Why Sweat the Small Stuff: the Importance of Microalgae in Hawaiian Stream Ecosystems

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Abstract

Microalgae are well known for their importance in aquatic ecosystems and for their utility as environmental indicators. These attributes are emphasized here for microalgae, especially diatoms, occurring in Hawaiian stream systems. Attention is paid to the influences stream morphology has on the distribution of algae in streams on Hawaiʻi and Kauaʻi. Maximum current velocities and flood frequency appear to be of particular importance in regulating community structure through re-initiation of the benthic algal successional cycle. The effects of variations in microalgal community structure on the grazing activities of native algivorous fishes are discussed, and suggestions are provided with regard to stream management strategies providing for the preservation of these fish.

Introduction

It is important to mention the background and perspective influencing the content of this manuscript. Discussion and examples are limited to observation and experimentation made over the last three plus field seasons on Hawaiʻi and Kauaʻi. The observations and experimentation summarized here are appropriate for this paper's objectives. These are:

1. understanding the major differences between Hawaiian and temperate stream systems;
2. explaining the spatial distribution of microalgal (not visible with naked eye) communities in Hawaiian streams;
3. describing the role of microalgal communities in Hawaiian stream ecosystems; and
4. explaining how these factors relate to one another in context of making management decisions for conserving native fishes in streams and estuaries.

The two islands dealt with represent the youngest and oldest, as well as, the range of naturally occurring variation in Hawaiian stream systems making them good examples for objective 1. Additionally, these two islands represent the extremes of mechanistic variations influencing algal community structure in terms of objectives 2 and 3. The specific endpoints driving the text are also limited; gobioid fishes for freshwater systems and mullet species for marine systems, but again these specific fishery endpoints lend themselves to the objectives of the manuscript. The two fish groups (goby and mullet) used as examples in this article are appealing because of their cultural and economic importance. Each fish group includes native species of cultural and economic interest. The mechanistic factors influencing algal communities also influence the distribution of native fishes. Both fish groups also include algal grazing species. These components allow objective 4 to be achieved in an efficient and relevant context.

Nature and Composition of Hawaiian Stream Systems

Hawaiian vs. temperate streams

To understand the composition and development of algal communities in Hawaiian streams, researchers must comprehend the structure and mechanics of these aquatic systems and their surrounding environments. As with most investigations of freshwater ecology, studies of lotic ecosystems have disproportionately focused on temperate zone systems with study sites smaller than 10 m^2

and individual investigations lasting less than one year (Lodge *et al.*, 1998). This investigative and literature bias must be recognized to avoid applying generalizations appropriate for temporal zone systems to Hawaiian streams. Notable structural and environmental differences in Hawaiian streams compared to temperate systems include the minimal (perhaps nonexistent) hyporheic zone, narrow seasonal variation, and the smaller, steeper overall stream system. These structural differences in Hawaiian streams directly influence mechanistic factors impacting stream biota. Not the least of these factors include nutrient regimes, flow regimes, and residence time.

The minimized hyporheic zone is a result of the islands' volcanic origins and the limited amount of sediment covering this volcanic substrate. This streambed morphology limits the degree to which nutrient buffering can occur in the stream system and generally restricts nutrient inputs from inflow activities to surface sediment runoff. Minimized seasonal variation creates a situation in which temperature and light regimes for many species are always near optimal conditions and reduce seasonal succcessional patterns observed in the biota of temperate systems. Perhaps the most dramatic structural difference from temperate systems is the short, steep morphology of the overall stream system. Influences of this stream architecture on flow regimes and residence time are obvious.

Nutrients, specifically nitrogen and phosphorus, in stream systems of moist tropical environments are typically considerably higher than those in temperate systems with typical total nitrogen exports around 998 kg km^{-2} yr^{-1} and total phosphorus exports approximating 46 kg km^{-2} yr^{-1} (Lewis, 1986). These are approximately three to four times greater than values for temperate regions lakes, 300 kg km^{-2} yr^{-1} of total nitrogen and 10 kg km^{-2} yr^{-1} of total phosphorus (Schindler *et al.*, 1974; Jansson, 1979). Runoff from the streams' riparian zone almost certainly accounts for a high proportion of the nutrient values given little trickling and filtration occurs via soils before storm runoff enters the stream systems. These runoff events and the short, steep architecture of the stream systems also produce a much shorter residence time for these systems in comparison to those in temperate regions. Average values for temperate regions are approximately 16 days for unimpounded stream systems (Vörösmarty *et al.*, 1997) compared to nearly daily flushing in Hawaiian systems. Related to the short residence times are the relatively high maximum flow rates of the Hawaiian stream systems. Heavy rain events (>100mm per day) are not uncommon and result in major flash flood events (Kodama & Barnes, 1997; Kodama & Bursinger, 1998). Based upon particle size, rubble to boulder sized (64 to 128+ mm) (Einsele, 1960) particles, in the stream beds flood events have to achieve maximum velocities in excess of 200 cm s^{-1} (Morisawa, 1968; Allan, 1995). The strong currents and frequent flooding events maybe the features most useful in understanding the biotic interactions in the Hawaiian stream systems. With the relatively high nutrients and consistent temperature and light regimes, these variable hydrologic regimes have a strong effect on the streams' biota (Poff & Ward, 1989). Bright (1980) identified flood periodicity among the most influential mechanisms for restructuring the invertebrate stream community on Palau, another Pacific island of volcanic origin, and conditions appear similar for Hawaiian islands.

Streams on Hawai'i vs. streams on Kaua'i
Differences worth noting exist between the streams of Hawai'i and Kaua'i. The oldest island, Kaua'i, formed over 5 mya and rose to approximately 2600 m before eroding down to its present maximum elevation of 1598 m. In contrast, the youngest island, the Island of Hawai'i emerged less than 0.5 mya and has eroded little from its maximum height of 4600 m. As a result of differences in elevational gradient, these islands do not contain identical stream systems. The erosion of Kaua'i has resulted in broad meandering streams with large estuaries. These streams are only rarely interrupted by waterfalls, which are usually located in stream headwaters. In contrast, streams on Hawai'i have steep slopes resulting in higher velocity streams with few (if any) estuaries. Moreover, frequent waterfalls that can exceed 100 m in height and include many that terminate directly on the beach or in the ocean interrupt streams on Hawai'i. Furthermore, weather movements across Hawai'i precipitate out moisture and create the arid conditions on the Kona side of the island and moist conditions on the Hilo side of the island where flood events occur on a near monthly scale (Kodama & Barnes, 1997). This is not the case on Kaua'i where flood events are less frequent. The frequent waterfall
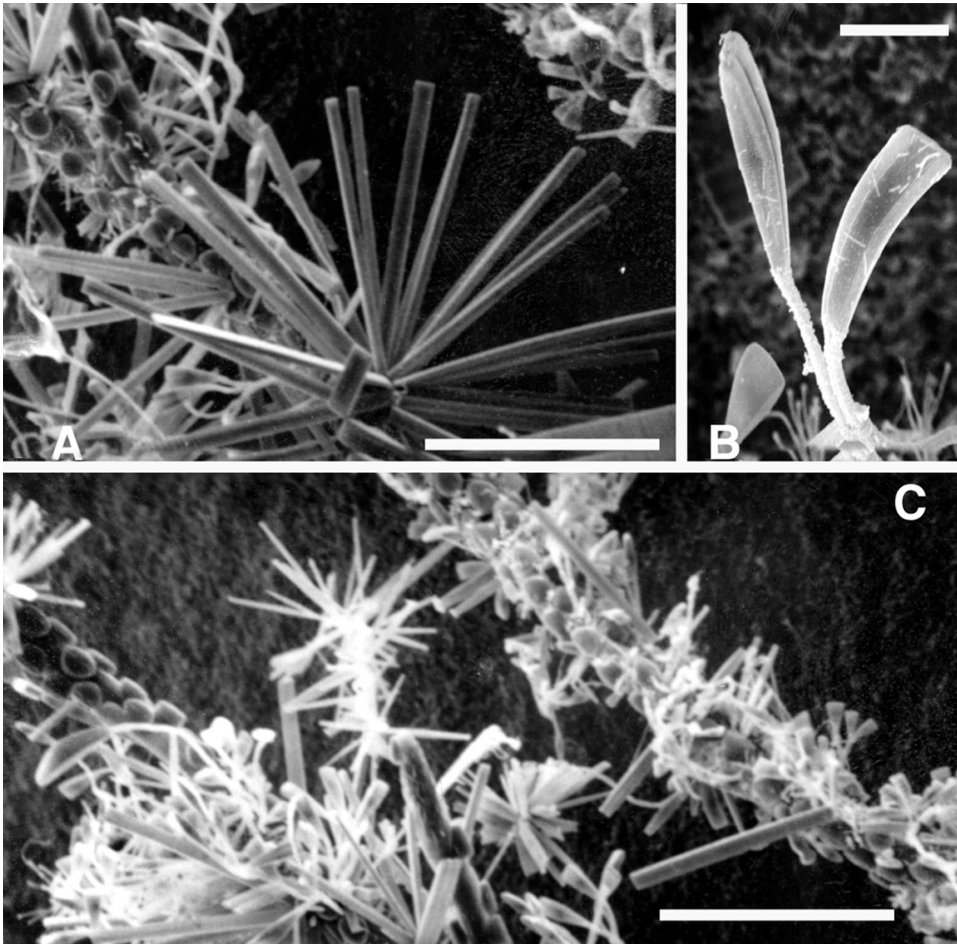
Figure 1. Scanning electron micrographs of benthic microalgae. **A:** the tuft forming diatom *Synedra acus*. **B:** the stalk forming diatom *Rhoicosphenia curvata*. **C:** epiphytic diatoms growing on a filamentous green algae. Scale bars equal 200 µm for A and C and 10 µm for B.

interruptions in stream systems on Hawai'i may limit the degree to which nutrient spiraling (Newbold *et al.*, 1983) can occur because of the inability of biota to move back upstream.

Distribution of microalgae in Hawaiian streams

The composition and mechanistic factors of Hawaiian streams discussed above directly influences the distribution of microalgae in the stream systems. The close association of microalgae with their surrounding environmental conditions dates to the earliest observations in aquatic ecology (Naumann, 1919), and they continue to be used as indicators of environmental health (Lowe & Pan, 1996). The nutrient regimes in the streams are conducive to algal growth with ratios of N:P averaging 22:1 (Lewis, 1986). This N:P ratio suggests phosporus is the limiting nutrient (Vallentyne, 1974) and results in eukaryotic microalgae being the dominant forms in Hawaiian stream systems. Studies of nutrient availability and periphyton on Oahu are consistent with this taxon/nutrient distribution pattern (Larned & Santos, 2000). The composition of this eukaryotic community is largely dominated by diatoms (Bacillariophyta), and further suggests that silica is in abundance in these streams. This is supported by Derry *et al.*'s (2005) observation that most of the silica released on Hawaiian islands is processed as biogenic silica.
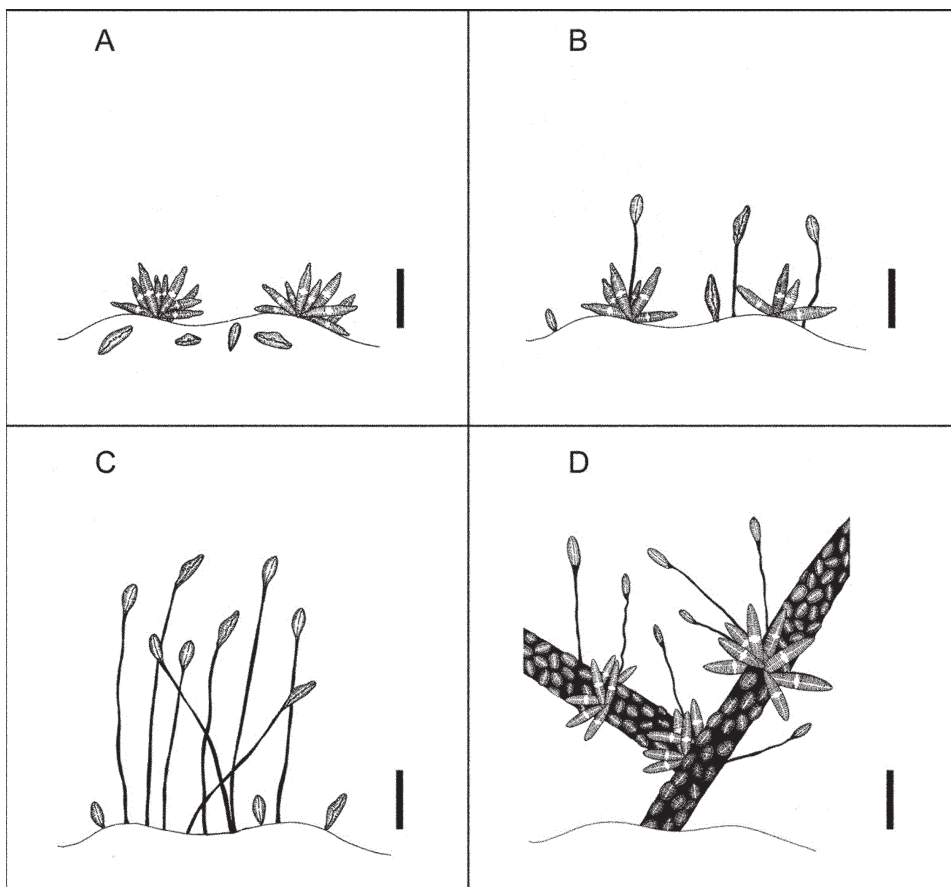
Figure 2. Hypothetical representation of benthic algal community succession, modified from Tuji (2000). **A:** First colonizers, characterized by colonies of tuft forming species and motile stalk growing forms. **B:** Early development of stalk forming species continuing. **C:** Dominant phase of stalk growing species. **D:** Community apex with macrophyte supporting numerous epiphytic species.

Among algae, the diatoms are the most widely used environmental indicators (Stoermer & Smol, 2000). The specimens observed from Hawaiian freshwater stream systems largely emphasize the environmental conditions of the streams described above. The diatom flora of the streams largely consists of benthic taxa occurring in one of two growth forms; tuft and stalk formers (Fig. 1A,B) (Julius *et al.*, 2005). Typical species assemblages comprise taxa associated with warm, nutrient-rich, hardwater, flowing systems with a pH ranging from 7.5 to 8.0 (Patrick & Reimer, 1966, 1975). Planktonic taxa are absent in the stream assemblages; these algae are a frequent component of most temperate systems (Stoermer & Julius, 2003). This is most likely a function of the absence of lakes draining into the Hawaiian stream systems.

Flow regimes are also important in structuring the overall algal community and directly influence when streams are dominated by filamentous macroalgae or by diatom microalgae. Peak algal biomass in high nutrient and high light environments occurs at modest stream velocities (30–60 cm s^{-1}) (Stevenson, 1996). Attached filamentous algae typically dominate in higher flow rates, and unattached filamentous forms persist in slower currents. Attached macroalgal filaments often act as a growth substrate for diatom microalgae (Fig. 1C), and unattached macroalgal filaments do not typ-

ically support diatom microalgal epiphytes. Only attached filamentous macroalgae and stalk forming diatoms are drag resistant and accumulate biomass in high flow environments (Reiter & Carlson, 1986; Dodds & Gudder, 1992).

During flash floods stream velocities become great enough to overturn the substrates of epilithic macro- and microalgae; based upon particle size discussed above these currents would exceed 200 cm s^{-1}. Flood events of this type will result in a clearing of the substrate surface initiating a distinct successional pattern (Hoagland *et al.*, 1982; Tuji, 2000; Fig. 2). Initially, a substrate is colonized by tumbling and motile species of diatoms, and short, tuft-like algal colonies develop (Fig. 2A). Stalk-forming species eventually begin to develop and coexist with tuft-forming taxa (Fig. 2B). As the stalk forming taxa become taller, the tuft-forming taxa are excluded via light competition (Fig. 2C). Eventually, macroalgae develop and exclude stalk-forming taxa from occurring directly on the rock substrate. At this point, stalk attachments shift from the rock to the stems of macrophyte algae, which are also colonized by tuft-forming and abundant adnate epiphytes (Fig. 2D). This last stage represents the development of peak biomass in benthic algal communities (Biggs, 1996). The entire successional process, from bare rock to epiphyte-supporting macroalgae, takes approximately one month to complete (Tuji, 2000). This timeframe has been corroborated with artificial substrate experiments in streams on Hawai'i (Julius, unpubl. data).

The frequency with which this successional pattern is initiated may well characterize the major differences in algal distribution between stream systems on Hawai'i and stream systems on Kaua'i. As previously mentioned, flash flood events on Hawai'i occur frequently. This is not the case for streams on Kaua'i where flash flood events are less frequent. The successional cycle is constantly being re-initiated in streams on Hawai'i. Periods of peak biomass are not persistent (Julius *et al.*, 2005) and microalgal taxa are in a near constant logarithmic growth phase (Biggs, 1996). In contrast, streams on Kaua'i are frequently found at peak biomass and the successional pattern is initiated only a few times per year. The best illustration of this dichotomy between streams on the two islands is abundance of the filamentous diatom *Hydrosera whampoensis* (Fig. 3). *Hydrosera* colonies are easily disturbed in strong currents and large colonies take several months to form. The taxon is extremely abundant in streams on Kaua'i, and form long filamentous colonies (hundreds of cells). In contrast, it is almost nonexistent in collections from streams on Hawai'i and, when present, occurs as a unicell or in short 2–5 cell filaments. This distribution contrasts streams on Hawai'i and Kaua'i and emphasizes the differences in periodicity of flood events.

Role of microalgal communities in Hawaiian stream ecosystems
Diatoms appear to be a particularly satisfactory food source for many aquatic animals, including fishes (Volkman *et al.*, 1989; Ahlgren *et al.*, 1990). This role as a quality food source is a function of the high energy lipid produced as a product of photosynthesis (Stoermer & Julius, 2003) like other members of the Stramenopile algal lineage, and contrasts with other major groups of algae which produce forms of starch as photosynthetic products. While discussions of microalgae as a food source frequently focus on members of the invertebrate community (Bott, 1996), the Hawaiian Islands provide some of the most spectacular examples of adult fish grazing on algal communities.

Gobioid fishes
The role of algae as a food source for the amphidromous gobioid fishes of Hawai'i is well documented (Kido, 1996a,b). Algae appear to be particularly important to climbing gobioid species, where grazing dietary habits appear to be reacquired with the development of climbing phylogenetically (Thacker, 2002). For at least one of these fishes, *Sicyopterus stimpsoni,* benthic diatoms appear to be the primary source of dietary sustenance. The adult jaw structure of the fish is highly modified for rasping and scraping benthic algal communities during early stages of their successional pattern (Julius *et al.* 2005). More dramatic is the evidence that this fish species can exist exclusively on thin coatings of epilithic diatoms exclusively (Schoenfuss *et al.*, 2004). This species also serves as an example illustrating the relationship between algal growth habit and availability to grazers. Steinman (1996) described limitations of stalked and tuft-forming taxa as a food source for invertebrate graz-

ers (see Fig. 2A–C) and filamentous algae with epiphytes as a food source for another class of graz-
ers (see Fig. 2D). This functional barrier appears to explain the coexistence of *Awaous guamensis*
and *S. stimpsoni*, where *A. guamensis* feeds on filamentous algae and its epiphytes and *S. stimpsoni*
feeds on the epilithic diatom taxa.

Native mullet

Preliminary investigation of the floristic composition of stomach contents from *Mugil cephalus*
revealed that the contents consisted almost exclusively of diatoms. This result is not surprising, since
Wells (1984) determined that algae comprised a major dietary source for this species. The floristic
composition of this diatom assemblage for the Hawaiian fish, however, was more restricted than
expected. A single diatom taxon, *Melosira moniliformis*, comprised the majority of the species iden-
tified. This taxon ranged from 70–90% of the total specimens recovered from the fish's stomachs.
This diatom species distribution is not reflective of the diatom community composition in Hawaiian
estuarine algal communities (Hustedt, 1942). This statement is accurate both in terms of total species
numbers and overall abundance of *M. moniliformis*; and strongly suggests the fish is selectively
feeding on this diatom species. The high abundance of *M. moniliformis* was present in the stomachs
of all specimens observed from collections made in both Hawai'i and Kaua'i and percent composi-
tion of Hawai'i or Kaua'i collections were roughly equivalent. This seems to suggest a preference
for the species by *Mugil cephalus* during foraging activities. The potential for this food preference
is further emphasized by the fact that the other diatom species identified in the stomachs readily
grow as epiphytes on *Melosira moniliformis*.

   Although *Mugil cephalus* and *Melosira moniliformis* are both estuarine taxa, they are men-
tioned in this article because of the strong role the stream systems have in maintaining their interde-
pendent ecologies. *Melosira moniliformis* is a colonial, centric diatom widely distributed throughout
the entire southern Pacific and Atlantic seaboard. Like other *Melosira* species, *M. moniliformis* is
tychoplanktonic, and exists both in benthic and planktonic communities. Typically, species are
brought into planktonic habitats during storm events when waters are actively circulating through
the benthic sediments of aquatic habitats due to the storm winds (Sicko-Goad *et al.*, 1986).
Resuspension of *Melosira* typically breaks the colonies from longer, large cell number colonies into
shorter, small cell number colonies. While in the plankton, the cells grow rapidly because light and
nutrient conditions are more favorable than those encountered in benthic habitats. Increased light is
a function of being higher in the water column, and increased nutrients are from resuspension of ben-
thic sediments by storm events where nitrogen and phosphorus are trapped via sedimentation. As cell
division proceeds in planktonic environments, *Melosira* colonies increase in length and become
heavier. Weight is especially critical in diatom species because of the silica cell wall. Once colonies
reach a certain length buoyancy can no longer be maintained, and the colonies settle into benthic
environments. This peculiar ecology often results in large "blooms" of *Melosira* in post storm event
waters. In the case of Hawaiian stream systems, blooms of *M. moniliformis* are regulated by flood
events from the freshwater systems into near shore marine environments. These blooming events
attract *Mugil cephalus.* This relation between the algae and the fish is so well understood that resi-
dents of Hilo actively harvest *Melosira moniliformis* after flood events to use as bait for *Mugil
cephalus* (R. Nishimoto, pers. comm.).

Implications for Management of Native Fishes

Allan (2004) completed a review of the relationship between land use and stream health. Of the six
factors mentioned in the article, hydrologic alteration appears to be the one of greatest concern in
managing Hawaiian freshwater stream systems. Given the relationship between stream current, flood
events, and biotic interactions described above there appears to be a distinct threshold or tolerance
level beyond which hydrologic conditions should not be altered. Most significant is the requirement
for periodic flooding events in the stream ecosystem; these could be on a near monthly scale for
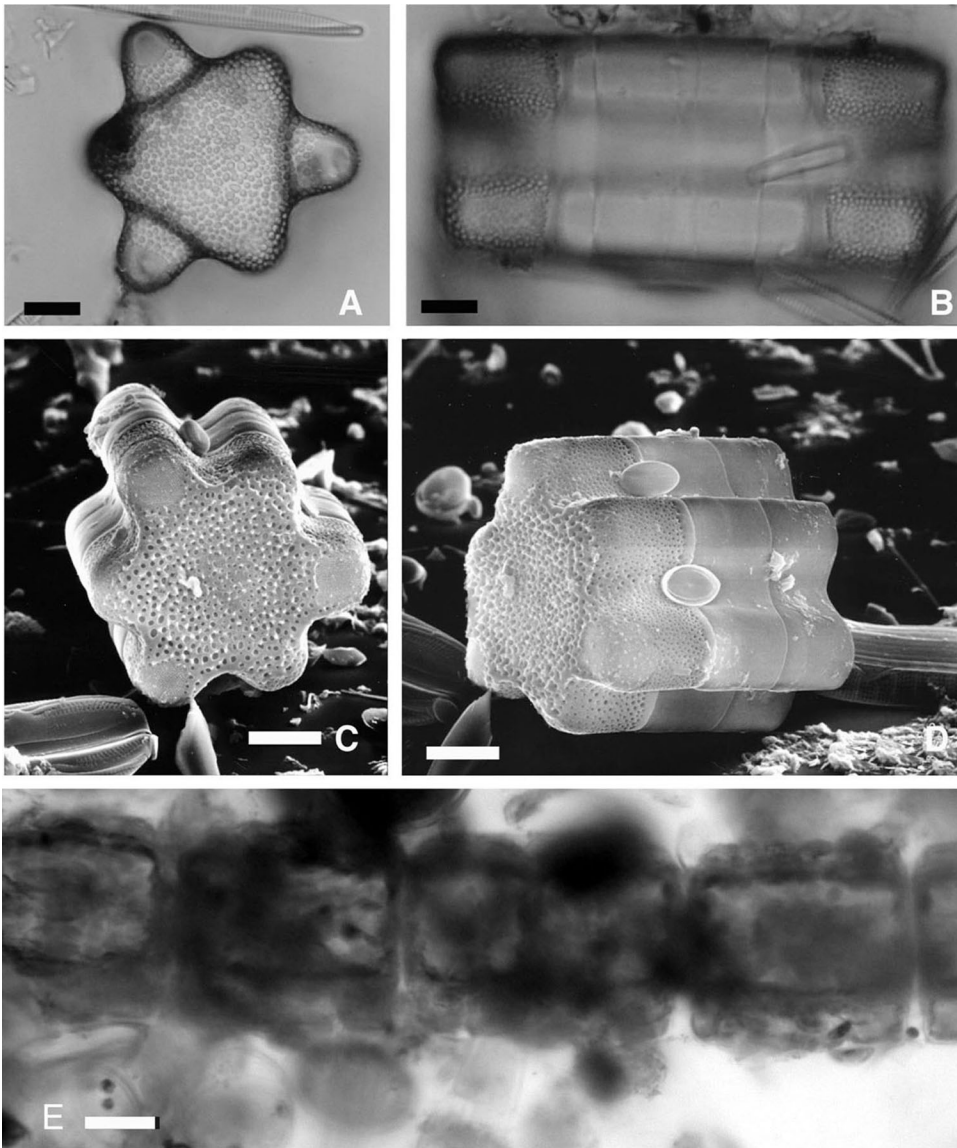
Figure 3. *Hydrosera whampoensis*. **A:** Light micrscope valve view of acid cleaned specimen. **B:** Light micrope girdle view of acid cleaned specimen.**C:** Scanning electon microscope oblique view. **D:** Scanning electron microscope girdle view. **E:** Light microscope view of live colony. Scale bars equal 10 µm.

streams on Hawai'i or semi-annual scale for streams on Kaua'i. Biotic responses to modifications in these threshold limited degredation events are non-linear (Allan, 2004), and once the threshold is broached the stream biota degrades rapidly.

Gobioid fishes

For *Sicyopterus stimpsoni* to continually gain access to its algal food, benthic algal succession must periodically be re-initiated through biological or physical disturbance events. Algal succession could

be re-initiated through repeated grazing or periodic limitation of light, but it might also be re-initiated by substrate disruption via water column turbulence. These disturbance events may be critical to the maintenance of suitable food sources for *S. stimpsoni* in stream systems.

Field observations of feeding behavior in *S. stimpsoni* are consistent with the hypothesis that this species contributes to the disturbance of benthic algae and thereby continually re-initiates algal succession. Adult fish appear to "farm" large feeding rocks in upper stream reaches by continually scraping the same rock over a period of several days or weeks (Fitzsimons *et al.*, 2003). This activity effectively re-initiates benthic algal succession and prevents the development of long filamentous algae, which would make the rock difficult for these fish to feed from. Such grazing could also help to exclude other grazing fish species (Schoenfuss *et al.*, 2004), which typically feed on longer filamentous algae (Kido, 1996b).

In terms of maintaining this fish species on Hawai'i and Kaua'i, the conservation approaches may vary slightly based upon differences in streams on each island. For streams on Hawai'i periodic flood events must be maintained on a near monthly schedule to re-initiate the benthic algal successional pattern. This will ensure a constant food source for *S. stimpsoni* and emulate current stream conditions on the island in the most appropriate fashion. For streams on Kaua'i, appropriate sized feeding rocks provided to support *S. stimpsoni* would have to be within a specific size range. The feeding rock should be (1) large enough to allow development of early succession benthic algal taxa on some portions of the rock while feeding took place on other portions and (2) small enough to allow complete grazing of the rock before filamentous taxa became well developed. These expectations are consistent with the descriptions of feeding rocks provided by Fitzsimons *et al.* (2003). Rocks of the specific size described will provide an adequate feeding substrate for *S. stimpsoni* and accounts for the limited periodicity of flood events on Kaua'i.

In some instances the stream flow tolerance threshold for gobioid fishes has been exceeded. Numerous stream branches on Hawai'i have been impounded or diverted to such an extent that stream velocities are well below 30 cm s^{-1}. In these instances, the unattached filamentous algae *Spirogyra* dominate the stream segment. These filamentous algae do not support the growth of epiphytes, and these stream segments are devoid of both *Awaous guamensis* and *S. stimpsoni* (Schoenfuss, personal observation). These segments should be flooded to clear out *Spirogyra* and re-initiate the benthic algal successional cycle.

Native mullet
Use of the alga *Melosira moniliformis* as bait may have developed on and be limited to Hawai'i, particularly the windward side of the island, rather than on the other Hawaiian islands because of topography. Frequent flash floods in streams on Hawai'i directly affect the frequency of *Melosira moniliformis* blooms along the windward coast of the islands. As turbidity is increased by flood waters along the coast, *Melosira moniliformis* is actively resuspended into planktonic environments, and blooms are triggered. This scenario makes *Melosira moniliformis* readily available for harvest by anglers on the windward side of Hawai'i and less available to anglers at other locations where *Melosira moniliformis* blooms are less frequent and predictable, such as Kaua'i.

The recent introduction of the mullet species *Valamugil engeli* has caused great concern over appropriate management strategies for protecting the native mullet *Mugil cephalus*. The invasive species appears to be more abundant on Kaua'i than on Hawai'i, and this may be a result of stream systems on Kaua'i approaching their tolerance threshold for hydrologic alteration. *Valamugil engeli* appears to consume a wider variety of algal species in coastal Hawaiian ecosystems than the native fish *Mugil cephalus.* With diminished flooding events, blooms of *Melosira moniliformis* become less frequent. This may well provide the opportunity for the invasive mullet species to garner a competitive advantage over the native fish. In terms of management strategies, flood events should be maintained in stream systems on Hawai'i to provide an optimal feeding environment for *Mugil cephalus*. Resources can then be disproportionately applied to preventing the spread of *V. engeli* on Kaua'i where it is unreasonable to try to use flood regulation as a control mechanism.

Conclusions

Our ability to understand and manage the health of Hawaiian streams is directly linked to how well we understand the ecology of the biota and mechanics of the system. Unfortunately, the ability to compare both biota and mechanics of Hawaiian systems with that of other well-studied ecological systems is limited. It is also difficult to predict how the new challenges and problems for maintaining Hawaiian aquatic ecosystem health may manifest themselves. This does not mean that research should be funded without expectation of its results having some practical application. Researchers must make an effort to derive general principles from studying applied problems (Harris, 1994), and these applied problems may well provide interesting large-scale and long-term studies of great interest to basic research questions (Lodge *et al.*, 1998). If this relationship can be achieved between researcher and manager, maximum benefit per research dollar both in terms of application and knowledge expansion will be produced.

An area lending itself to this research relationship is a study focusing on interactions between Hawaiian freshwater streams and coastal marine environments to control the spread of *V. engeli*. This invasive mullet species moves between coastal marine and freshwater habitats as juveniles, and the regulation of the native mullet species food source appears to be linked with freshwater discharges into coastal marine environments. The following research objectives should be pursued in context of this problem:

- A floristic survey of the gut contents of *M. cephalus* and *V. engeli* should be conducted.
- The feeding mechanics of each fish should be examined and documented.
- Feeding trials and competition studies using varying food sources should be conducted.

Once these research objectives are complete, management decisions can be made to create environments favoring the behaviors and ecology of *M. cephalus*. This research will also expand the limited knowledge base concerning the feeding behaviors and mechanics of algivorous fish by relating specific algal taxa and growth forms with mechanistic constraints.

Acknowledgments

Literature Cited

Ahlgren, **G**., **L**. **Lundstedt**, **M**. **Brett & C**. **Forsberg**. 1990. Lipid composition and food quality of some freshwater phytoplankton for cladoceran zooplankters. *Journal of Plankton Research* **12**: 809–818.

Allan, **J**.**D**. 1995. *Stream ecology: structure and function of running waters*. Chapman & Hall, London. 388 p.

———. 2004. Landscapes and riverscapes: the influence of land use on stream ecosystems. *Annual Review of Ecology, Evolution, & Systematics* **35**: 257–284.

Biggs, **B**.**J**.**F**. 1996. Patterns in benthic algae of streams, p. 31–56. *In*: R.J. Stevenson, M.L. Bothwell & R.L. Lowe (eds.), *Algal ecology: freshwater benthic ecosystems.* Academic Press, San Diego.

Bott, **T**.**L**. 1996. Algae in microscopic food webs. *In*: R.J. Stevenson, M.L. Bothwell & R.L. Lowe (eds.), *Algal ecology: freshwater benthic ecosystems*. Academic Press, San Diego. p. 574–607.

Bright, **G**.**R**. 1980. Secondary production in a tropical island stream. *Limnology & Oceanography* **27**: 472–480.

Derry, **L.A.**, **A.C. Kurtz**, **K. Ziegler & O.A**. **Chadwick**. 2005. Biological control of terrestrial sil-ica cycling and export fluxes to watersheds. *Nature* **433**: 728–731.

Dodds, **W.K**. **& D.A**. **Gudder**. 1992. The ecology of *Cladophora*. *Journal of Phycology* **28**: 415–427.

Einsele, **W**. 1960. Die Strömungsgeschwindigkeit als beherrschender Faktor bei der limnologishcen Gestaltung der Gewasser. *Österreichs Fischerei* **2**: 1–40.

Fitzsimons, **J.M.**, **M.G**. **McRae**, **H.L**. **Schoenfuss & R.T**. **Nishimoto**. 2003. Gardening behavior in the amphidromous Hawaiian fish *Sicyopterus stimpsoni* (Osteichthyes: Gobiidae). *Ichthyological Explorations of Freshwaters* **14**: 185–191.

Harris, **G.P**. 1994. Pattern, process, and prediction in aquatic ecology. A limnological view of some general ecological problems. *Freshwater Biology* **32**: 143–160.

Hoagland, **K.D.**, **S.C**. **Roemer & J.R**. **Rosowski**. 1982. Colonization and community structure of two periphyton assemblies, with emphasis on the diatoms (Bacillariophyceae*). American Journal of Botany* **69**: 188–213.

Hustedt, **F**. 1942. Süsswasser-Diatomeen des indomalyayischen Archipels und der Hawaii-Inseln. *Internationalen Revue der Gesamten Hydrobiologie und Hydrographie* **42**: 1–252.

Jansson, **M**. 1979. Nutrient budgets and regulation of nutrient concentrations in a small subarctic lake in Northern Sweden. *Freshwater Biology* **9**: 213–231.

Julius, **M.L.**, **R**. **Blob & H.L**. **Schoenfuss**. 2005. The survival of *Sicyopterus stimpsoni*, an endem-ic amphidromous Hawaiian gobiid fish, relies on the hydrological cycles of streams: evidence from changes in algal composition of diet through growth stages fish. *Aquatic Ecology* **39**: 473–484.

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.

Kodama, **K.P. & G.M**. **Barnes**. 1997. Heavy rain events over the south-facing slopes of Hawaii: attendant conditions. *Weather & Forecasting* **12**: 347–367.

———. **& S**. **Businger**. 1998. Weather and forecasting challenges in the Pacific region of the National Weather Service. *Weather & Forecasting* **13**: 523–546.

Larned, **S.T. & S.R**. **Santos**. 2000. Light- and nutrient-limited periphyton in low order streams of Oahu, Hawaii. *Hydrobiologia* **432**: 101–111.

Lewis, **W.M.**, **Jr**. 1986. Nitrogen and phosphorus runoff losses from a nutrient-poor tropical moist forest. *Ecology* **67**: 1275–1282.

Lodge, **D.M.**, **S.C**. **Blumenshine & Y**. **Vadeboncoeur**. 1998. Insights and application of large-scale, long-term ecological observations and experiments, p. 202–235. *In*: W.J. Resettarits, Jr. & J. Dernardo (eds.), *Experimental ecology: issues and perspectives*. Oxford University Press, New York.

Lowe, **R.L**. **& Y Pan**. 1996. Benthic algal communities as biological monitors, p. 705–739. *In*: R.J. Stevenson, M.L. Bothwell & R.L. Lowe (eds.), *Algal ecology: freshwater benthic ecosystems*. Academic Press, San Diego.

Morisawa, **M**. 1968. *Streams: Their dynamics and morphology*. McGraw-Hill, New York. 175 p.

Naumann, **E**. 1919. Några Synpunkter Angående Limnoplanktons Ökologi med Särskild Hänsyn till Fytoplankton. *Svensk Botanisk Tidskrift* **13**: 129–163. [English Translation by the Fresh-water Biological Association, publication #49.**]**

Newbold, **J.D.**, **J.W**. **Elwood**, **R.V**. **O'Neill & A.L**. **Sheldon**. 1983. Phosphorus dynamics in a woodland stream ecosystem: A study of nutrient spiraling. *Ecology* **64**: 1249–1265.

Patrick, **R**. **& C.W**. **Reimer**. 1966. *The diatoms of the United States I*. Academy of Natural Sciences Philadelphia, Monograph **13**. 688 p.

———. **& C.W**. **Reimer**. 1975. *The diatoms of the United States II, part 1*. Academy of Natural Sciences Philadelphia, Monograph 13. 213 p.

Poff, **N.L**. **& J.V**. **Ward**. 1989. Impications of streamflow variability and predictability for lotic community structure: A regional analysis of streamflow patterns. *Canadian Journal of Fisheries and Aquatic Sciences* **46**: 1805–1818.

Reiter, **M.A**. **& R.E**. **Carlson**. 1986. Current velocity in streams and the composition of benthic algal mats. *Canadian Journal of Fisheries and Aquatic Sciences* **43**: 1156–1162.

Schindler, **D.W**., **H.E**. **Welch**, **J**. **Kalff**, **G.J**. **Brunskill & N**. **Kritsch**. 1974. Physical and chemical limnology of Char Lake, Corwallis Island (75? N Lat.). *Canadian Journal of Fisheries and Aquatic Sciences* **31**: 585–607.

Schoenfuss, **H.L**., **M.L**. **Julius & R**. **Blob**. 2004. Colonization of a recent, volcanically formed freshwater habitat: an example of primary succession. *Icthyological Exploration of Freshwaters* **15**: 83–90.

Sicko-Goad, **L.M**., **E.F**. **Stoermer & G**. **Fahnenstiel**. 1986. Rejuvenation of *Melosira granulata* (Bacillariophyceae) resting cells from the anoxic sediments of Douglas Lake, Michigan, 1. Light microscopy and 14C uptake. *Journal of Phycology* **22**: 22–28.

Steinman, **A**. 1996. Effects of grazing on freshwater benthic algae, p. 341–347. In*: R.J. Stevenson, M.L. Bothwell & R.L. Lowe (eds.), *Algal ecology: freshwater benthic ecosystems.* Academic Press, San Diego.

Stevenson, **R.J**. 1996. The stimulation and drag of Current. *In*: R.J. Stevenson, M.L. Bothwell & R.L. Lowe (eds.), *Algal ecology: freshwater benthic ecosystems*. Academic Press, San Diego. p. 321–340.

Stoermer, **E.F**. **& J**. **Smol**. 2000. *The diatoms: applications for earth and environmental sciences*. Cambridge University Press, London. 469 p.

———. **& M.L**. **Julius**. 2003. Centric diatoms. *In*: J.D. Wehr & R.G. Sheth (eds.), *Freshwater algae of North America: classification and ecology*. Academic Press, San Diego. p. 559–594.

Thacker, **C.E**. 2002. Molecular phylogeny of the gobioid fishes (Teleostei: Perciformes: Gobioidei). *Molecular Phylogenetics & Evolution* **26**: 354–368.

Tuji, **A**. 2000. Observation of developmental processes in loosely attached diatom (Bacillariophyceae) communities. *Phycological Research* **48**: 75–84.

Vallentyne, **J.R**. 1974. *The algal bowl: lakes and man*. Ottawa: Department of the Environmental, Fisheries, & Marine Services. 185 p.

Volkman, **J.K**., **S.W**. **Jeffery**, **P.D**. **Nichols**, **G.I**. **Rogers & C.D**. **Garland**.1989. Fatty acid and lipid composition of 10 species of microalgae used in mariculture. *Journal of Experimental Marine Biology & Ecology* **128**: 219–240.

Vörösmarty, **C.J**., **K.P**. **Sharma**, **B.M**. **Gekete**, **A.H**. **Copeland**, **J**. **Holden**, **J**. **Marble & J.A**. **Lough**. 1997. The storage and aging of continental runoff in large reservoir systems of the world. *Ambio* **26**: 210–219.

Wells, **R**. 1984. The food of the grey mullet (*Mugil cephalus* L.) in Lake Waahi and the Waikato River at Huntly, *New Zealand Journal of Marine and Freshwater Research* **18**: 13–19.