SPECIES PROFILES: LIFE HISTORIES AND ENVIRONMENTAL REQUIREMENTS OF COASTAL VERTEBRATES AND INVERTEBRATES PACIFIC OCEAN REGION

Report 3

AMPHIDROMOUS MACROFAUNA OF HAWAIIAN ISLAND STREAMS

by

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Report 3 of a Series

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**Abstract:** This species profile summarizes information on a group of amphidromous Gobioid fishes (Electris sandwicensis, Stenogobius genivittatus, Awaous stamineus, Sicyopterus stimpsoni, and Lentipes concolor), crustaceans (Athyoida bisulcata, Macrobrachium grandimanus, and Macrobrachium lar), and Mollusca (Hermitina spp. and Clithon spp.) that, while taxonomically unrelated, share a common life history pattern and similar environmental conditions for their survival. The term "amphidromous" describes organisms that migrate to and from the sea but not specifically for reproductive purposes. Amphidromous fishes and invertebrates occur on continents and oceanic islands in both tropical and warm temperate regions. They occur in lotic freshwater systems flowing into the marine environment. This profile concentrates on species occurring in the Hawaiian Islands, one of the few regions where this fauna has been studied. It summarizes information on the taxonomy, morphology, life history, and environmental requirements of the species.
PREFACE

This report is designed to provide coastal managers, engineers, and biologists with a brief comprehensive sketch of the biological characteristics and environmental requirements of the amphidromous macrofauna of island streams of Hawaii and to describe how populations of these species in Hawaiian waters may be expected to react to environmental changes caused by coastal development. The report has sections on taxonomy, life history, ecological role, environmental requirements, growth, exploitation, and management.

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The report was prepared by Dr. Robert A. Kinzie III, Hawaii Institute of Marine Biology and the Department of Zoology, University of Hawaii at Manoa. Technical reviews were provided by Dr. John A. Baker of the Aquatic Habitat Group and Drs. Douglas G. Clarke and Mark W. LaSalle of the Coastal Ecology Group (CEG), Environmental Laboratory (EL), US Army Engineer Waterways Experiment Station (WES); Dr. James E. Maragos and Mr. Mike Lee of the US Army Engineer Division, Pacific Ocean; Mr. Bill Devick of the State of Hawaii; Mr. John I. Ford of the US Fish and Wildlife Service; Messrs. James Uchiyama and Doyle E. Gates of the National Marine Fisheries Service; and Drs. Paul Jokiel and Richard H. Titgen of the Hawaii Institute of Marine Biology. Ms. Susan Monden provided the excellent illustrations.

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Commander and Director of WES during publication of this report was COL Larry B. Fulton, EN. Dr. Robert W. Whalin was Technical Director.

This report should be cited as follows:

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AMPHIDROMOUS MACROFAUNA OF ISLAND STREAMS

INTRODUCTION

The purpose of this species profile is to summarize pertinent information on a group of organisms that, while taxonomically unrelated, share a common life history pattern and require similar environmental conditions for their existence.

The term "amphidromous" was first used by Myers (1949) to describe diadromous fishes that migrate to and from the sea but not specifically for reproductive purposes. These life history patterns and their evolution have been recently reviewed by Gross (1987) and McDowall (1987, 1988). The species dealt with here consist of animals that live their entire adult lives in running freshwater habitats, but spend their larval period as marine zooplankton.

Three phyla will be covered: Chordata, Class Osteichthyes; Mollusca, Class Gastropoda; and Arthropoda, Class Crustacea. These comprise the three major animal groups that have taken up the amphidromous mode of life. In some regions, they coexist with other animals that have different life history patterns, such as aquatic insects, itinerant (Myers 1949) marine fishes, primary and secondary division freshwater fishes (Myers 1938), introduced organisms, and smaller, less conspicuous animals (notably crustaceans, nematodes, and annelids) that are likely to be important components of aquatic systems but about which little is known.

Amphidromous fishes and invertebrates occur on continents and on continental and oceanic islands in both tropical and warm temperate regions (McDowall 1987, 1988). The common environmental parameter is the occurrence of lotic freshwater systems flowing into the marine environment. Because of the paucity of attention amphidromous animals have received, this report will almost exclusively concentrate on species occurring in the Hawaiian Islands, one of the few regions where this fauna has been studied to any extent. However, it should be pointed out that related species with very similar life history patterns occur in many areas of particular concern to agencies of the United States government or areas where these agencies operate or cooperate with other governments. Areas under direct US jurisdiction include Puerto Rico, US Virgin Islands, American Samoa, northern Marianas Islands, and Guam. Additional areas of interest include nations formerly a part of the US Trust Territories, Federated States of Micronesia (Truk, Pohnpei), Belau, and areas where the
United States maintains some continued presence or interest (e.g. the Philippines, Japan, Caribbean island nations). Where appropriate, reference will be made to available information on the amphidromous fauna of these regions.

HAWAIIAN AMPHIDROMOUS MICROFAUNA

Table 1 lists the Hawaiian amphidromous animals together with their common name(s) and biogeographical status. Several very important groups of stream animals, often rich in endemic and potentially threatened species, are not included in this table. Notably absent are the endemic lymnaeid snails (Hubendick 1952, Burch 1968, Morrison 1968), stream insects (particularly the endemic damselfly genus *Megalagron* (Cowles 1977, Maciolek and Howarth 1979), as well as sponges and polychaetes (Bailey-Brock 1987). The common feature that links the species in Table 1 is that they all share the amphidromous life history pattern, and so require free access to the sea both for the downstream movement of the newly hatched individuals, and the recruitment and upstream migration phase of the juveniles.

Due to the small number of amphidromous species in Hawaiian streams and their distinct appearance, no keys for identification are needed. Rather, characteristic features useful for field identification will be given in the following descriptive section.

SPECIES ACCOUNTS: GOBIOID FISHES

*Eleotris sandwicensis* (Vaillant and Sauvage, 1875)

There has been little study either of the systematics or the ecology of *Eleotris sandwicensis* (Figure 1). Its systematics were briefly discussed by Mainland (1939), and Gosline and Brock (1960) gave the most recent treatment. Currently, *E. sandwicensis* is considered to be endemic to the Hawaiian Islands, but this status could change with further study of the genus throughout the Pacific. It has at times been included in *E. fusca* (Schneider, 1901), a widespread Pacific species (Mainland 1939).

*Eleotris sandwicensis* is common on all the Hawaiian islands that support streams, even in very altered streams such as those that occur on O'ahu (where it is frequently attacked by the North American leech *Myzobdella lugubris*).

*Eleotris sandwicensis* attains a standard length (SL) of at least 25 cm. The color is generally dark brown or black. Eleotrids with two fairly distinct head shapes occur in Hawaiian streams, but it is not known if there is a continuum or two distinct types. Because of the unfused pelvic fins, there is no problem distinguishing even very small individuals of *E. sandwicensis* from the true stream gobies.

Nothing is known about the reproduction of this species, but eleotrid larvae are commonly taken in plankton tows as far as 11 km off windward O'ahu (T. Clarke, Hawai'i Institute of Marine Biology, pers. comm.).

*Eleotris sandwicensis* is typically found in estuaries and lower stream reaches, though it does occur farther inland in low gradient streams (Mainland 1939). Norton, Timbol, and Parrish (1978) report that this species is euryhaline. Because it lacks the paired pelvic fins of the true gobies, it cannot climb waterfalls, and its upstream limit is often set by the first substantial waterfall.
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* These two snails are almost entirely restricted to estuaries as are many populations of *N. vespertina*, but because of their systematic relationship with the truly freshwater *Neritina granosa*, and because of their amphidromous life history pattern, they are included in this table.
Eleotris sandwicensis is a voracious carnivore preying both on invertebrates and fishes (Timbol 1972, Maciolek 1981, Maciolek and Timbol 1981). Its potential impact on other stream gobies is discussed in Kinzie and Ford (1982), who hypothesized that, in streams entering the sea through estuaries or as relatively flat runs, the presence of the carnivorous eleotrid would reduce numbers of small gobies, including the juveniles of all species and the adults of Sicyoperus stimpsoni and Lentipes concolor. On the other hand, the eleotrid is not able to recruit to streams that terminate in falls or steep rapids. In these streams, the absence of the predator allows the development of substantial populations of the two smaller species even very near the ocean.

**Stenogobius genivittatus** (Cuvier and Valenciennes, 1837)

*Stenogobius genivittatus* (Figure 2) is a true goby that occurs throughout the Indo-Pacific (Jordan and Seale 1906; Norton, Timbol, and Parrish 1978) making it the only nonendemic native Hawaiian stream fish. Very little is known about its biology. Until recently, it was included with *Awaous stamineus* in the genus Chonophorus by Gosline and Brock (1960) and in the genus *Awaous* by Timbol and Maciolek (1978). However, a recent treatment of gobioid fishes (Birdsong, Murdy, and Pezold 1988) tentatively placed the genus *Stenogobius* in the Gobionellus group separate from *Awaous*.

Adults of *S. genivittatus* are easily identified by the black patch extending down and posterior from the eyes. While this color can fade when the fish are excited, it soon reappears. This black patch can be seen in juveniles as small as 14 mm (SL) and is useful in identifying small specimens. Gosline and Brock (1960) stated that this species has 13 anal fin rays, but counts of 11-13 are common. Adults may reach a size of 10 cm (SL) or more.

*Stenogobius genivittatus* occurs in lower stream reaches in most streams on the major Hawaiian islands, although there is some evidence that it is more common on O'ahu than the other main islands (Timbol and Maciolek 1978). Norton, Timbol, and Parrish (1978) stated that this species is euryhaline and can be found in brackish water. It commonly occurs in estuarine habitats or just upstream from estuarine conditions. While it has fused pelvic fins, it is not known to be able to climb waterfalls. It typically occurs on soft bottoms rather than on rocks and boulders. It feeds by burrowing with its snout into the substratum, and where densities are high, the bottom can have a characteristic dimpled appearance from the feeding activities of this species. *Stenogobius genivittatus* and *E. sandwicensis* are the only native stream fishes that occur in any
abundance on O'ahu, occurring even in altered streams.

*Stenogobius genivittatus* has been reported to be omnivorous (Norton, Timbol, and Parrish 1978), but nothing is known of its food preferences. The reproductive biology of this species in Hawai'i is unstudied. Little is known about its distribution and habitat preferences. A study of otoliths from recent recruited juvenile *S. genivittatus* has shown that the larvae may spend up to 135 days in the plankton (Radtke, Kinzie, and Folsom 1988). This planktonic period is very long when compared with typical coral reef dwelling gobies. However, there is currently no information on the amount of variation in the length of larval life of this species, so it is not known if this long planktonic life is typical of the species or not. However, the ability to remain in the plankton for such an extended period may be related to the necessity of locating a suitable adult habitat before settling can occur.

*Awaous stamineus* (Eydoux and Souleyet, 1841)

*Awaous stamineus* (Figure 3) is the largest of the Hawaiian stream gobies with males reaching total lengths (TL) of 34 cm and females 28 cm (Ego 1956). These sizes correspond to weights of 484 and 340 g, respectively. This species is fished for home consumption. *A. stamineus* is endemic to the Hawaiian Islands.

Birdsong, Murdy, and Pezold (1988) tentatively placed the circumtropical genus *Awaous* with the Sicydiine gobies, though they had reservations about this relationship. In Hawai'i, the species is found on all the major islands, although on O'ahu the population sizes and the number of streams inhabited are small. There has been no statewide survey of the distribution and abundance of *A. stamineus*, so its apparent decline on O'ahu needs to be verified. Although this species was listed as being of special concern by the American Fisheries Society due to destruction or modification of its habitat (Deacon et al. 1979), it has been given no legal protection (Johnson 1987).

*Awaous stamineus* is readily identified in the field by vertical light and dark stripes on the dorsal and caudal fins (Figure 3). Additionally, there is a dark patch at the base of the caudal fin that is helpful in identifying individuals as small as 15 mm. Males are generally larger and darker than females and tend to have broader heads and mouths. The genital papilla of females is bilobed or rounded while that of males is pointed.

The biology of *A. stamineus* was studied by Ego (1956), and most of our knowledge of this fish comes from his report. Ego (1956) found
that the longitudinal distribution pattern of this fish in Wainiha River on the island of Kaua‘i is centered in lower stream reaches, although individuals were seen 13 km inland at an elevation of 450 m. Densities above 22/100 sq m extended from 1.2-6 km inland, at corresponding elevations of 7.6-168 m above sea level. The maximum density, 74/100 sq m, occurred at a distance of 3.6 km from the stream mouth at an elevation of 46 m.

From analysis of gut contents, Ego (1956) concluded that the diet of A. stamineus consists primarily of filamentous green algae (84% by volume) with the remainder being made up of animal matter including chironomid larvae, earthworms, and snails. There was no evidence that A. stamineus eats fishes. Field observations indicate that this species feeds on the bottom, but will also frequently swim up into the water column to take material moving downstream. In an analysis of habitat utilization, Kinzie (1988) found that A. stamineus tends to occur in deeper, slower moving waters characterized by fine sediments or gravel. This species often burrows into the bottom with only its eyes showing.

Observations of nonbreeding adult A. stamineus suggest that they are not territorial, but occur in schools. They move slowly along the bottom or remain stationary while feeding together. Spawning takes place from August through November and may extend into December (Ego 1956). Apparently, spawning is initiated during the first heavy rains of the fall rainy season. The fish are thought to migrate downstream to breed. Ego (1956) never found eggs in the upper stream reaches even during the height of the breeding season in the large Kaua‘i streams he studied. Eggs are laid on the sides and upper surfaces of rocks and are guarded by both the male and female (Ego 1956). This behavior, untypical in many gobies, was substantiated by Heacock and Kido (Hawai‘i Department of Land and Natural Resources, pers. comm.). Egg masses range in size from 200-390 sq cm; Ego (1956) estimated that a 28-cm female laid 1.5 million eggs. In major spawning runs, nests may reach densities as high as 1/sq m (Heacock and Kido, Hawai‘i Department of Land and Natural Resources, pers. comm.). Ego (1956) indicated that spawning is debilitating because many dead fish were found in the lower stream reaches for several weeks following a spawning migration. More recent observations support this suggestion. One week after a major spawning run, many dead and dying A. stamineus were seen in Wainiha Stream, Kaua‘i (Heacock and Kido, Hawai‘i Department of Land and Natural Resources, pers. comm.). While some of this
mortality may have been due to the excessive use of gill nets by fishermen during the spawning run, the emaciated appearance of many of the dead fish suggests that spawning itself was at least partially responsible.

Ego (1956) reported that the fry hatch within 48 hr and are subsequently swept out to sea. Experiments with newly hatched fry indicated they have reduced tolerance to fresh water soon after hatching. This observation was substantiated by Heacock and Kido (Hawai‘i Department of Land and Natural Resources, pers. comm.). Postlarval *A. stamineus* were found entering river mouths from December through July, with peak recruitment from March to April. Previously, there was a fishery for the large numbers of returning postlarvae in Hawai‘i (Titcomb 1972). Because of diminishing numbers, this practice is now illegal, though still practiced to some extent. Radtke, Kinzie, and Folsom (1988), using otolith analyses, determined that the length of larval life of *A. stamineus* can be as long as 160 days. This estimate is very similar to that of Ego (1956), who based his value on the difference in times of peak spawning and peak recruitment. As discussed earlier for *S. genivittatus*, this extremely long larval period may be related to the amphidromous life history pattern of this fish (see page 5).

*Sicyopterus stimpsoni* (Gill, 1860)

*Sicyopterus stimpsoni* (Figures 4a, b) is a relatively small (up to 17 cm) goby. Originally known as *Sicydium stimpsoni*, this endemic species was placed in the genus *Sicyopterus* by Akihito and Meguro (1979). The genus *Sicydium* has an amphip-Amerian distribution (Fowler 1938; Erdman 1961, 1986; Bussing 1987; Birdsong, Murdy, and Pezold 1988), while *Sicyopterus* is an Indo-Pacific genus (Birdsong, Murdy, and Pezold 1988). *Sicyopterus stimpsoni* was listed as being of special concern by Deacon et al. (1979), but has no legal protection (Johnson 1987).

*Sicyopterus stimpsoni* is restricted to relatively undisturbed streams with good water quality and high rate of discharge. It is not found in streams where the habitat of this fish has been extensively altered, where exotics are abundant, or where development in the watershed has increased siltation in the habitat. This species is rare on O‘ahu; only a few individuals have been recorded in the few remaining large unaltered streams such as Kaluanui, Kahana, and Waimea (Tomihama 1972; Timbol and Maciolek 1978; Kinzie, pers. obs.). It is not known why this species has been almost eliminated from O‘ahu streams, but stream alteration (Timbol and Maciolek 1978) and diminishing water quality may be factors. O‘ahu streams are the only ones where *S. stimpsoni* have been found to be parasitized by the leech *Myzobdella lugubris*. This fish is common in good quality streams on Kaua‘i, Maui, Moloka‘i, and Hawai‘i. Streams that have been degraded by a number of causes appear to lack this species, whereas streams that have experienced little degradation often have substantial populations. On these islands, it tends to occur in middle stream reaches (from about 10-300 m elevation), though individuals can be found near stream mouths co-occurring with *A. stamineus* and *E. sandwicensis*. *Sicyopetrus stimpsoni* tends to be found in swifter water than *A. stamineus* and is more frequently seen on hard substrata rather than gravel or sand (Kinzie 1988).
Field identification of *S. stimpsoni* is most easily accomplished by observation of its characteristic feeding behavior on hard substrata. The upper jaw is extended, and the rock surface is rapidly and repeatedly scraped with the tricuspid upper jaw teeth. The coloration of this species is quite variable, and an individual can rapidly change its color pattern. Females tend to be mottled brown or gray (Figure 4a). Males may be similarly colored, but they can also rapidly show a characteristic bright white longitudinal stripe against an almost black background (Figure 4b). This stripe runs around the anterior of the head to the caudal peduncle. When displaying, males often exhibit a bright blue fluorescent margin to the caudal and anal fins. The first ray of the first dorsal fin is greatly elongated in mature males (Figure 4b). The genital papilla of females is bilobed while that of males is pointed. In most average-sized specimens, this difference is difficult to see without magnification.

*Sicyopterus stimpsoni* can be distinguished from *Lentipes concolor* by the fact that it has both a median cleft and lateral alveoli in the upper lip, whereas *L. concolor* has only a median cleft (Figure 5). This difference is useful in identifying immature and small female specimens, which are sometimes difficult to distinguish by color alone.

The biology of *S. stimpsoni* has been studied by Tomihama (1972) and Yuen (1987). Its ecology has been studied by Kinzie and Ford (1982), Kinzie et al. (1984), and Kinzie (1988). Tomihama (1972) reported that adults of *S. stimpsoni*, unlike
Figure 5. Comparison of upper lip morphology between *Lentipes concolor* (on left) with only a medial notch and *Sicyopterus stimpsoni* (on right) with a median and two lateral notches.

The other Hawaiian freshwater gobies, are strictly herbivorous, obtaining their food by scraping epilithic algae. He suggested that postlarvae returning to streams are probably omnivorous, but juveniles became more restricted in their diet with the attaining of adult morphology. Perhaps because of its restricted diet, it is very difficult to maintain *S. stimpsoni* in aquaria, whereas the other species can be maintained on a range of food items.

Yuen (1987) studied the behavioral biology of *S. stimpsoni*. He found that males are strongly territorial with typical territory size being about 1 sq m. Males are particularly aggressive to conspecific males, though aggressive behavior is also directed towards other species and sometimes to conspecific females. Males display elaborate courting behavior towards conspecific females.

*Sicyopterus stimpsoni* lays demersal eggs. Tomihama (1972) found ripe ovaries from August through February, although neither he nor Yuen (1987) ever observed spawning. Tomihama (1972) found ovaries with as many as 160,000 eggs (8.9 cm SL female). A nest with eggs that may have been from *S. stimpsoni* had about 20,000 eggs, but Tomihama (1972) did not see the parent, so the species attribution is not certain. Hatching from egg masses collected from the stream occurred in 24 hr. Fry lived 7 days in seawater and 5 days in fresh water. This is similar to the findings of Ego (1956) for *A. stamineus*. Postlarvae were seen returning to streams from January to August. From the time difference between peak spawning and the return of postlarvae, Tomihama (1972) estimated that larval life is about 5 months in duration. No age determination studies (e.g. daily otolith increments) have been carried out on this species.

*Lentipes concolor* (Gill, 1860)

*Lentipes concolor* (Figures 6a, b) is the rarest of the Hawaiian stream gobies. It was listed as threatened by the American Fisheries Society (Deacon et al. 1979) and is currently a category one endangered species candidate (Dodd et al. 1985), although it has no protected status at the state level (Johnson 1987).

Prior to 1973, there were two names used for Hawaiian *Lentipes*: *L. concolor* and *L. seminudus*. The taxonomy of the Hawaiian species was clarified by Lau (1973) and Maciolek (1977). Until 1979, the genus was monotypic making *Lentipes* an endemic genus, a rarity on the Pacific plate.
Figure 6a. *Lentipes concolor* 4.0-cm (SL) female

Figure 6b. *Lentipes concolor* 5.8-cm (SL) male

(Springer 1982). Sakai and Nakamura (1979) described *L. armatus* as a new species from Ishigaki Island in the Ryukyus. However, the status of the genus is still not settled.

While *L. concolor* was found on O'ahu in the last century (Gunther 1880), it has been extirpated on that island. It still occurs on other islands, and a statewide survey (Timbol, Sutter, and Parrish 1980) found it in 36 streams and estimated that approximately 20 more streams might harbor this species. This total accounts for only 15% of the perennial streams in the state. Maciolek's (1977) earlier estimate put the number of streams in the state with this species at only 6%.

*Lentipes concolor* generally occurs at middle to higher elevations (to 500 m) in perennial stream on the windward sides of all the major Hawaiian Islands except O'ahu. This species is a strong climber and has been reported to surmount single waterfalls 100 m high as well as a series of six falls with a combined height of 300 m (Maciolek 1977). *Lentipes* is generally restricted to relatively undisturbed streams in remote areas. Decline of this species on O'ahu and on other islands correlates with intensity of human impact, but specific causes have not been identified. Channelization and other forms of stream alteration are the most likely factors at this time (Norton, Timbol, and Parrish 1978; Parrish et al. 1978). In addition, Lau (1973) observed that populations of *L. concolor* in Pi'ina'au Stream on Maui declined markedly after the construction of an arboretum near the stream. The few remaining fish in the stream were all found to be infected with the epizootic protozoan *Ichthyophthirius multifilis*.

While *L. concolor* is typically found at the upper end of the longitudinal distribution of Hawaiian stream fishes, adults are sometimes found at stream mouths. This pattern generally occurs in small streams that enter the sea as waterfalls rather than in estuaries or low gradient reaches. It has been suggested that streams that enter the sea as waterfalls, thereby excluding the carnivorous *E. sandwicensis*, may allow
*L. concolor* to occur at low elevations in these streams (Kinzie and Ford 1979).

Adults of *L. concolor* are readily identified in the field. Males, particularly when interacting aggressively, have a very marked color pattern (Timbol, Sutter, and Parrish 1980; Nishimoto and Fitzsimons 1986). The anterior half of the body of displaying males is almost black and is divided from the bright red or orange posterior by a distinct vertical margin at about the anterior end of the second dorsal fin (Figure 6b). At the most intense levels of this display, both dorsal fins and the anal fin are brilliant white; these, plus the caudal fin, may have a fluorescent blue margin. Nishimoto and Fitzsimons (1986) related various levels of aggression to the gradual escalation of the male coloration pattern. The male coloration pattern can change rapidly, fading to the nonaggressive overall olive-to-brown mode in less than a minute, as well as back to the display pattern as quickly. Even when not displaying, adult males generally have some suggestion of the bicolor pattern, facilitating field identification. Adult females typically have a marbled olive-green to yellow-brown color over all of the body. It is often quite difficult to differentiate between males and females in specimens less than 35 mm TL. The most likely source of confusion between species in the field is in attempting to separate juvenile or small adult *S. stimpsoni* from female and small male *L. concolor*. In general, the pectoral fins of *L. concolor* are somewhat larger and rounder and are held almost perpendicular to the body. The lack of lateral alveoli in the upper lip in *L. concolor* can be used for positive separation from *S. stimpsoni*, which possesses them, when specimens are in hand (Figure 5). This difference is noticeable even with very small specimens.

*Lentipes concolor* has received a good deal of attention because of its rarity. Lau (1973) surveyed gut contents and concluded that this species is omnivorous, with atyid shrimps and microalgae (including diatoms) making up the majority of the diet. He suggested that smaller specimens tend to be more herbivorous while larger fish consume more animal material. Males are also more carnivorous than females, though it was not determined if this is due to the larger average size of males or to differences in dentition between the sexes (Lau 1973, Maciolek 1977). Personal observations in streams and aquaria suggest that, in addition to the bottom-foraging behavior also commonly observed, *L. concolor* readily swims up into the water column to actively take drift particles.

Little attention had been paid to the breeding biology of *L. concolor* until recently. Maciolek (1977) noted that ovaries from two females (46 and 57 mm TL) had 7,000 and 14,000 eggs respectively. Timbol, Sutter, and Parrish (1980) surveyed gonads in 25 females (mean 50.6 mm SL and a range of 38.6-50.6 mm SL) and found a mean of 14,000 eggs with a range of 4,000-30,000. Unfortunately, they did not give collection dates for the gonad samples. Until very recently, there had been only a single report of *L. concolor* nesting. A recent program to investigate breeding biology of *L. concolor* involved an intensive search for nests in the field, as well as an experimental breeding study in a large aquarium (Kinzie, pers. obs.). Nests were found from October to May in the field, and eggs were laid in the tank on four occasions from January to early June. These observations suggest a breeding season running from fall to late spring.
Clutch sizes were estimated from egg density (approximately 3.5 eggs/sq mm) and total area of the egg masses. Estimates of total number of eggs per clutch ranges from 5,900-24,700. The diameter of fresh eggs is about 0.5 mm, a value similar to preserved material. Field observations suggest that hatching may occur as soon as 24-48 hr after laying, a value similar to that reported by Tomihama (1972) for Sicyopterus stimpsoni, by Manacop (1953) for S. extraneus, and Dotu and Mito (1955) for S. (as Sicydium) japonicus. Results from observations in aquaria suggest, however, that hatching does not occur under laboratory conditions until day 4-6. Newly hatched fry are approximately 1.8 mm TL, a value only slightly larger than that reported by Dotu and Mito (1955) and Manacop (1963) for Sicyopterus spp. Apparently, the larvae cannot survive more than a few days in fresh water, a finding similar to that of Ego (1956) for A. stamineus. No data exist pertaining to length of larval life of this species, and recruitment has been poorly documented. Kinzie and Ford (1982) reported that returning postlarvae were observed from February to May.

**CRUSTACEA**

*Atyoida bisulcata* (Randall, 1840)

*Atyoida bisulcata* (Figure 7) is a caridean decapod crustacean endemic to the Hawaiian Islands. It is one of two freshwater atyids that have been described from Hawai'i: *A. bisulcata* (Randall, 1840) and *Ortmannia henshawi* (Rathbun, 1901). Edmondson (1929) suggested that these might be the same species. In an extensive study of the Hawaiian freshwater atyids, Couret (1976) concluded that Edmondson's suspicion was correct and that there is but a single freshwater species known. Recently, Chace (1983) revised the group and reestablished the genus *Atyoida*, which includes the Hawaiian stream species. Two other genera of atyid shrimps occur in Hawai'i but are found in anchialine ponds and not streams (Holthuis 1973, Maciolek 1983). The genus *Atyoida* is found on high islands of the Indo-Pacific from Madagascar to as far East as Hawai'i, the Marquesas, and the Gambier Islands.

*Atyoida bisulcata* is widespread in Hawai'i. Couret (1976) stated that it is found in the upper reaches of nearly every perennial stream in Hawai'i and that it has an upper limit of at least 100 m. While this shrimp apparently can tolerate brackish water, it is not normally found at stream mouths. Edmondson (1929) gave its lower distributional limit as 5-m elevation. While it has been found somewhat lower than this more recently, it is not a typical inhabitant of estuaries. It can be found in habitats ranging from quiet pools to shooting velocities (2-3 m/sec) under falls. Typically, this species is found in streams with swiftly flowing water. It is frequently found in dense aggregations and is probably the most abundant and widespread of the native Hawaiian amphidromous species.

There is little difficulty in identifying adult *A. bisulcata* because they are the only stream carideans lacking a pronounced rostrum and having small chelae. Determination of the sex of specimens can be more difficult. Couret (1976) gave several morphological characters that are useful in making sex determinations. Females are typically larger than males and have shorter antennal flagella (typically not reaching the tip of the telson). The pleural cavity of females, where the embryos are carried, is wider and deeper than in males. The
endopod of the first pleopod of females lies perpendicular to the
exopod and is somewhat larger, while
that of males is "S" shaped and
parallel to the exopod. Addition-
ally, the endopod of males is some-
what shorter than the exopod. The
postlarvae of *Atyoida bisulcata* can be
confused with postlarvae of either
of the two species of *Macrobrachium*
described below. The easiest way of
separating postlarvae of the two
genera is by rostral length. Atyid
postlarvae have a very small
rostrum, while rostra of postlarvae
of both prawn species are
pronounced.

Couret (1976) gave a detailed
account of the feeding behavior of
*Atyoida bisulcata*, pointing out that this
species exhibits two feeding modes.
In moderately fast-moving water, the
shrimp act as passive filter feeders
taking particulate material from the
downstream drift. The shrimp orient
themselves into the current and
extend the fanlike setae of the
chelipeds up into the current.
Periodically, the chelipeds alter-
nately close and bring the trapped
material to the mouth. When densi-
ties are high, these shrimp may
align themselves side-by-side in
rows or concentric arcs facing into
the current. This behavior has also
been noted in Caribbean atyids by
Covich (1988). In slower water
flow, the second method of feeding
is employed. The substratum is
brushed with the setae of the cheli-
peds, and detritus and epilithic
algae are collected and brought to
the mouth for feeding.

*Atyoida bisulcata* appears to
reproduce throughout the year.
Couret (1976) reported continual
reproduction with a suggestion of a
late summer peak in O‘ahu streams.
Kinzie and Ford (1982) found no
marked seasonality in percent
ovigerous females in two Maui
streams. Generally, at least 50% of
the females are ovigerous at any
time, and Couret (1976) found values
as high as 80%. He also presented
data suggesting that females may
produce a clutch as frequently as
every 66 days. Couret (1976) found
that the average clutch is about
3,000 eggs, suggesting a possible
annual fecundity of
16-17,000 larvae/year. Hatching

Figure 7. *Atyoida bisulcata* 8 mm (Post-Orbital Carapace Length (POCL)).
takes place at about day 63. While unsuccessful in rearing larvae to settlement, Couret (1976) found that the larvae apparently require saltwater for survival, a condition similar to that found for the gobiid fish larvae. While he was not able to metamorphose the experimental larvae, he did maintain them to a length of 8.5 mm (TL) and an age of 100 days.

There is little information on seasonality or timing of recruitment. Postlarval A. bisulcata have been seen in most months. A mass settling event was observed in February in Pepeaolepo Stream on East Maui (Kinzie and Ford 1982), when thousands of postlarval A. bisulcata were observed in the brackish water flowing through boulders between the stream mouth and the sea. Individuals as small as 2 mm (postorbital carapace length) were observed. Animals this size were estimated by Couret (1976) to be in their first week of benthic existence.

**Macrobrachium grandimanus** (Randall, 1840)

Macrobrachium grandimanus (Figure 8) was originally described from the Hawaiian Islands as *Palemon grandimanus* by Randall (1840) and for some time was thought to be endemic to Hawai‘i. More recently, the species has been reported from the Ryukyu Islands by Holthuis (1950, 1973); however, there have been no other reports of this species from elsewhere in the Pacific. Lovett (1981) included *M. grandimanus* in his compilation of carideans from the Malaysia-Singapore region, though he stated that his keys were assembled from the literature and he made no statement as to the presence or absence of this prawn in Malaysia. Its small size, relative to many congeners, makes it of less interest as a food item, so it has not received much attention from aquaculturists.

Macrobrachium grandimanus is typically a low elevation species. Kubota (1972) found that *M. grandimanus* reached elevations of 64 m, 4.9 km inland from the mouth of Kahana Stream, O‘ahu. However, the species was common only below about 12-m elevation. While no study has been devoted to this species, the works of Kubota (1972), Timbol (1972), Maciolek (1981), and Maciolek and Timbol (1981) indicate that *M. grandimanus* can be quite common in estuaries. In their study of Kahana Estuary on O‘ahu, Maciolek and Timbol (1981) found *M. grandimanus* to be the most common crustacean in their study area. It is also commonly found in anchialine ponds and brackish coastal wetlands (Holthuis 1950, Brock and Norris 1988). This species probably occurs on all the main Hawaiian Islands though there has been no systematic collecting.

There are presently two introduced species of *Macrobrachium* in Hawai‘i. One of these, *M. lar*, is widespread in most natural streams. The other, *M. rosenbergii*, has been found in Kahana estuary (Kubota, 1972; Timbol, 1972), in the Opaeula and Helemano Streams on O‘ahu, and in the Kuiaha Stream on Maui (Div. of Aquatic Resources, Dept. of Land and Natural Resources, State of Hawai‘i, unpublished data). *Macrobrachium grandimanus* is most easily identified by the greatly inflated chela of the males. Generally, one of the chelae of males is much larger than the other. Both appendages typically have a longitudinally striped pattern. Both males and females can be differentiated from *M. lar* by the rostral teeth. Rostra of *M. grandimanus* have 15 dorsal and 4 ventral teeth while *M. lar* generally have 8 dorsal and 2 ventral teeth. The much larger *M. rosenbergii* has 13-14 dorsal and 8-14 ventral rostral teeth. *Macrobrachium grandimanus* is
typically smaller than both of its congeners, reaching a maximum size of about 7 cm TL.

*Macrobrachium grandimanus* is probably a generalist bottom scavenger. Maciolek (1981) reported that 92% of the stomach contents was "detritus," but because of the mode of feeding of most crustaceans, the preponderance of unidentifiable material is expected. Kubota (1972) stated that *M. grandimanus* is truly euryhaline, occurring in water with salinities reaching 25 parts per thousand (ppt). Walsh (1963) carried out salinity tolerance tests on *M. grandimanus* and found that it can survive salinities ranging from 0.46-35 ppt.

Almost nothing is known about the reproductive biology of *M. grandimanus*. Maciolek and Timbol (1981) reported only that breeding *M. grandimanus* were found in their Kahana Estuary study area. Maciolek (1972) suggested that *M. lar* might be responsible for the diminished numbers of *M. grandimanus* in some streams, but this possibility has not been studied.

*Macrobrachium lar* (Fabricius, 1798)

While *Macrobrachium lar* (Figure 9) is an introduced species, it has the same amphidromous life history pattern as the native species discussed previously. This fact and its abundance in many otherwise pristine streams are the reasons for its inclusion in this report. *Macrobrachium lar* is a very widespread and common Indo-Pacific prawn that ranges from East Africa to the Marquesas. It was introduced to the Hawaiian Islands from Guam in 1956 and from Guam and Tahiti in 1957. Kubota (1972) and Maciolek (1972) traced the stocking efforts and spread of this species through Hawai‘i. Maciolek (1972) indicated that by 1969 *M. lar* was sighted in 42 streams and occurred on all islands. He extrapolated that by 1972 *M. lar* would be found in every inhabitable stream in Hawai‘i, a
prediction strongly supported by subsequent observations.

Kubota (1972) carried out extensive studies on the distribution and biology of *M. lar*, focusing on the population in Kahana Estuary. As stated previously, *M. lar* generally has 8 dorsal and 2 ventral rostral teeth which serve to distinguish it from the other two species of *Macrobrachium* in Hawai‘i. Kubota (1972) reported a range in dorsal rostral teeth of 7-10. The dentition of the rostrum of Hawaiian *M. lar* more closely resembles those from Tahiti than those from Guam, suggesting that the former location provided the source of the successful introduction.

Although males of *Macrobrachium lar* reach 16 cm (SL), females as large as 14 cm are not common. Males have very large, chelate second walking legs that are up to 36 cm from tip to base of the coxa and can make up to 20% of the total mass. Females have smaller chelate second walking legs usually making up less than 10% of the total mass.

Postlarval *Macrobrachium* spp. can be differentiated from postlarval *A. bisulcata* by the presence of a much larger rostrum. Kubota (1972) observed that larval and postlarval individuals of the three *Macrobrachium* species are very difficult to distinguish.

Kubota (1972) found that *M. lar* is an omnivorous bottom scavenger. By analyses of stomach contents and observations of individuals in aquaria, he determined that *M. lar* consumes both animal (fish, insects, crustaceans) and plant material. Feeding generally took place at night as evidenced by full guts in early morning and empty stomachs late in the day. Kubota (1972) also analyzed courtship and mating behavior of *M. lar*.

Berried females were found in Kahana throughout the year, but there is a peak in winter and spring (Kubota 1972). Kinzie and Ford (1982) found a different trend in streams on Maui and Kaua‘i, with percent berried females being highest in summer and fall. Kubota (1972) determined that females can potentially breed every 30-40 days under ideal conditions, with females carrying the developing embryos for 27-31 days. He attempted to rear the larvae but succeeded in obtaining only five zoeal stages. Kubota (1972) found some suggestion of a downstream breeding migration in *M. lar* based on relative numbers of berried and spent females in different parts of Kahana Stream. However, he cited several instances
both from Kahana and from other areas where such a migration probably did not occur. Kubota (1972) suggested that most of the females that migrate to the estuary to spawn die there. He based this conclusion on low recaptures of marked individuals. However, he did not see any evidence of mortality such as is common with *Awaous stamineus*.

Kubota (1972) estimated that the planktonic larval period lasts 30-50 days based on comparison with the development time of the congener *Macrobrachium rosenbergii*. Kubota (1972) stated that recruitment occurs throughout the year, without giving any indication of seasonal peaks in this process. Similarly, Kinzie and Ford (1982) found evidence of recruitment throughout the year, although they suggested that a broad and poorly defined recruitment peak might occur in summer and fall.

**MOLLUSCA**

*Neritina granosa* (Sowerby, 1825)

The circumtropical genus *Neritina* is represented in Hawai‘i by two endemic species. *Neritina granosa* is the only fully freshwater neritid in the state. While some early accounts listed *N. granosa* from other Pacific Islands, the locality data are apparently in error (Ford 1979). The biology of this prosobranch gastropod was studied by Ford (1979), whose thesis forms the basis of much of this account.

Island groups to the west of Hawai‘i have a richer representation of *Neritina* in their freshwater habitats (Haynes 1988). Haynes (1984) listed 11 species of *Neritina* from fresh and brackish water in Fiji, and Maciolek and Ford (1987) listed four species from Pohnpei. This west-to-east decrease in species richness, also seen in the amphidromous fishes and crustaceans, is a common biogeographical pattern in the tropical Pacific.

In Hawai‘i, *N. granosa* is generally restricted to the lower and middle reaches of perennial streams. Ford (1979) estimated that less than 50 streams in the state have large populations of *N. granosa*. The species is uncommon on O‘ahu, perhaps due to alteration of streams associated with human activities. Ford (1979) found *N. granosa* in only two streams on O‘ahu.

This species is apparently attracted to shallow, well-oxygenated streams with clean basalt boulders and coarse gravel. Individuals are typically located on the undersides of rocks in falls or under boulders often partly buried in gravel. Silty or shifting sandy substrata are not utilized. The upper elevation limit of *N. granosa* is approximately 400 m (Maciolek 1978), and individuals can be found to sea level. Ford (1979) reported that the upper elevation limit differed among streams depending to some extent on discharge and the presence of stream diversions. Streams with high flows have populations of *N. granosa* at higher elevations than smaller streams with low flows. Additionally, Ford (1979) did not find significant numbers in estuarine or low elevation, low gradient reaches. He hypothesized that the sluggish flows, strong thermal stratification, and silty substrata served to exclude this snail from these habitats. Populations have been found in very small rheocrenes or seeps near the shoreline. Snails in these very shallow habitats can have the dorsal part of the shell out of the water, though moist. It is likely that postlarvae were recruited to these unsuitable habitats and, once metamorphosis had occurred, the snails were forced to
remain there. Predation, particularly by sea birds, appears to be intense in these peculiar habitats.

Maciolek (1978) described an apparent shell dimorphism in this species which was further studied by Ford (1979). Specimens from lower elevations have the adult shell compressed with a reduced spire (Figure 10a). The lips of the outer growth margin are irregularly crenelated, and the lateral extensions of the outer margins of the growth region form winglike projections. The dorsal shell surface is covered with small concentric ribs and closely spaced granulations. The periostracum is black with irregularly spaced light brown spots. Individuals from higher elevations lack the flared winglike projections resulting in a shell that is longer than wide. The shell surface is generally smooth or bears only fine concentric striations (Figure 10b). The shell opening of both types is white, while the colure area is yellow to orange. The uncalcified operculum is red to maroon. Newly recruited individuals are less than 3 mm in length and have smooth, globose shells with prominent concentrically placed light-brown spots. Adults reach lengths of almost 49 mm, although individuals in the range of 24-46 mm are more common.

The low elevation morph is generally restricted to reaches below the first waterfall while the smooth upstream morph occurs above the falls. Ford (1979) experimentally demonstrated that these two forms are environmentally induced ecotypes. An individual transplanted to the alternate habitat will lay down the alternate shell type.

_Neritina granosa_ is herbivorous, rasping epilithic algae from rock surfaces. Ford (1979) found that diatoms, desmids, and filamentous algae comprise much of the diet of this snail. Ford (1979) listed possible competitors of this species, but the very high population densities sometimes attained by _N. granosa_ suggest that food availability may not be limiting in many populations. Predation on adults is probably restricted to birds. In addition to sea bird predation, Ford (1979) observed both the Hawaiian black-crowned night-heron (_Nycticorax nycticorax hoactli_) and the migratory wandering tattler (_Heteroscelus incanus_) feeding on _N. granosa_. This species is sometimes gathered for human consumption, and the low frequency of very large individuals in streams with easy access may be attributable to this factor.

_Neritina granosa_ is gonochoric. The males may be recognized by the presence of a penis, located medial to the right cephalic tentacle. Ford (1979) found sex ratios close to 1:1 in his study streams. Fertilization is internal, and eggs are laid in capsules attached to rocks or the shells of other _N. granosa_. Ford (1979) found an average of 250 eggs/capsule and about 30 capsules/clutch. Most laying appears to occur between June and August, though fresh egg capsules may be found throughout the year. Ford (1979) attempted to rear veligers, and although unsuccessful, he found that the larvae, like those of the amphidromous fishes and crustaceans, survived longer if they were transferred to saline conditions soon after hatching. Ford (1979) suggested, based on peak spawning and recruitment times, that the larval life may be as long as 1 year. Recruitment is highest in the summer months. Frequently, very large numbers of newly recruited animals can be found moving upstream apparently following mucus trails with "parades" of up to 80 snails. Ford (1979) reported densities of over 1,000 individuals/sq m in some
of his samples. These newly recruited individuals are about 3 mm in length and, at this size, the potential for predation is great. While it has not been documented, it is likely that, besides birds, both fishes and crustaceans take significant numbers of the recruits.

Other Mollusca

Kay (1979) listed three species of Theodoxus occurring in Hawai‘i, all three being endemic estuarine species. Recently Haynes (1988) has revised this group transferring Theodoxus vespertinus (Sowerby, 1849) to the genus Neritina. Neritina vespertina (Figure 11) is the most common of the three, occurring in fair numbers in estuaries and lower stream reaches on all islands in the State. This snail is pale brown, and the shell is thin relative to the other fresh and brackish water neritids. Haynes (1988) placed the two remaining species which had been in Theodoxus into Clithon. Clithon cariosus (Wood, 1828) has a smooth black shell marked by fine growth lines.

This species tends to have the lateral margins developed into "wings" similar to Neritina granosa and N. vespertina. The other species Clithon neglectus (Pease, 1861) has a smooth black shell with white flecks. The "wings" are not as broadly developed as in the other species. There is very little information on the biology of any of these three species.

GENERAL CHARACTERISTICS OF THE AMPHIDROMOUS FAUNA

As indicated in the species accounts, the two primary ecological requirements common to all of the Hawaiian stream species listed are the presence of a marine planktonic larval stage and the need to pass through a stream mouth two times in the life of each individual. These requirements limit the distribution of the species to streams that have a permanent (perennial) or at least seasonal (intermittent) exorheic flow. Streams that have a
A serious deterrent to the formulation of rational management practices for native amphidromous species is the lack of knowledge of their population biology, general life history, genetic structure and island and statewide distributions. Two possible extreme scenarios illustrate the problems involved. In the first instance, while a species may be found in both large and small streams, only a few or even one breeding population may be responsible for the bulk of the reproductive output of the entire species. In this case, habitat destruction in the majority of the streams would have little impact on the species as a whole, but any degradation of the primary breeding stream could be disastrous. Because so little is known about the genetic structure of any of these species or about the ocean current patterns among the islands, we could not identify which streams would be the important ones if this scenario were true.

At the other extreme, it is possible that each stream with a population of adults contributes recruits to the total species pool in proportion to the adult population size, modified by chance events including unusual streamflow events, offshore currents, and conditions at potential settling sites. In this case, reduction of the suitability of any stream would reduce the reproductive potential of the total population in proportion to the reduction in numbers of adults in the stream.

The actual situation probably lies somewhere between these two extremes, but because of an almost total lack of information, judgments cannot be made about the relative expendability of any potential breeding population. Given this situation, the most careful review should be given to any proposed action that could potentially
interfere with the link between the freshwater habitats and the sea. Because we cannot evaluate the potential effect of an action on the species, extreme caution is advised in each instance where any of the native populations are threatened by a proposed activity, particularly in the critical lower elevations.

Where projects will result in diminished discharge, particularly in the dry months, a site-specific study should be made to assess the potential impact of the reduced flows. Of particular concern are the two migratory life history stages when fry move out to the sea and when the postlarvae migrate back to the freshwater habitat.

A further consideration when discharge will be diminished is that periodic flushing flows may be eliminated. While there has been no study of the importance of these natural channel-clearing events in Hawaiian streams, the opening and closing of bars across stream mouths are likely to be major environmental events in the lives of Hawaiian amphidromous animals. Additionally, the importance of these periodic high flow events in clearing the habitat of silt and detritus has not been evaluated. It is known that most of the endemic species appear to prefer clean rather than detritus and silt-covered substrata. This would suggest that periodic high flows may be necessary to maintain habitat quality for these species.

When channel modification is being considered, every effort should be made to maintain the complex natural substratum. Additionally, riparian vegetation should be allowed to remain to provide cover and shading reduce temperature extremes. Past attempts to provide substratum enhancement by embedding boulders in the concrete floor of channelized streams have not been shown to provide any useful habitat for migrating amphidromous animals.

Impacts caused by hydropower development are of two sorts. First, the damming of flows at the intake for the water supply may result in reduced or complete elimination of passage habitat below the dam. Secondly, there is the possibility of entrainment into the penstock. The former impact may be avoided by ensuring adequate flow at all seasons in the reaches between the dam intake and the point where the water is returned to the channel. The latter impact may be minimized by proper designing of the intake screens and by maintaining adequate water flow patterns near the intakes.

Another possible mitigation procedure for any project that would substantially dewater a stream would be to require the purchase of water for rewatering of a currently dry stream. This would be practical in areas where ditches, flumes, pipelines, etc., intercept one or more streams leaving them dry below the diversion. While there has been no study of the extent that dry streams, once restored to a flowing state, might attract recruits, the possibility should be investigated.

In addition to the short-term measures outlined here, there is a great need to increase understanding of the most basic biology of these organisms and the stream systems that are their habitat. Recommended further research includes investigation of the breeding structure, population dynamics, distributions, larval life history, and genetic structure of these populations. Also, the lack of information on the effects of exotic species must be addressed both in terms of direct impact and in terms of indirect effects when native and exotic species come into contact in altered
habitats. Without this information it is not possible to make reasonable and responsible resource management decisions.
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