

Alien Rainbow Trout (*Oncorhynchus mykiss*) (Salmoniformes: Salmonidae) Diet in Hawaiian Streams¹

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ABSTRACT: Diet of rainbow trout, *Oncorhynchus mykiss* (Walbaum), introduced by the State of Hawai'i into tropical headwater streams of the Waimea River in the Kōke'e area of the Hawaiian island of Kaua'i, was examined in this study through gut content analysis. In Wai'alaie Stream, rainbow trout were found to be opportunistic general predators efficient at feeding on invertebrate drift. Foods eaten ranged from juvenile trout, to terrestrial and aquatic arthropods, to algae and aquatic mosses. Native aquatic species, particularly dragonfly (*Anax strennus*) and damselfly (*Megalagrion heterogamias*) naiads, lymnaeid snails (*Erinna aulacospira*), and atyid shrimp (*Atyoida bisulcata*), were determined to be major foods for alien trout. Terrestrial invertebrates (primarily arthropods), however, provided a substantial (albeit unpredictable) additional food supply. Based on results of the study, it is cautioned that large numbers of rainbow trout indiscriminantly released into lower- to middle-elevation reaches of Hawaiian streams could do substantial damage to populations of native aquatic species through predation, competition, and/or habitat alteration.

RAINBOW TROUT, *Oncorhynchus mykiss* (Walbaum), along with several other Salmoniformes (Salmonidae), were introduced into Hawaiian Island streams early in the century to create a freshwater sportfishery in a tropical setting. Rainbow trout were first imported into Hawai'i by the Board of Agriculture and Forestry in 1920, eastern brook trout (*Salvelinus fontinalis* (Mitchill)) in 1876, chinook salmon (*Oncorhynchus tshawytscha* (Walbaum)) in 1876, and brown trout (*Salmo trutta* Linnaeus) in 1935 (Needham and Welsh 1953). Despite large numbers of imported salmonid fry releases in streams on all of the major islands during those early years, only rainbow trout took hold, and only in two streams (Kōke'e and Kuaikananā) in

the high-elevation (ca. 3500 ft [1067 m]) Kōke'e area of Kaua'i Island (Figure 1) (Needham and Welsh 1953). By 1941, only Kōke'e streams were being stocked. From 1955 to the present, rainbow fry reared from fertile eggs imported from a California hatchery by the Hawai'i Department of Land and Natural Resources have been released in various streams and reservoirs in the Kōke'e area to supplement fishery stocks seasonally open to public fishing. From 1990 to 1996, 28,122 licensed anglers captured 62,364 rainbow trout during annual open fishing seasons in Kōke'e (D. Shinno, pers. comm.).

In the early years of the Hawai'i salmonid stocking program, little attention was given to the potential adverse effects these aliens might have on native aquatic species through predation and competition or disease and parasite transmission. And why should there have been? At the time in the United States, introduction of nonindigenous fishes was a primary management tool for fisheries workers and enhancement of sportfisheries was a motivational feature of most fisheries programs (Radonski et al. 1984). Indeed, alien trout as opposed to natives were the value-

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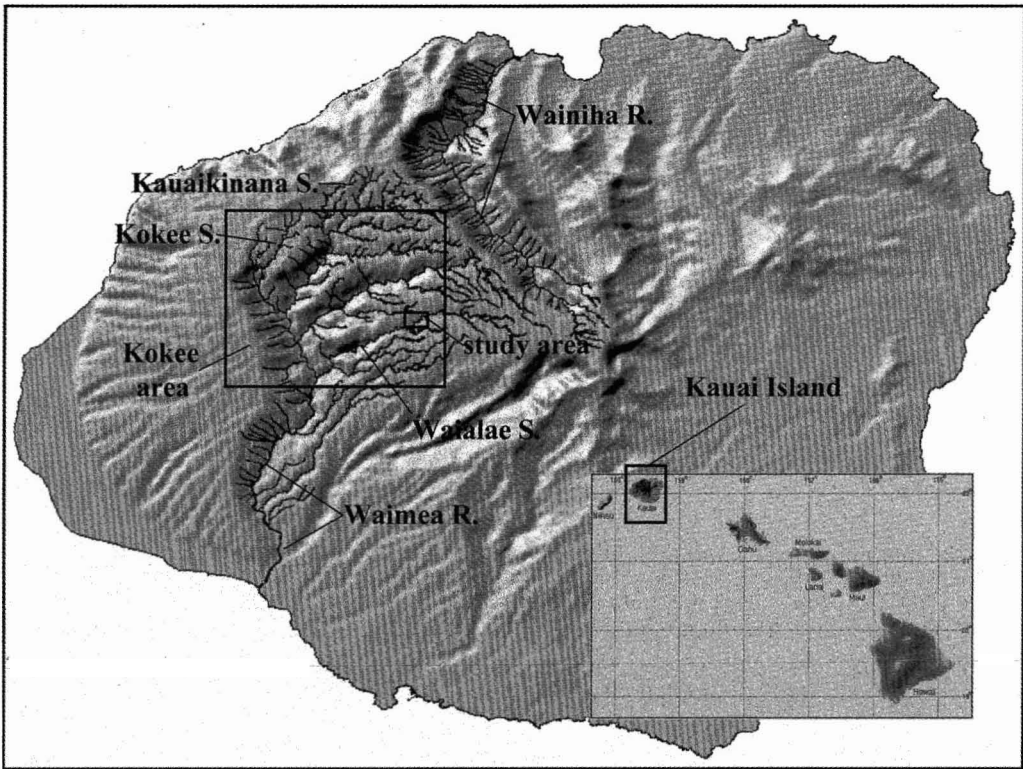


FIGURE 1. Kōke'e area on the Hawaiian island of Kaua'i: location of Wainiha River and headwater streams of the Waimea River (Kōke'e, Kauaikananā, and Wai'ālae Streams) where alien rainbow trout have been introduced. Boxed area in Wai'ālae Stream delineates approximate study area at ca. 1097 m (3600 ft) elevation.

laden species. For example, Needham and Welsh (1953), on contract to develop the potential food and sport value of a Hawaiian trout fishery, remarked on enormous populations of native torrent midges (*Telmatogeton* spp.: Chironomidae) that might serve as an abundant food source for trout. Introductions of mayflies (Ephemeroptera), caddisflies (Trichoptera), and stoneflies (Plecoptera), insect orders absent in Hawaiian streams, were suggested to supplement food for trout, and native dragonfly and damselfly (Odonata) naiads were considered "the principal predators on small trout" (Needham and Welsh 1953).

Since then, native species have been given greater appreciation and more careful scrutiny has been directed at the ecological impact of alien fish introductions on native

aquatic species in Hawai'i (e.g., Maciolek 1984) and in the remainder of the United States (Courtenay and Stauffer 1984). Moyle (1976) classed alien fish impacts into ecosystem alteration and reduction or elimination of native organisms. Potential habitat alterations involve primarily removal of aquatic vegetation and various cascading effects of such removal, which may degrade water quality and eliminate refugia for native species, as well as disrupt their behavior, reproduction, and growth (Taylor et al. 1984). Reduction/elimination effects are mediated through predation and competition or via the transmission of disease and parasites. Font and Tate (1994) provided strong evidence that poeciliid fishes (Poeciliidae) introduced into Hawai'i for mosquito control in 1905 infected native stream fishes with helminth

parasites. Smallmouth bass (*Micropterus dolomieu* Lacépède), first introduced from California into Hawai'i for sportfishing in 1953, has been implicated as a "serious piscine predator on native stream fauna" (Maciolek 1984).

Little is known, however, about the ecological impacts of rainbow trout in tropical Hawaiian streams. Trout have been occasionally observed in other Kaua'i stream locale inhabited by large populations of native aquatic species, such as in lower- to middle-elevation reaches of the Wainiha River on the island's north shore (M.H.K., unpubl. data) (Figure 1). Predation on native freshwater species in these habitats is of paramount concern, yet for trout in Hawaiian streams, little food habit data are available. Needham and Welsh (1953) concluded from gut content analysis that rainbow trout captured in the Kōke'e area were more reliant on food items of terrestrial rather than aquatic origin. Based on gut content analysis of eight trout captured in the only stream sampled (Kōke'e Stream), terrestrial angleworms (earthworms) were reported as providing the bulk of the trouts' diet (36.4% by volume per fish) followed by native damselflies (*Megalagrion* spp.: Odonata) (18.1%), terrestrial millipedes (17.4%), and algae (11.5%). Because of the continuation of rainbow trout stocking efforts on Kaua'i and current proposals from sportfishing enthusiasts for trout stocking in lowland reservoirs, it is essential that more current and detailed information become available to adequately assess the implications of these actions.

The underlying purpose of this study, therefore, was to examine the ecological implications of widespread alien trout introductions into Hawaiian streams through a dietary study of an established trout population in a Kaua'i Island stream. The study objectives were to (1) obtain data on the range, abundance, and significance of food items taken by trout; (2) evaluate the importance of terrestrial versus aquatic food sources; (3) determine if individual trout were actively selecting certain foods or randomly taking foods in proportion to their availability in the habitat; and (4) evaluate prey im-

portance, feeding strategy, and niche width for foraging individuals.

MATERIALS AND METHODS

Sampling Methodology and Analyses

To evaluate alien rainbow trout diet, fish were captured with artificial lures in a ca. 3 km (2 mile) reach of Wai'ālae Stream in the Kōke'e area of Kaua'i Island in September 1993. Wai'ālae Stream is a headwater tributary of the Waimea River (Figure 1). The fish capture site was at ca. 1097 m (3600 ft) elevation and (for practical purposes) only accessible by helicopter. Immediately after capture, the fish were sexed and measured for standard length, and the gut (esophagus to anus) was removed and subsequently stored in 10% buffered formalin. In the laboratory, gut contents were removed, sorted, and identified to lowest taxonomic category. Food items by taxa were subsequently dried at 60°C for 48 hr and weighed to the nearest 0.001 g.

The availability of food resources within site were estimated through benthic sampling after fish captures were completed. Five randomly located square-meter quadrats were sampled in each of four wadable fish capture sites. Random sampling locations within quadrats were determined as in Kido (1996a). Substrates within quadrats were sampled using a Surber-type sampler (250- μ m mesh) (Surber 1937) and through cobble removal as in Kido (1996b). Three randomly located 0.09-m² squares within quadrats were scraped clean of biotic material using the Surber sampler and a stiff brush. Five cobbles, randomly selected (Kido 1996b), were placed in a bucket, scraped clean of biotic material with a stiff brush, and measured for maximum length and width at right angles using a sliding tree caliper. These measurements were used to estimate cobble surface area. All material collected was washed into a nitex fabric square (21 by 21 cm, 200- μ m mesh), tied, and stored in 10% buffered formalin. In the laboratory, material washed from the nitex squares was processed as

described previously for gut samples. Dried weights of collected benthic species were used with substrate surface area measures to calculate density (biomass gm^{-2}) and subsequently proportionate abundances of total benthic biomass ("population proportion").

Diet, Feeding Strategy, Prey Selection

To evaluate the frequency with which individual rainbow trout selected particular foods, a frequency of occurrence index (% F) (Hynes 1950) was calculated that gave the sample proportion of individuals in the population having a particular food item in the gut. The relative importance of a food item in the diet is expressed as a percentage of its dry weight to total dry weight of all foods found in the gut (% DW) (Zander 1982). Diet data (% DW) were compared by using an analysis of covariance procedure (ANCOVA) (GLM procedure [SAS Institute 1992]) in which the covariate, fish standard length, was incorporated into the model to increase precision. Initially, dietary abundances were compared through ANCOVA for "terrestrial" versus "aquatic" origins to determine which source provided greater dietary biomass for rainbows. Main aquatic food groups were subsequently evaluated through ANCOVA to determine their relative dietary importance.

A graphical approach was used to obtain information about prey importance, feeding strategy, and niche width for foraging rainbow trout, through plots of % F against prey-specific abundance (Amundsen et al. 1996). Prey-specific abundance (% PSA) is "the percentage a prey taxon comprises of all prey items in only those predators in which the actual prey occurs" (Amundsen et al. 1996). The distribution points of prey items along the lower left–upper right diagonals of the plot provide a measure of prey importance, with dominant prey being plotted in the upper right quadrant and rare or unimportant prey in the lower left. The niche width contribution of a prey item is evaluated along the diagonal from upper left to lower right, with specialized prey appearing in the upper left quadrant and generalized prey in the lower right. The position of prey along the vertical

axis (upper half versus lower half) elucidates feeding strategy in terms of specialization or generalization, respectively.

For comparisons of selection (Manly et al. 1993) and preference (Johnson 1980), a "Standard Index" was used that allows comparisons of the relative probabilities of selection of available aquatic foods (Manly et al. 1993). This index was calculated as in Manly et al. (1993) utilizing combined percentage abundance (% DW) data of foods in the diet of rainbows ("used sample proportion"), which were compared with their availability as estimated by benthic sampling ("population proportion"). Two log-likelihood chi-squared values, which compared expected to actual resource use (calculated as in Manly et al. 1993), were used to determine if: (1) individual trout were utilizing resource categories in a similar way (i.e., expected resource use was calculated as if all animals utilize resources similarly); and (2) there were evidence of selection by at least some individuals for certain foods (i.e., expected resource use was calculated as if proportional to availability). The design utilized in developing chi-squared values considered the animals as the primary sampling units, and statistical inferences are based on the use of animals as replicates (Manly et al. 1993).

RESULTS

In total 22 rainbow trout were collected in 3 days of sampling (September 1993) from Wai'ālae Stream on Kaua'i (59% female, 36% male, and 5% juvenile). Mean standard length for females was 26.7 ± 1.151 cm (10.5 ± 0.453 in.), ranging from 19.0 to 34.0 cm (7.5 to 13.4 in.). Males ranged in standard length from 18.0 to 32.0 cm (7.1 to 12.6 in.) with a mean of 23.8 ± 3.474 cm (9.4 ± 1.368 in.). The one juvenile trout captured was 11.5 cm (4.5 in.) in standard length. All guts examined were at least 80% full.

Based on the results of gut content analysis, aquatic foods were found in significantly greater amounts than foods of terrestrial origin ($F = 6.35$, $df = 1$, $P = 0.0119$) (Figure 2). For aquatic foods, native odonates (drag-

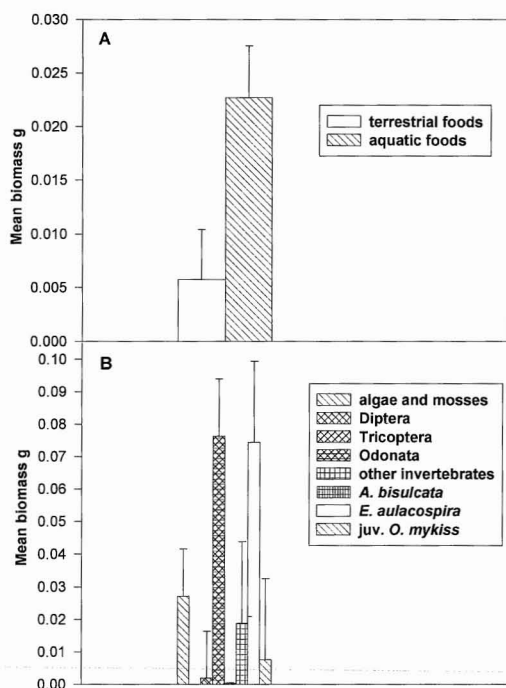


FIGURE 2. Comparison of mean weights (biomass g adjusted for covariate fish standard length): A, combined aquatic versus terrestrial foods; B, main aquatic food taxa in the diet of rainbow trout (*O. mykiss*) from Wai'alealae Stream, Kōke'e, Kaua'i.

onfly and damselfly naiads) and native lymnaeid snails (*Erinna aulacospira* Ancey) composed a significantly greater portion of the trouts' diet ($P < 0.05$) (Figure 2) than other foods, composing 31.5% and 15.4% of the diet, respectively (Table 1). A majority of the trout examined had *Anax strennus* Hagen naiads and *E. aulacospira* in their gut (% F = 72.7 and % F = 68.2, respectively), which composed 35.6% and 22.1% (% PSA), respectively, of the collective diet of these individuals (Table 1). No significant differences were determined in the abundances of other aquatic foods ($P > 0.05$) (Figure 2). Native damselfly naiads (*Megalagrion heterogamias* (Perkins)) and atyid shrimp (*Atyoida bisulcata* Randall) were other native animals preyed upon by trout in fair to moderate quantities (% DW = 1.3 and % DW = 3.9, respectively) and with moderate frequency (% F = 40.1 and % F = 31.8, respectively).

The most frequently eaten foods were alien caddisfly immatures (*Cheumatopsyche pettiti* (Banks)) (% F = 86.4) and an aquatic moss, *Ectropothecium sandwichense* (Hook. & Arnott) (Bryales: Hypnaceae) (% F = 81.8) (Table 1). Remains of a small fish, probably a juvenile rainbow, were found in the gut of a 26.2-cm (10.3-in.) (standard length) female.

Terrestrial invertebrates also provided a substantial food source for trout, composing 29.6% of their total diet (Table 1). Individual species, however, were found in relatively low dietary frequency (Table 1). This would be expected of a food source dependent upon prey that unpredictably fall into the stream. Click beetles (Elateridae) (% F = 40.1, % DW = 4.6) and isopods (% F = 50.0, % DW = 2.4) were eaten in highest frequency and amounts. Terrestrial food items exhibited relatively high prey-specific abundances, indicating that numbers of like species fall into the water at similar times and/or are large-bodied species that provide high food biomass (Table 1). Arthropods composed nearly half of the trouts' food from terrestrial origins (45.0% by dry biomass), contributing 9.5% to total food biomass (Table 1).

The trout sampled fed on aquatic species as generalists, with all items falling in the lower half of the plot of % F versus % PSA (Figure 3). Most of the smaller invertebrates as well as algae were unimportant prey falling in the lower left quadrant of the plot. Native odonates, lymnaeid snails, atyid shrimps, and the aquatic moss were of greater prey importance, being eaten with relatively high frequency but in only moderate prey-specific abundances (Figure 3). Dragonfly naiads (*A. strennus*) came closest to being a dominant aquatic prey (Figure 3). Major prey items fell in the lower right quadrant of the niche width diagonal (upper left–lower right), indicating that trout fed as generalists, each exploiting a wide range of overlapping resources.

Algae and mosses composed 87.7% (population proportion) of the available food biomass on the stream bottom as determined by benthic sampling (Table 2). If plant material were removed from the analysis, alien caddisfly immatures (Tricoptera), lymnaeid

TABLE 1

DIETARY FREQUENCY OF ABUNDANCE (% F) (HYNES 1950), TOTAL DRY BIOMASS (% DW) (ZANDER 1982), AND PREY-SPECIFIC ABUNDANCE (% PSA) (AMUNDSEN ET AL. 1996) OF AQUATIC AND TERRESTRIAL PLANTS AND ANIMALS FOUND IN THE GUT OF 22 RAINBOW TROUT (*Oncorhynchus mykiss*) COLLECTED IN WAI'ALAE STREAM, KAUAI, IN SEPTEMBER 1993

| GUT CONTENTS ^a | % F | % DW | % PSA |
|---|--------|--------|--------|
| Aquatic foods | | | |
| Arthropoda | | | |
| Insecta | | | |
| Diptera (flies) | | | |
| <i>Cricotopus bicinctus</i> (Chironomidae) (midges) | 18.182 | 0.009 | 0.048 |
| <i>Limonia</i> spp. (Tipulidae) (crane flies) | 18.182 | 0.016 | 0.043 |
| Odonata | | | |
| <i>Anax strenuus</i> ^a (Aeshnidae) (dragonflies) | 72.727 | 30.212 | 35.566 |
| <i>Megalagrion heterogamias</i> ^a (Coenagrionidae) (damselflies) | 40.909 | 1.312 | 2.691 |
| Tricoptera | | | |
| <i>Cheumatopsyche pettiti</i> (Hydropsychidae) | 86.364 | 1.085 | 1.224 |
| <i>Hydroptila arctia</i> (Hydroptilidae) | 18.182 | 0.026 | 0.189 |
| <i>Oxyethira maya</i> (Hydroptilidae) | 13.636 | 0.044 | 0.262 |
| Arachnida: Hydracari (Acari) (water mites) | 13.636 | 0.003 | 0.025 |
| Mollusca: <i>Errina aulacospira</i> ^a (Lymnaeidae) | 68.182 | 15.367 | 22.073 |
| Crustacea: <i>Atyoida bisulcata</i> ^a (Atyidae) (shrimps) | 31.818 | 3.870 | 7.642 |
| Turbellaria: <i>Dugesia</i> sp. (Planariidae) (flatworms) | 18.182 | 0.099 | 0.606 |
| Chordata | | | |
| Teleostei (probably juvenile <i>O. mykiss</i>) | 4.546 | 1.558 | 27.155 |
| Algae | | | |
| <i>Nostoc</i> sp. (Cyanophyta) | 27.273 | 0.078 | 0.334 |
| <i>Rhizoclonium</i> sp. (Chlorophyta) | 9.091 | 0.111 | 1.431 |
| Mosses (Bryophyta): <i>Ectropothecium sandwichense</i> (Hypnaceae) | 81.818 | 16.602 | 22.870 |
| Terrestrial foods | | | |
| Arthropoda | | | |
| Insecta | | | |
| Coleoptera | | | |
| Carabidae (ground beetles) | 4.546 | 0.032 | 0.915 |
| Elateridae (click beetles) | 40.909 | 4.604 | 14.051 |
| Nitidulidae (sap-feeding beetles) | 9.091 | 0.115 | 1.163 |
| Scarabaeidae (lamellicorn beetles) | 4.546 | 0.216 | 6.190 |
| Hemiptera: <i>Nabis</i> spp. ^a (Nabidae) (damself bugs) | 13.636 | 0.258 | 2.177 |
| Reduviidae (assassin bugs) | 22.727 | 0.445 | 2.127 |
| Homoptera: <i>Oliarus</i> spp. (Cixiidae) (planthoppers) | 4.546 | 0.012 | 0.213 |
| Hymenoptera: <i>Apis mellifera</i> (Apidae) (honey bee) | 13.636 | 0.972 | 7.485 |
| Lepidoptera (caterpillars) | 9.091 | 0.254 | 3.672 |
| Diplopoda (millipedes) | 9.091 | 0.041 | 0.462 |
| Isopoda | 50.000 | 2.383 | 3.497 |
| Arachnida: Araneae (spiders) | 9.091 | 0.208 | 2.134 |
| Annelida: Lumbricidae (earthworms) | 13.636 | 1.045 | 10.628 |
| Amphibia: Anura: probably <i>Rana rugosa</i> (Wrinkled Frog) | 4.546 | 1.553 | 22.046 |
| Mollusca: <i>Oxychilus alliarius</i> (garlic snail) | 22.727 | 0.644 | 5.599 |
| Reptilia: Scincidae: probably <i>Leiopisma mettalicum</i> (Metallic Skink) | 4.546 | 6.248 | 77.735 |
| Miscellaneous arthropod parts | 81.818 | 10.581 | 15.933 |

^a Known native species.

snails (*E. aulacospira*), alien midge immatures (*Cricotopus bicinctus* (Meigen)), and native odonates would account for 94.0% of the available aquatic invertebrate food biomass

(48.2%, 32.7%, 11.3%, and 1.8%, respectively). Chi-square comparisons of expected to actual resource use (algae and mosses included) showed that: (1) fish were not uti-

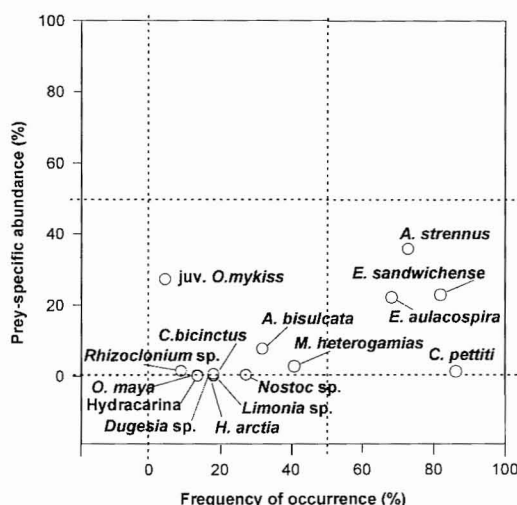


FIGURE 3. Use of algal, aquatic bryophyte, and aquatic invertebrate foods by rainbow trout (*O. mykiss*) in terms of feeding strategies, niche width contribution, and prey importance.

lizing resources differently, implying that resource categories were utilized by all individuals sampled in a similar way (chi-square = 31.887, $df = 336$, $P = n.s.$); and (2) there was no evidence of selection by individual fish (chi-square = 20.892, $df = 352$, $P = n.s.$); therefore, foods were taken according to their availability in the environment. Based upon probabilities of dietary occurrence in relation to availability (standard index), *A. strennus* naiads had nearly a 95% probability of being eaten as compared with any other aquatic food (Table 2). Given the nonsignificant chi-square tests for selection, however, this is more likely related to their availability rather than to trout preference.

DISCUSSION

Rainbow trout, even in tropical Hawaiian stream habitat, remain true to form, being opportunistic general predators particularly

TABLE 2

PROPORTIONATE BENTHIC AVAILABILITY (POPULATION PROPORTION), DIETARY ABUNDANCE (USED SAMPLE PROPORTION), AND RELATIVE PROBABILITIES OF SELECTION (STANDARD INDEX) (MANLY ET AL. 1993) FOR AQUATIC PLANT AND ANIMAL FOODS OF RAINBOW TROUT (*O. mykiss*) CAPTURED IN WAI'ALAE STREAM, KAUA'I, SEPTEMBER 1993

| AQUATIC FOODS | POPULATION PROPORTION | USED SAMPLE PROPORTION | STANDARD INDEX |
|--|--------------------------|---------------------------|-------------------|
| Invertebrates | | | |
| Insecta | | | |
| Diptera | | | |
| <i>Cricotopus bicinctus</i> (Chironomidae) | 0.01397 | 0.00014 | 0.00002 |
| <i>Limonia</i> spp. (Tipulidae) | 0.00000 | 0.00023 | 0.00000 |
| <i>Hemerodromia stellaris</i> (Empididae) | 0.00001 | 0.00000 | 0.00000 |
| Odonata | | | |
| <i>Anax strennus</i> (Aeshnidae) | 0.00092 | 0.43893 | 0.94330 |
| <i>Megalagrion heterogamias</i> (Coenagrionidae) | 0.00131 | 0.01906 | 0.02882 |
| Tricoptera | | | |
| <i>Cheumatopsyche pettiti</i> (Hydropsychidae) | 0.01117 | 0.01576 | 0.00277 |
| <i>Hydroptila arctia</i> (Hydroptilidae) | 0.04313 | 0.00038 | 0.00002 |
| <i>Oxyethira maya</i> (Hydroptilidae) | 0.00511 | 0.00063 | 0.00024 |
| Arachnida: Hydracari | 0.00001 | 0.00004 | 0.00717 |
| Mollusca: <i>Errina aulacospira</i> (Lymnaeidae) | 0.04036 | 0.22325 | 0.01088 |
| Crustacea: <i>Atyoida bisulcata</i> (Atyidae) | 0.00000 | 0.05623 | 0.00000 |
| Turbellaria: <i>Dugesia</i> sp. (Platyhelminthes: Planariidae) | 0.00051 | 0.00143 | 0.00553 |
| Hirudinea (Annelida) | 0.00680 | 0.00000 | 0.00000 |
| Algae | | | |
| <i>Nostoc</i> sp. (Cyanophyta) | 0.49782 | 0.00113 | 0.00001 |
| <i>Rhizoclonium</i> sp. (Chlorophyta) | 0.00000 | 0.00160 | 0.00000 |
| Bryophyta: <i>Ectopothecium sandwichense</i> (Hypnaceae) | 0.37891 | 0.24119 | 0.00125 |

adept at feeding on invertebrate drift (e.g., Faragher 1983, Waters 1969). The range of foods eaten by trout in Wai'ālae Stream ranged from large-bodied animals like frogs and skinks to tiny arthropods to aquatic mosses. Individual trout fed similarly, not preferring particular food species but rather selecting foods randomly based on their availability in the habitat. The results of this study differ, in some ways, from the findings of Needham and Welsh (1953). In our study, food species from aquatic rather than terrestrial sources were found to play a more important role in sustaining rainbow trout. Resident native aquatic species, particularly odonates (*A. strennus* and *M. heterogamias*), lymnaeid snails (*E. aulacospira*), and atyid shrimp (*A. bisulcata*), were determined to be the most important foods of foraging trout. Terrestrial sources, however, do provide a substantial alternative food supply. Moderate to large numbers of animals (primarily arthropods) apparently fell into the stream at similar times, and some trout examined in this study fed exclusively on such items. Spatial/temporal variability in occurrence as well as the magnitude of such events in the landscape surrounding streams, therefore, may be an important factor influencing food selection by trout.

The implications are that rainbow trout set free in Hawaiian streams in large numbers could do major damage to populations of native stream organisms through predation. Predation is of particular concern in lower-to middle-elevation habitat where trout would be exposed to higher abundances of the full range of native swift-water species from fish to insects to algae. Native stream arthropods would be at very high risk because of the robust size of adult rainbow trout and the diet results of this study. Trout exhibit cannibalistic behavior when high population densities limit space (Chapman 1966), and at least one juvenile trout was found in the gut of a large adult. Native Hawaiian stream fishes would also be easy prey for rainbow trout because of their smaller size, benthic habit, and inexperience with efficient fish predators. Because of the propensity of trout for preying on drifting forms, native amphidromous macro-

fauna may be particularly vulnerable to predation during early life history stages when newly hatched individuals drift to the ocean to begin marine larval phases. These natives are also at risk on their return migration as juveniles into mountainous stream reaches.

Rainbow trout were also found to consume substantial quantities of plant material with high frequency (Table 1). This is apparently the only trout species known to do so (Needham and Welsh 1953). Needham and Welsh (1953) reported that nearly all fish examined in their study had a filamentous green alga, *Stigeoclonium tenue* (Agardh) (Kutz), in their gut. Algae are known to be important dietary components of most native Hawaiian stream fishes (e.g., Kido 1997) and play a central role in the ecology of native aquatic insects as well (e.g., Hardy 1960). With the sparse information available, it is difficult to determine if rainbows would compete with native fish or invertebrates for algae or if Moyle's (1976) concern for habitat alteration with associated side effects would be realized. This potential, however, is certainly present depending upon trout densities. Salmonid use of food and space is highly density-dependent, resulting in widespread utilization of upstream-downstream habitat when densities are high (Chapman 1966). Rainbow trout would, then, likely distribute themselves across wide geographical ranges if large numbers of fish are introduced into a particular Hawaiian stream. It is this potential situation that should cause the greatest concern.

The results of this study indicate that rainbow trout would negatively impact populations of native stream organisms if introduced in high densities to middle- to lower-elevation reaches of Hawai'i's streams. The list of existing threats to native aquatic species is already too long (e.g., Maciolek 1984). Dwindling populations of native stream fishes have resulted in their scientific names reaching lists of "special concern" (Williams et al. 1989), several native damselflies are already believed to be extinct (Polhemus and Asquith 1996), and a native stream-adapted lymnaeid snail (*Erinna newcombi* (H. & A. Adams)) is currently being

considered for federal listing as an endangered species (proposal in *Federal Register* 62 FR 38953–38958). Indiscriminant introductions of generalist fish predators into Hawaiian streams will certainly not help the tenuous situation of many of our native aquatic species. Although there may be a place for freshwater game fish introductions into Hawai'i for recreational purposes, more stringent protocols for evaluation of alien species introductions are essential (Kohler and Stanley 1984) because there are no guarantees that alien species will be restricted to the habitat in which they are released. The nearly complete disappearance of the magnificent razorback sucker from its native range in the vast Colorado River Basin of the American West, due in large part to the introduction of exotic game fish species (Minckley et al. 1991), is a sobering call for caution.

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