Effects of barge traffic on distribution and survival of ichthyoplankton and small fishes in the Upper Mississippi River. *Transactions of the American Fisheries Society* **115**: 162–165.
- Irschick, D.J.** 2003. Measuring performance in nature: implications for studies of fitness within populations. *Integrative and Comparative Biology* **43**: 396–407.
- Julius, M.L., R.W. Blob & H.L. Schoenfuss.** 2005. The survival of *Sicyopterus stimpsoni*, an endemic amphidromous Hawaiian gobiid fish, relies on hydrological cycles of streams: evidence from changes in the algal composition of diet through growth stages. *Aquatic Ecology* **39**: 473–484.
- Juvik, S.P. & J.O. Juvik.** 1998. *Atlas of Hawai'i*. 3rd ed. University of Hawai'i Press, Honolulu, 333 p.
- Keith, P.** 2003. Biology and ecology of amphidromous Gobiidae of the Indo-Pacific and Caribbean regions. *Journal of Fish Biology* **63**: 831–847.
- Kido, M.H.** 1996a. Diet and food selection in the endemic Hawaiian amphidromous goby, *Sicyopterus stimpsoni* (Pisces: Gobiidae). *Environmental Biology of Fishes* **45**: 199–209.
- . 1996b. Morphological variation in feeding traits of native Hawaiian stream fishes. *Pacific Science* **50**: 184–193.
- Krueger, C.C. & D.J. Decker.** 1993. The process of fisheries management, p. 33–54. *In*: C.C. Kohler & W.A. Hubert (eds.), *Inland Fisheries Management in North America*. American Fisheries Society, Bethesda, Maryland.
- Maie, T., H.L. Schoenfuss & R.W. Blob.** In press. Ontogenetic scaling of body proportions in waterfall-climbing gobiid fishes from Hawai'i and Dominica: implications for locomotor function. *Copeia*.

- McDowall, R.M.** 2003. Hawaiian biogeography and the islands' freshwater fish fauna. *Journal of Biogeography* **30**: 703–710.
- . 2004. Ancestry and amphidromy in island freshwater fish faunas. *Fish & Fisheries* **5**: 75–85.
- Munday, P.L., S.J. Pierce, G.P. Jones & H.K. Larson.** 2002. Habitat use, social organization and reproductive biology of the seawhip goby, *Bryaninops yongei*. *Marine & Freshwater Research* **53**: 769–775.
- Nelson, S.G., J.E. Parham, R.B. Tibbatts, F.A. Camacho, T. Leberer & B.D. Smith.** 1997. Distribution and microhabitats of the amphidromous gobies in streams of Micronesia. *Micronesica* **30**: 83–91.
- Nishimoto, R.T. & J.M. Fitzsimons.** 1999. Behavioral determinants of the instream distribution of native Hawaiian stream fishes, p. 813–818. *In*: Seret, B. & J.-Y. Sire (eds.), *Proceedings of the 5th Indo-Pacific Fish Conference*. Noumea.
- . & **D.K.G. Kuamo'o.** 1997. Recruitment of goby postlarvae into Hakalau stream, Hawai'i Island. *Micronesica* **30**: 41–49.
- Novotny, V., A. Bartosova, N. O'Reilly & T. Ehlinger.** 2005. Unlocking the relationship of biotic integrity of impaired waters to anthropogenic stresses. *Water Research* **39**: 184–198.
- Parenti, L.R. & K.R. Thomas.** 1998. Pharyngeal jaw morphology and homology in sicydiine gobies (Teleostei: Gobiidae) and allies. *Journal of Morphology* **237**: 257–274.
- Pezold, F.** 1993. Evidence for a monophyletic Gobiinae. *Copeia* **1993**: 634–643.
- Privitera, L.A.** 2002. Reproductive biology of the coral-reef goby, *Asterropteryx semipunctata*, in Kaneohe Bay, Hawaii. *Environmental Biology of Fishes* **65**: 289–310.
- Radtke, R.L. & R.A. Kinzie III.** 1991. Hawaiian amphidromous gobies: Perspectives on recruitment processes and life history events, p. 125–141. *In*: Devick, W.S. (ed.), *New directions in research, management, and conservation of Hawaiian freshwater stream ecosystems*. State of Hawaii, Honolulu.
- , **R.A. Kinzie & S.D. Folsom.** 1988. Age at recruitment of Hawaiian freshwater gobies. *Environmental Biology of Fishes* **23**: 205–213.
- Schoenfuss, H.L.** 1997. Metamorphosis of the Hawaiian stream goby *Sicyopterus stimpsoni*: a structural, functional, and behavioral analysis. Ph.D. Dissertation. Louisiana State University. 145 p.
- . & **R.W. Blob.** 2003. Kinematics of waterfall climbing in Hawaiian freshwater fishes (Gobiidae): vertical propulsion at the aquatic-terrestrial interface. *Journal of Zoology* **261**: 191–205.
- , **M.L. Julius & R.W. Blob.** 2004. Colonization of a recent, volcanically formed freshwater habitat: an example of primary succession. *Ichthyological Exploration of Freshwaters* **15**: 83–90.
- , **T.A. Blanchard & D.K.G. Kuamo'o.** 1997. Metamorphosis in the cranium of postlarval *Sicyopterus stimpsoni*, an endemic Hawaiian stream goby. *Micronesica* **30**: 93–104.
- Schwenk, K.** 2000. *Feeding: form, function, and evolution in tetrapod vertebrates*. Academic Press, San Diego.
- Steinmann, A.** 1996. Effects of grazing on freshwater benthic algae, p. 341–373. *In*: Stevenson, R.J., M.L. Bothwell & R.L. Lowe (eds.), *Algal ecology: freshwater benthic ecosystems*. Academic Press, San Diego.
- Tate, D.C.** 1997. The role of behavioral interactions of immature Hawaiian stream fishes (Pisces: Gobiodei) in population dispersal and distribution. *Micronesica* **30**: 51–70.
- Taylor, M.S. & M.E. Hellberg.** 2003. Genetic evidence for local retention of pelagic larvae in a Caribbean reef fish. *Science* **299**: 107–109.
- Thacker, C.E.** 2002. Molecular phylogeny of the gobioid fishes (Teleostei: Perciformes: Gobioidei). *Molecular Phylogenetics & Evolution* **26**: 354–368.
- Todd, E.S.** 1975. Vertical movements and development of the prolarvae of the eleotrid fish, *Dormitator latifrons*. *Copeia* **1975**: 564–568.



- Voegtle, B., M. Larinier & P. Bosc.** 2002. Etude sur les capacités de franchissement des cabot bouche-rondes (*Sicyopterus lagocephalus*, Pallas, 1770) en vue de la conception dispositifs adaptés aux prises d'eau du transfert Salazie (île de la Réunion). *Bulletin Français de la Pêche et de la Pisciculture* **364**: 109–120.
- Vogel, S.** 1994. *Life in moving fluids: the physical biology of flow*. Princeton University Press, Princeton, New Jersey. 467 p.
- Wainwright, P.C., D.R. Bellwood & M.W. Westneat.** 2002. Ecomorphology of locomotion in labrid fishes. *Environmental Biology of Fishes* **65**: 47–62.
- Walker, J.A.** 2000. Does a rigid body limit maneuverability? *Journal of Experimental Biology* **203**: 3391–3396.
- Webb, P.W.** 1984. Body form, locomotion, and foraging in aquatic vertebrates. *American Zoologist* **24**: 107–120.
- Westneat, M.W.** 2003. A biomechanical model for analysis of muscle force, power output, and lower jaw motion in fishes. *Journal of Theoretical Biology* **223**: 269–281.
- . 2004. Evolution of levers and linkages in the feeding mechanisms of fishes. *Integrative & Comparative Biology* **44**: 378–389.
- Wolter, C.** 2001. Conservation of fish species diversity in navigable waterways. *Landscape & Urban Planning* **53**: 135–144.
- . & **R. Arlinghaus.** 2003. Navigation impacts on freshwater fish assemblages: the ecological relevance of swimming performance. *Reviews in Fish Biology & Fisheries* **13**: 63–89.
- Yamamoto, M.N. & A.W. Tagawa.** 2000. *Hawai'i's Native and Exotic Freshwater Animals*. Mutual Publishing, Honolulu, p. 200.
- Zink, R.M.** 1991. Genetic variation within and between populations of *Lentipes concolor* from Hawai'i and Kaua'i, p. 96–105. In: Devick, W.S. (ed.), *New directions in research, management, and conservation of Hawaiian freshwater stream ecosystems*. State of Hawaii, Honolulu.
- , **J.M. Fitzsimons, D.L. Dittman, D.R. Reynolds & R.T. Nishimoto.** 1996. Evolutionary genetics of Hawaiian freshwater fishes. *Copeia* **1996**: 330–335.

