Asian Fisheries Science 12(1999):1-16
Asian Fisheries Society, Manila, Philippines

https://doi.org/10.33997/j.afs.1999.12.1.001

Diet of the Exotic Mosquitofish, *Gambusia holbrooki*, in an Australian Lake and Potential for Competition with Indigenous Fish Species

A.H. ARTHINGTON and C.J. MARSHALL

Centre for Catchment and In-Stream Research
Griffith University, Nathan
Queensland 4111, Australia

Abstract

The exotic mosquitofish, *Gambusia holbrooki* Girard, has become established in fresh-water systems on sand islands of high conservation significance off the coast of southeast-ern Queensland, Australia. These freshwater systems support indigenous fish species with very restricted distributions and the mosquitofish has been listed as a threat to at least three rare species. This paper records the diet of *G. holbrooki* in an oligotrophic dune lake and explores the potential for competition for food between the mosquitofish, the Ornate Rainbowfish, *Rhadinocentrus ornatus* (Melanotaeniidae), and the Firetail Gudgeon, *Hypseleotris galii* (Eleotrididae). There was a high degree of similarity in mean population diets of *R. ornatus* and *G. holbrooki* (overlap index=0.83), moderate dietary overlap be-tween *G. holbrooki* and *H. galii* (overlap index=0.49) and low dietary overlap between *R. ornatus* and *H. galii* (overlap index=0.18). In some months, the mosquitofish switched to feeding on aquatic invertebrates normally consumed by gudgeons, and levels of dietary overlap between these species increased markedly. The capacity of *G. holbrooki* to feed opportunistically on a wide variety of aquatic prey, confirmed again in this study, could ex-ert a significant pressure on small populations of both indigenous fishes. Of the two spe-cies studied here, the restricted Ornate Rainbowfish appears to be particularly vulnerable to the effects of dietary interactions with the mosquitofish.

Introduction

The mosquitofish, *Gambusia holbrooki* Girard, is exotic to Australia and has become widely distributed in freshwater systems since its introduction in the 1920s (Arthington and Lloyd 1989). It is commonly found in warm, slowly flowing or still waters amongst aquatic vegetation and in backwaters of lotic systems (Arthington *et al.* 1983; Lloyd and Walker 1986; Penn and Potter 1991), but has been reported less often in lakes (McDowall 1996). *G. holbrooki* is usually associated with disturbed systems close to rural and urban areas, but a lacustrine population has become established in a National Park situated on North Stradbroke Island, one of several large sand islands of high conservation significance off the coast near Brisbane, southeastern Queensland. Lakes in coastal sand dunes support up to 15 fish species, including three species with very restricted distributions (Arthington 1984; Arthington *et al.*

1986). The mosquitofish has been listed as one of the threats to these rare species (Wager and Jackson 1993).

The mosquitofish is a very tolerant, competitive species with flexible feeding and habitat requirements and a range of behaviors that may adversely affect other fishes (Arthington and Lloyd 1989; Meffe 1985). Previous research on the diet of the mosquitofish in Brisbane streams (Arthington 1989) has indicated the potential for high levels of dietary overlap with fishes indigenous to Australia, especially small species with similar foraging behavior. This paper examines the diet of the mosquitofish and the potential for competition with two indigenous fishes in an extremely oligotrophic dune lake. One of these species, the Ornate Rainbowfish (*Rhadinocentrus ornatus* Regan; Melanotaeniidae), has been classified as "restricted" and is vulnerable to habitat loss and water pollution (Leiper 1985; Wager and Jackson 1993). It has been suggested that additional pressure in the form of resource competition exerted by *G. holbrooki* may be a deciding factor in the fate of small populations (Leiper 1984).

Study Area

Blue Lake is situated within a small National Park near the east coast of North Stradbroke Island, southeastern Queensland (Fig. 1). It is an oligotrophic water-table window lake of exceptional water clarity (Secchi disc depths of up to 11 m), low pH (4.9-6.5) and very low conductivity (81-91μS cm^{-1}) (Bensink and Burton 1975). There are relatively few lakes of this type in the

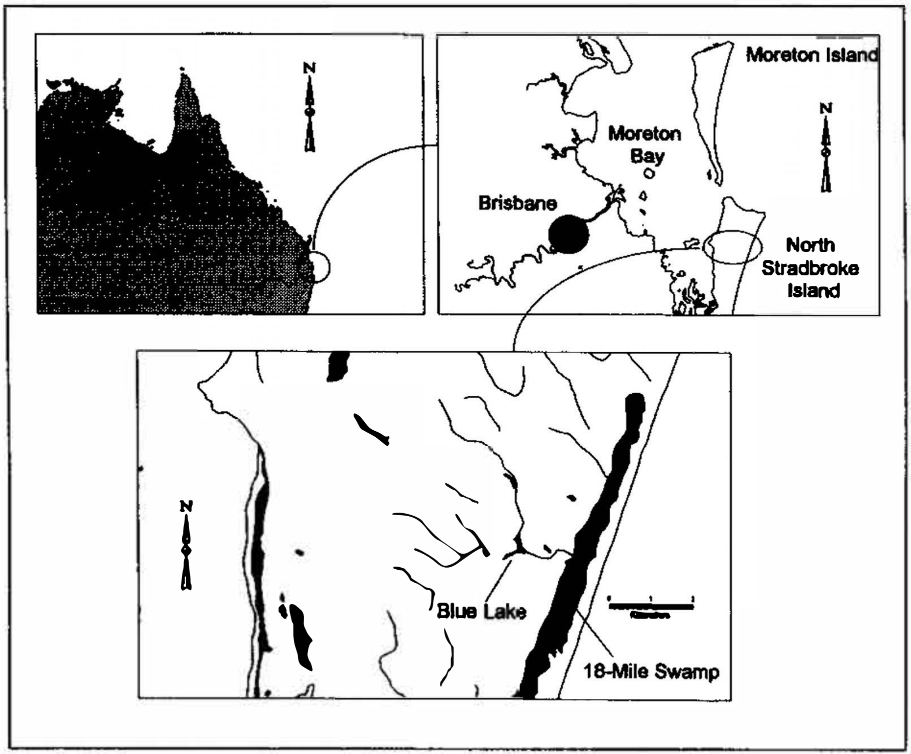

Fig. 1. North Stradbroke Island, southeastern Queensland.

coastal lowlands of southern Queensland, perched lakes being far more common (Bayly *et al.* 1995; Arthington *et al.* 1986).

During this study conducted in 1990-1991, the entire shoreline of Blue Lake and the creek draining from the lake into the large coastal 18-Mile Swamp (Fig. 2) were surveyed to establish the distribution of *G. holbrooki* and indigenous fishes, and to select a site suitable for collection of fish for dietary comparisons.

Materials and Methods

Fish sampling

Fish sampling in Blue Lake involved dragging a 2.5m seine net (constructed from 70% shade cloth, mesh size range 2-5mm) through shallow beds of submerged aquatic plants and across areas with a sandy substrate close to the bank (Fig. 2). This collecting technique was standardized so that the main study site was sampled with five hauls of the net, providing data on the relative abundance of each fish species throughout the study period (May 1990 to July 1991). The same catch-per-unit-effort approach was applied to the general survey of fish species in the lake.

Preliminary sampling in Blue Lake showed that the three fish species generally feed from dusk to late morning and fish caught between 1500-1700h have empty guts. Since the purposes of sampling were to document fish abundance and to simultaneously collect specimens for dietary and reproductive studies, fish were sampled during daylight in the morning feeding period (0800-1100h).

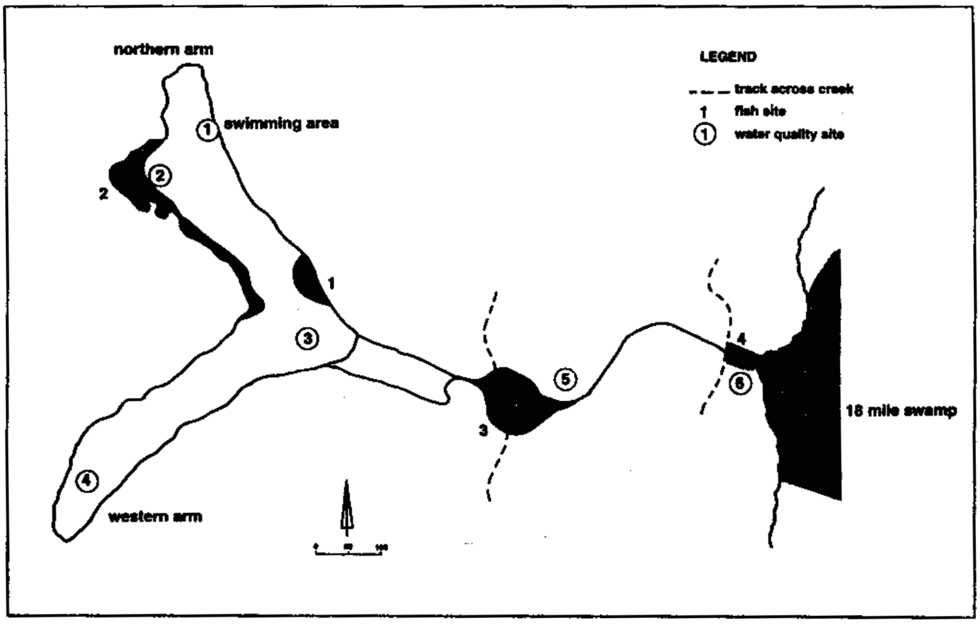

Fig. 2. Map of Blue Lake and creek flowing to 18-Mile Swamp, North Stradbroke Island, showing the sites sampled for fish during 1990-1991, and the main sampling site for the study of fish diets (site 1).

Fish caught during each seine haul were identified and assigned to abundance ranks, and the numbers required for laboratory study removed and stored on ice in an esky. Most of the other fish were returned to the water alive.

Diet composition

Freshly-caught fish were stored on ice and then frozen until they were measured and dissected. The standard length of all fish was measured to the nearest millimeter using Vernier callipers. Whole guts were removed and their contents emptied into a Petrie dish. Gut contents were separated into 27 food categories. Since gut volumes and food items were generally too small to permit rapid volumetric or calorific analysis of the diet, an approximation of the volumetric method of Hellawell and Abel (1971) was used. The items within each food category were firmly squashed together to a depth approximating 1mm and the area of each squash measured in mm^2. This method resembles the indirect volumetric method of Hyslop (1980), which has been estimated as having an error of about 3.5%. It has been used successfully in other studies on the dietary ecology of small fish species (Arthington 1992; Pusey 1992).

Statistical analysis

Fish guts with a fullness index of >20% were used in statistical analyses of diet composition and dietary overlap. Empty and near-empty guts were excluded to avoid bias in the estimation of diet diversity and proportional contributions of prey. The quantitative importance of each food type in the diet of each fish species was expressed as the mean proportional contribution of a category of food to the diet of all fish in a sample (defined by sampling site and date), and as the incidence of each food category expressed as the number and proportion of fish consuming it.

Fish diets were also described by the Shannon-Weaver indices of diversity and evenness; the proportional contribution of unidentified material was excluded from the latter calculations. Shannon-Weaver diversity was used as a measure of dietary niche breadth (after Pusey 1992).

Seasonal comparisons of diet composition and overlap in Blue Lake fish were based on 20 or more individuals of the three fish species. In order to provide larger sample sizes for analysis of dietary overlap, the data for individual sampling dates were collapsed down into 1990 and 1991 collections, on the basis of similarities in diet composition within each of these six-month periods.

Seasonal and inter-annual variations in diet composition were examined by ordination of the mean diet of each species on each sampling occasion, using Detrended Correspondence Analysis (DECORANA) (Hill 1979). Unidentified material was excluded from this analysis and the mean diet adjusted to 100% prior to analysis. All options in this analysis were set to the default. Mean diet composition of each fish species on each sampling occasion was plotted in the ordination space defined by the first two principal axes; the position of each food category was also plotted in the same ordination space.

Dietary overlap was examined among fish species collected each month to assess their utilization of food resources and the possibility of close interactions between species pairs. Measures of similarity or overlap in resource use by sympatric species are frequently used to estimate the intensity of interspecific competition. However, when information on the status (i.e. quantity and availability) of food resources is not available, as in the present study, high dietary overlap between species may be interpreted both as evidence that interspecific competition occurs and also that it does not (Holbrook and Schmidt 1989). Low overlap in resource use may also be interpreted in several ways in the absence of data on resource availability. It may be taken to indicate that interspecific competition has resulted in resource partitioning, or that competition is not likely to occur, or that competition has occurred in the evolutionary past of sympatric taxa (Connell 1980).

Dietary overlap was estimated during this study as the first step towards assessing the possible interactions of indigenous fishes with *G. holbrooki*. Morisita's index of overlap (Morisita 1959) was used and its variation estimated by the jackknife (or bootstrap) procedure (Smith 1985). Overlap values exceeding 0.6 are considered to describe biologically important interactions (see Mathur 1977) and this criterion of significance was adopted here. When resource categories are numerous, estimates of overlap tend to be conservative (Pusey 1992).

Results

Fish distributions

The indigenous fish fauna of Blue Lake consisted of *Rhadinocentrus ornatus*, the Firetail Gudgeon, *Hypseleotris galii* (Eleotrididae) and the Long-finned Eel, *Anguilla reinhardtii* (Anguillidae) as well as *Gambusia holbrooki*. Within Blue Lake, *G. holbrooki* was patchily abundant along the eastern shoreline and more common along the western shore in the northern arm of the lake (Fig. 2), where it was frequently the only species recorded. *H. galii* and *R. ornatus* were present at various sites around the lake with the exception of the area along the western shore. Site 1 (Fig. 2) on the eastern shoreline of the lake was selected as the collecting site for the dietary study. This site supported relatively large numbers of mosquitofish, rainbowfish and gudgeon, and was also readily accessible and suitable for deployment of the seine net.

Fish diets in Blue Lake

Samples of at least 20 individuals were included in the analysis of seasonal variations in the diet of *H. galii, R. ornatus* and *G. holbrooki.* The standard lengths of the fish examined each month are given in Table 1.

The composition of the mean diet of each fish species is presented for two time periods, June-December 1990 and January-June 1991, to show gross changes in diet over time (Tables 2-4). Diets are expressed quantitatively as the mean proportional contribution of each food category to the diet and the standard deviations of these means, as well as the incidence and the proportional occurrence of each food category (minus unidentified material) in the species' diet. Indices of dietary diversity (breadth) and evenness are also given for each species.

Diet of H. galii

The diet of *H. galii* in Blue Lake comprised Crustacea, aquatic Insecta, other aquatic invertebrates, filamentous algae, and a small component of terrestrial Insecta, Arachnida and plant material (Table 2). Chironomid larvae made up over 30% of the diet in both years but chironomid pupae were unimportant in 1990 (5%) and absent from the diet in 1991. There was further variation in the population diet between the two years of study. For instance, in 1991, Crustacea were more important (1990, 36%; 1991, 52%), especially the decapod, *Caridina* sp. *H. galii* had a relatively low dietary niche breadth in Blue Lake with monthly Shannon-Weaver indices of diversity varying from 0.47 to an exception high of 0.93.

Diet of R. ornatus

This species consumed a wider variety of aquatic and terrestrial taxa than *H. galii* and took a greater proportion of its diet from food items associated with the water's surface (overall >60%, including chironomid pupae, adult Diptera, Hymenoptera, and Lepidoptera, Araneae, flower parts and other plant tissues) (Table 3). Chironomid pupae were the most important dietary component in 1990 (25%) and adult Diptera in 1991 (26%). Small quantities of filamentous algae were consumed in both years but other algae (e.g. desmids and diatoms) were not recorded. Prey diversity and evenness were higher than in

Table 1. Number of fish examined, mean standard length (S.L.), standard error (S.E.), F and z values and the significance level of differences in mean standard length of each fish species collected from Blue Lake in 1990 and 1991.

Species/Year	Number	Mean S.L. (in mm)	S.E.	F	z	Significance
G.H.						
1990	162	20.3	0.32	1.398	3.72	$p<0.01$
1991	113	18.6	0.32			
R.O.						
1990	148	27.0	0.60	1.416	0.96	ns
1991	122	26.2	0.55			
H.G.						
1990	132	19.0	0.42	1.263	2.10	$p<0.05$
1991	128	20.2	0.39			

Note: *G.H.* = *Gambusia holbrooki*, *R.O.* = *Rhadinocentrus ornatus*, *H.G.* = *Hypseleotris galii*

Table 2. Composition of the diet of *H. galii* from Blue Lake in 1990-1991.

Food Categories	Mean		S.E.		Incidence		Proportion	
	1990	1991	1990	1991	1990	1991	1990	1991
Aquatic								
Crustacea								
Copepoda	0.0516	0.0276	0.050	0.042	29	10	0.23	0.08
Cladocera	0.1795	0.1167	0.090	0.095	71	37	0.56	0.29
Decapoda								
Caridina sp.	0.1300	0.3796	0.115	0.185	21	55	0.17	0.43
Insecta								
Trichoptera, larvae	0.0249	0.0686	0.050	0.094	7	13	0.06	0.10
Chironomidae, larvae	0.2148	0.3092	0.098	0.160	73	60	0.57	0.47
Chironomidae, pupae	0.0230	0.1080	0.041		8		0.06	
Other aquatic invertebrates	0.0301	0.0297	0.045	0.058	12	7	0.09	0.05
Filamentous algae	0.0218	0.0013	0.044	0.006	6	1	0.05	0.01
Terrestrial								
Insecta								
Diptera	0.233	0.0088	0.051	0.034	4	2	0.03	0.02
Other Insecta	0.0128	0.0530	0.024	0.019	7	2	0.06	0.02
Plants								
Other plant tissues		0.0026		0.012		1		0.01
Mixed aquatic and terrestrial material								
Acarina	0.0755	0.0375	0.050	0.048	53	22	0.42	0.17
Unidentified Insecta	0.0017		0.007		1		0.01	
Unidentified material	0.2110	0.0130	0.108	0.026	60	6	0.47	0.05

diversity = 0.9128; evenness = 0.6614; S.E. = standard error

Table 3. Composition of the diet of *R. ornatus* from Blue Lake in 1990-1991.

Food Categories	Mean		S.E.		Incidence		Proportion	
	1990	1991	1990	1991	1990	1991	1990	1991
Aquatic								
Crustacea								
Copepoda	0.0016	0.0029	0.007	0.014	1	1	0.01	0.01
Cladocera	0.0007	0.0024	0.003	0.006	1	6	0.01	0.04
Decapoda								
Caridina sp.	0.0439	0.0107	0.061	0.031	10	3	0.08	0.02
Insecta								
Trichoptera, larvae	0.0099	0.205	0.025	0.046	5	6	0.04	0.04
Chironomidae, larvae	0.0380	0.0396	0.055	0.059	11	23	0.09	0.16
Chironomidae, pupae	0.2147	0.2485	0.120	0.124	61	82	0.50	0.56
Coleoptera		0.0065		0.023		3		0.02
Hemiptera		0.0029		0.011		5		0.03
Other aquatic invertebrates	0.0146	0.0181	0.027	0.042	5	7	0.04	0.05
Filamentous algae	0.0043	0.0219	0.013	0.054	2	5	0.02	0.03
Terrestrial								
Insecta								
Diptera	0.2575	0.1354	0.126	0.087	63	55	0.52	0.37
Hymenoptera	0.0520	0.0262	0.071	0.048	22	16	0.18	0.11
Formicidae	0.0935	0.0793	0.092	0.091	23	21	0.19	0.14
Coleoptera	0.0295	0.0272	0.045	0.490	11	10	0.09	0.07
Lepidoptera	0.0371		0.063		6		0.05	
Trichoptera	0.0394	0.0097	0.064	0.034	7	2	0.06	0.01
Other Insecta	0.0196	0.0259	0.025	0.036	18	25	0.15	0.17
Plants								
Fruits	0.0135		0.033		3		0.02	
Flower parts		0.0007		0.003		1		0.01
Other plant tissues		0.0015		0.005		2		0.01
Mixed aquatic and terrestrial material								
Acarina	0.0008	0.0081	0.003	0.011	2	19	0.02	0.13
Araneae	0.0674	0.0455	0.076	0.065	17	17	0.14	0.12
Unidentified Insecta	0.0098	0.0279	0.018	0.042	6	13	0.05	0.09
Unidentified material	0.0234	0.2144	0.029	0.115	14	79	0.11	0.54

diversity = 1.0243 (1990), 1.0312 (1991); evenness = 0.7423 (1990), 0.7471 (1991); S.E. = standard error

Table 4. Composition of the diet of *G. holbrooki* from Blue Lake in 1990-1991.

Food Categories	Mean		S.E.		Incidence		Proportion	
	1990	1991	1990	1991	1990	1991	1990	1991
Aquatic								
Crustacea								
Copepoda	0.0232		0.055		8		0.05	
Cladocera	0.0191	0.0027	0.025	0.005	37	5	0.23	0.04
Decapoda								
Caridina sp.	0.0847	0.1349	0.094	0.133	20	17	0.12	0.15
Insecta								
Trichoptera, larvae	0.0317	0.0898	0.048	0.093	13	17	0.08	0.15
Chironomidae, larvae	0.0530	0.0903	0.063	0.092	27	28	0.17	0.25
Chironomidae, pupae	0.0883	0.0958	0.066	0.076	51	33	0.31	0.29
Coleoptera	0.0073		0.019		4		0.02	
Hemiptera		0.0054		0.019		2		0.02
Other aquatic invertebrates	0.0228	0.0439	0.043	0.079	10	6	0.06	0.05
Filamentous algae	0.0014	0.0208	0.006	0.043	1	7	0.01	0.06
Terrestrial								
Insecta								
Diptera	0.1324	0.2149	0.100	0.136	47	42	0.29	0.38
Hymenoptera	0.0224	0.0044	0.051	0.012	12	3	0.07	0.03
Formicidae	0.0571	0.0619	0.072	0.071	22	16	0.14	0.14
Coleoptera	0.0357	0.0192	0.054	0.048	10	4	0.06	0.04
Lepidoptera	0.0217	0.0179	0.052	0.054	4	2	0.02	0.02
Trichoptera	0.0105	0.2022	0.029	0.050	3	3	0.02	0.03
Other Insecta	0.0280	0.0068	0.031	0.017	37	6	0.23	0.05
Plants								
Flower parts		0.0010		0.004		1		0.01
Fruits	0.0078	0.0108	0.031	0.029	2	3	0.01	0.03
Other plant tissues	0.0069	0.0045	0.030	0.015	2	2	0.01	0.02
Mixed aquatic and terrestrial material								
Acarina	0.0076	0.0062	0.010	0.013	21	6	0.13	0.05
Araneae	0.108	0.0665	0.027	0.079	6	15	0.04	0.13
Unidentified Insecta	0.0551	0.0186	0.063	0.046	22	4	0.14	0.04
Unidentified material	0.2475	0.0541	0.110	0.071	94	14	0.58	0.13

diversity = 1.1379; evenness = 0.8244; S.E. = standard error

H. galii in both years of study and in each month of survey except December 1990 (Table 3).

Diet of G. holbrooki

The diet of *G. holbrooki* in Blue Lake was composed of aquatic invertebrates, filamentous algae, terrestrial Insecta, Arachnida, fragments of fruit and other plant tissues (Table 4). As for *R. ornatus*, over 50% of the diet in both years was comprised of items found at the water's surface (aquatic prey such as chironomid pupae, Arachnida and terrestrial insects). There was inter-annual and monthly variation in the mean diet of *G. holbrooki*. Copepoda, Cladocera, Formicidae and unidentified aquatic and terrestrial insects made up a greater proportion of the diet in 1990, whereas filamentous algae, Trichoptera larvae, adult Diptera and Arachnida were more important in 1991. However, the dominant dietary item in both years was adult Diptera (>20%). Overall, *G. holbrooki* had the most diverse diet among the species found in Blue Lake and indices of diversity were higher than those recorded for *R. ornatus* in all months except in May 1990, and in March and May 1991 (Table 4).

Comparison of fish diets

The similarities and differences and the seasonal variations in fish diets in Blue Lake are further clarified in the ordination plot of individual species' diets on each monthly sampling occasion (Fig. 3a). Axes 1 and 2 accounted for 60.11% and 19.34%, respectively, or a total of 79.45%, of the explained variation in diet composition and hence are the only ones plotted. The distribution of food categories in the same ordination space is shown in Fig. 3b.

Axis 1 of the ordination clearly separates *H. galii* from *R. ornatus* and *G. holbrooki*, largely on the basis of the gudgeon's consumption of aquatic invertebrates, which are arrayed to the right of Axis 1 in ordination of prey taxa in Fig 3b (i.e. Acarina, Cladocera, Copepoda, chironomid larvae, *Caridina* sp., Trichoptera larvae and other aquatic invertebrates). The high degree of similarity in the diets of *R. ornatus* and *G. holbrooki* is shown clearly by the cluster of points representing the diets of these two species in ordination space (Fig. 3a), driven by the consumption of terrestrial insects, Araneae, chironomid pupae, plant parts and filamentous algae (Fig. 3b).

A further comparison of dietary similarity was achieved by calculation of indices of dietary overlap for the entire study period (Table 5). Over all sampling occasions, there was a high degree of similarity in the population diets of *R. ornatus* and *G. holbrooki* (overlap index=0.83) and very low overlap between *R. ornatus* and *H. galii* (overlap index=0.18). Mean overlap between *G. holbrooki* and *H. galii* was somewhat higher (0.49) as a consequence of the higher diet diversity in the Mosquitofish and, hence, the consumption on some occasions of certain aquatic taxa which are normally the province of *H. galii* (Table 5).

A more detailed analysis computed indices of overlap between fish species pairs for each sampling occasion. Levels of dietary overlap between *R. ornatus*

Table 5. Jackknifed estimates (±95% c.i.) of Morisita's index of dietary overlap for fish species pairs in Blue Lake, 1990 - 91 (all data combined).

	G.h.	H.g.	R.o.
G.h.		0.49 ±0.08	0.83 ±0.06
H.g.			0.18 ±0.05

G.h. = *G. holbrooki* (275 individuals), H.g. = *H. galii* (260 individuals), R.o. = *R. ornatus* (275 individuals).

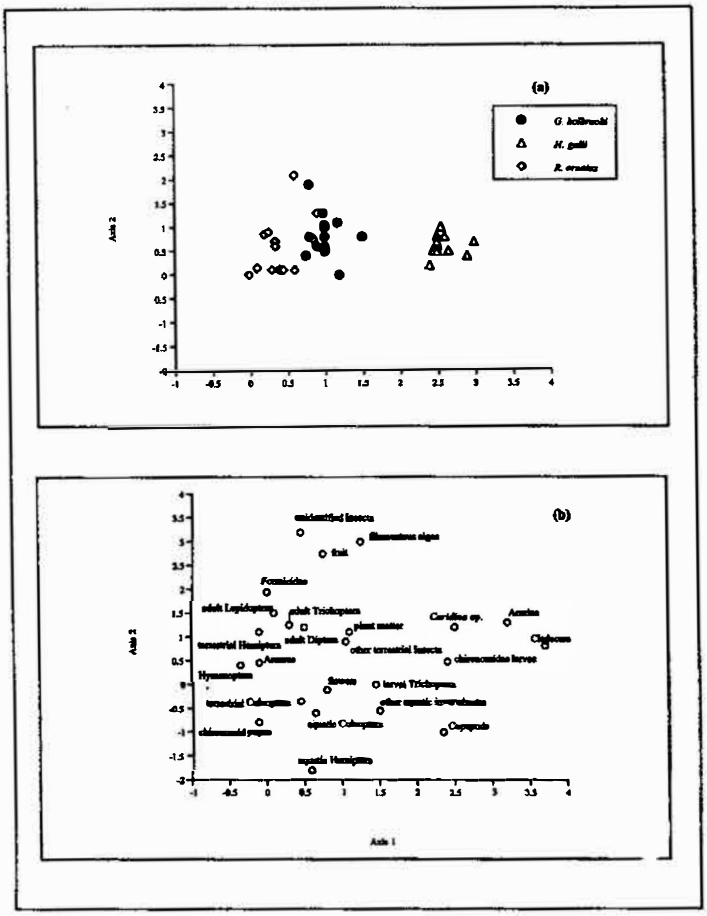

Fig. 3. a) Ordination plot of spatial and temporal variation in diets of fish from Blue Lake, 1990-1991. Each point represents the mean diet of each species collected on a particular date to demonstrate the seasonal spread of variation in diet composition. b) Ordination plot of prey taxa with taxon groups indicated.

and *G. holbrooki* varied with time of year and were >0.6 on all sampling occasions except in July, November and December 1990, and January 1991 (Fig. 4a). At these times, and in May 1991, the diets of *G. holbrooki* and *H. galii* showed greater similarity, with exceptionally high indices of overlap for this species pair in December 1990 and May 1991. *R. ornatus* and *H. galii* in contrast had very dissimilar diets and low indices of dietary overlap in all months of 1990 and 1991 (<3.6 to as low as 0.01; Fig. 4a). The endemic species consistently partitioned food resources despite seasonal and temporal variations in dietary diversity (Fig. 4b).

The fluctuating occurrence of high overlap in the diets of *G. holbrooki* and the two endemic species could be due to variations in diet breadth and diet composition of all three species. Temporal variations in dietary overlap (Fig. 4a), diet breadth (Fig. 4b) and evenness (Fig. 4c) indicate that the high overlap between *G. holbrooki* and *H. galii* in December 1990 and in May 1991 coincided with a narrowing of dietary diversity in *G. holbrooki* (compared to most months of the year) and similar diet diversity for *G. holbrooki* and *H. galii*.

At these times, *G. holbrooki* consumed an unusually large component of the decapod, *Caridina* sp., one of the most important items in the diet of *H. galii* (Fig. 4d). In addition, in December 1990 and in May 1991, the proportion of chironomid pupae in the diet of *G. holbrooki* declined compared to the previous months, reaching the low values more characteristic of *H. galii* (Fig. 4f). However, Chironomid larvae remained more important in the diet of *H. galii* than in *G. holbrooki* diets (Fig. 4e).

Low dietary overlap between *G. holbrooki* and *R. ornatus* in December 1990 was associated with decreasing diet breadth and a low index of evenness, particularly in *R. ornatus* (0.62). At this time, chironomid pupae made up 49% of the diet of *R. ornatus* but were insignificant in the diet of *G. holbrooki* (Fig. 4f). In May 1991, diet overlap between *G. holbrooki* and *R. ornatus* was only just in excess of 0.6 and the indices of dietary niche breadth and evenness were very similar.

Discussion

H. galii and *R. ornatus* had very dissimilar diets and low indices of dietary overlap in Blue Lake in all months (<3.6 to as low as 0.01). These species consistently partitioned food resources, despite seasonal and monthly variations in diet breadth. The diets of these indigenous species were similar to those recorded in other studies (Bayly *et al.* 1975; Merrick and Schmida 1984; Arthington *et al.* 1986; Arthington 1992), which have shown that *H. galii* feeds mainly on aquatic invertebrates, whereas *R. ornatus* is predominantly a surface feeder, consuming materials trapped at the meniscus, such as adult Insecta, flowers, fruits, pollen and other plant materials (Bayly *et al.* 1975), as well as aquatic taxa associated with the surface (e.g. chironomid pupae) and water column.

Levels of dietary overlap between *R. ornatus* and *G. holbrooki* varied with time of year and were >0.6 on all sampling occasions except in July, November and December 1990, and in January 1991. At these times, and in May 1991, the diets of *G. holbrooki* and *H. galii* showed greater similarity, with exceptionally high indices of overlap in December 1990 and in May 1991.

Intermittent high levels of dietary overlap between *G. holbrooki* and both endemic fishes in Blue Lake suggest the possibility that these species pairs may interact during foraging, even to the extent of competing for food resources. Interspecific competition may occur if the food resources shared by two sympatric species are in short supply. Whilst it was not possible to quantify

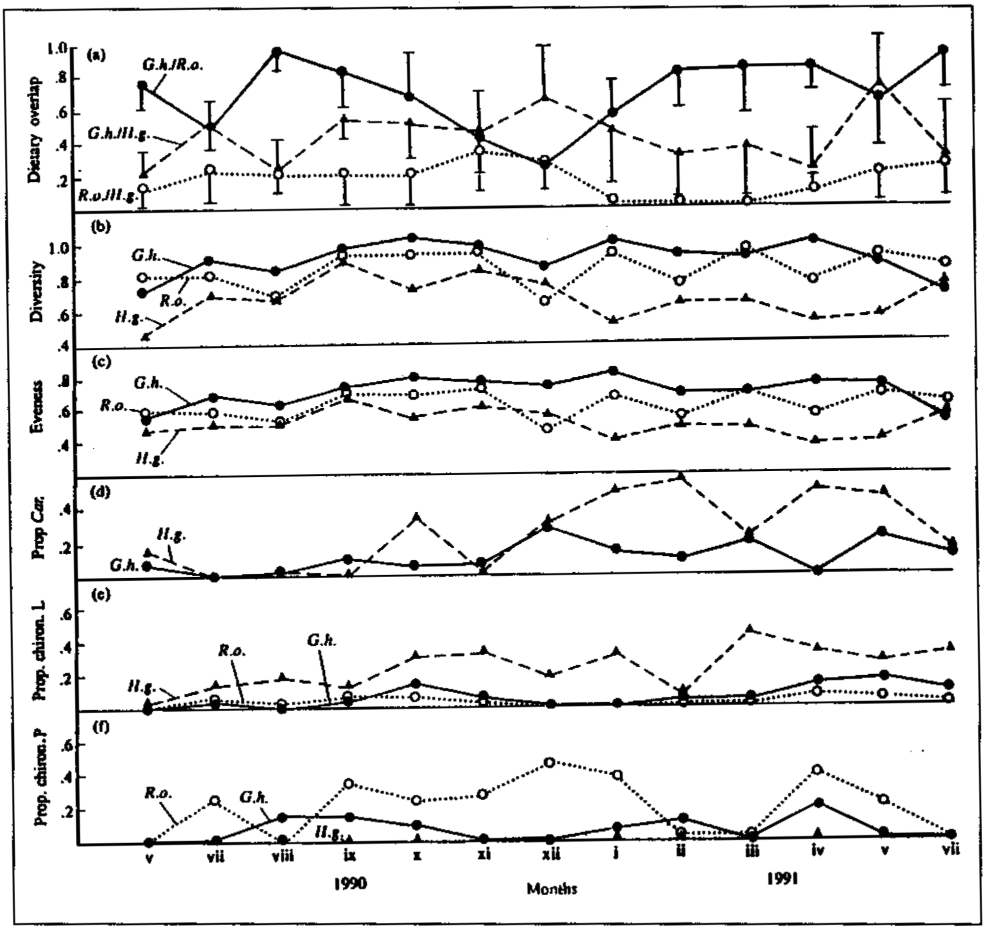

Fig. 4. Mean monthly fish diets: a) mean dietary overlap and confidence intervals; b) dietary diversity; c) evenness; d) proportion of *Caridina* in diet; e) proportion of chironomid larvae in diet; f) proportion of chironomid pupae in diet.

food resources during this study, two issues can be discussed on the basis of the data available. These are the issue of resource availability and the issue of sympatry.

Caridina sp. (probably *indistincta*) is found often in oligotrophic and dystrophic waterbodies of southeastern Queensland (Bensink and Burton 1975; Bayly *et al.* 1975; Arthington *et al.* 1986). In Blue Lake, this decapod inhabits both the littoral zone and the open water of the lake, and, in the latter zone, has a distinct diurnal vertical migration (Arthington and Burton, unpublished data). Breeding is seasonal and, in the spring and early summer months, large numbers of small planktonic larvae are released by the females (Williams 1980). The larvae of several chironomid species are also found in the littoral zone, in benthic sediments and in open water (Bensink and Burton 1975). Chironomid recruitment is seasonal and larvae in the limnetic zone migrate diurnally (Arthington and Burton, unpublished data), whereas pupae become abundant at the water's surface shortly before emergence of the adult stage, especially in summer months.

High overlap in the diets of *G. holbrooki* and *H. galii* in December 1990 coincided with similar levels of consumption of *Caridina* sp., which was usually relatively unimportant in the diet of *G. holbrooki*. At this time of year, the planktonic larvae of this decapod may have been unusually abundant as a result of seasonal recruitment. It is possible that *Caridina* sp. was sufficiently abundant as to minimize any possibility of shortages of supply and hence of interspecific competition between *G. holbrooki* and *H. galii* for this prey item. It is also possible that *G. holbrooki* and *H. galii* need not necessarily forage at the same depth in the water column in order to feed on *Caridina* sp. because this species occurs at various depths throughout the diet cycle (Arthington and Burton, unpublished data). The intermittent high dietary overlap between *G. holbrooki* and *H. galii* may be merely a consequence of each species foraging at the preferred depth on *Caridina* (and other abundant aquatic prey) that occur throughout the water column. Under these circumstances, interspecific competition for these common food resources would be unlikely, unless the total supply of the common food resources was reduced by predator pressure in one or more areas used for foraging.

It has been suggested that in Blue Lake, *G. holbrooki* may feed on *Caridina* sp. at any water depth. The consistent dominance of the diet of *R. ornatus* by prey associated with the water's surface (see also Bayly *et al.* 1975) indicates that *R. ornatus* may not have the same capacity to forage deeper in the water column, explaining the high intake of chironomid pupae and low consumption of chironomid larvae and *Caridina* sp. at times when both taxa were abundant. Another possibility is that *R. ornatus* does not prefer or cannot handle *Caridina*. Broad dietary niche breadth and prey switching seem to characterize the diet and foraging behavior of *G. holbrooki* but not the two indigenous species in Blue Lake.

Prey switching in response to the differential availability of alternative prey is common in the genus *Gambusia* (Greenfield *et al.* 1981) and other opportunistic carnivorous fishes (Dill 1983; Schlosser and Toth 1984; Winemiller 1989). *G. holbrooki* is particularly well adapted morphologically to feed at the water's surface, having a flattened head and a terminal, upwardly directed mouth (Scott *et al.* 1974). However, the position of the mouth during feeding is flexible, involving protraction of the premaxilla so that the mouth opening may shift from a dorsal terminal to a ventral terminal position (Dussault and Kramer 1981). These shifts permit all styles of foraging - at the surface, midwater and benthic (Alexander 1967; Dussault and Kramer 1981) and there is abundant evidence that the diet of *G. holbrooki* varies from the extremes of planktonic to benthic foraging under different circumstances (see references in Arthington 1989). In Blue Lake, *G. holbrooki* appears to adopt different foraging tactics in relation to the relative abundance of prey, switching to abundant food items such as *Caridina*, which are generally consumed mainly by *H. galii*, even when its own typical food resources may not be in short supply.

A tentative conclusion from this study is that *G. holbrooki* may present a threat to both *R. ornatus* and *H. galii* in Blue Lake, even though these indigenous species have very different foraging strategies and consistently utilize different food resources in the littoral shallows. The trophic flexibility of *G.*

holbrooki and the ability of individuals to successfully regulate food intake in the presence of potential competitors are regarded as key features governing both its success as an invasive species, and its potential for adverse interactions with indigenous fishes (Shakuntala 1977; Arthington and Lloyd 1989).

G. holbrooki occurs in other coastal waterbodies supporting *R. ornatus* and *H. galii,* the two most common indigenous fish species inhabiting oligotrophic lakes, swamps and streams on dune islands and along the coastal mainland of southeastern Queensland (Arthington 1994). The dietary similarity of *G. holbrooki* and *R. ornatus*, and occasionally of *G. holbrooki* and *H. galii,* in Blue Lake is probably highly indicative of the interspecific interactions likely to occur in other waterbodies of these coastal dune systems. The capacity of *G. holbrooki* to feed opportunistically on a wide variety of aquatic prey (for references see Arthington 1989), confirmed again by this study, coupled with consumption of fish eggs and larvae (Ivantsoff and Aarn 1999) and its innate aggressiveness towards other fish (Myers 1965; Meffe 1985), certainly could exert a significant pressure on small populations of indigenous fishes already under threat from habitat loss and water pollution. Of the two species studied here, the restricted Ornate Rainbowfish appears to be particularly vulnerable to the effects of dietary interactions with the mosquitofish.

References

Alexander, R.M. 1967. The function and mechanisms of the protrusible upper jaws of some acanthopterygian fish. Journal of Zoology 151:43-64.

Arthington, A.H. 1984. Freshwater fishes of Stradbroke, Moreton and Fraser Island. In: Focus on Stradbroke (ed. J. Covacevich and P. Davie), pp. 279-82. Boolarong Press, Brisbane.

Arthington, A.H. 1989. Diet of *Gambusia affinis holbrooki, Xiphophorus helleri, X. maculatus* and *Poecilia reticulata* (Pisces: Poeciliidae) in streams of southeastern Queensland, Australia. Asian Fisheries Science 2:193-212.

Arthington, A.H. 1992. Diets and trophic guild structure of freshwater fishes in Brisbane streams. Proceedings of the Royal Society of Queensland 102:31-48.

Arthington, A.H., H. Burton, R. Williams and P.M. Outridge. 1986. The ecology of humic and non-humic dune lakes, Fraser Island, with emphasis on the effects of sand infilling in Lake Wabby. Australian Journal of Marine and Freshwater Research 37:743-764.

Arthington, A.H. and L.N. Lloyd. 1989. Introduced Poeciliidae in Australia and New Zealand. In: Evolution and Ecology of Livebearing Fishes *(Poeciliidae)* (ed. G.K. Meffe and F.F. Snelson), pp. 333-348. Prentice-Hall, New York.

Arthington, A.H., D.A. Milton and R.J. McKay. 1983. Effects of urban development and habitat alterations on the distribution and abundance of native and exotic freshwater fish in the Brisbane region, Queensland. Australian Journal of Ecology 8:87-101.

Bayly, I.A.E., P. Ebsworth and Hang Fong Wang. 1975. Studies on the lakes of Fraser Island, Queensland. Australian Journal of Marine and Freshwater Research 26:1-13.

Bensink, A.H.A. and H. Burton. 1975. North Stradbroke Island - a place for freshwater invertebrates. Proceedings of the Royal Society of Queensland 86:29-45.

Connell, J.H. 1980. Diversity and coevolution of competitors, or the ghost of competition past. Oikos 35:131-138.

Dill, L.M. 1983. Adaptive flexibility in the foraging behaviour of fishes. Canadian Journal of Fisheries and Aquatic Sciences 40:398-408.

Dussault, G.V. and D.L. Kramer. 1981. Food and feeding behaviour of the guppy, *Poecilia reticulata* (Pisces: Poeciliidae). Canadian Journal of Zoology 59:684-701.

Greenfield, D.W., C.F. Rakocinski and T.A. Greenfield. 1981. Spatial and temporal interactions in wet and dry seasons between *Gambusia luma* and *Gambusia sexradiata* (Pisces:Poeciliidae) in Belize, Central America. Fieldiana Zoology New Series 14:1-16.

Hellawell, J. M. and R. Abel. 1971. A rapid volumetric method for the analysis of the food of fishes. Journal of Fish Biology 3:29-37.

Hill, M.O. 1979. DECORANA - a Fortran program for detrended correspondence analysis and reciprocal averaging. Ecology and Systematics Section, Cornell University, Ithaca, New York.

Holbrook, S.J. and R.J. Schmidt. 1989. Resource overlap, prey dynamics and the strength of competition. Ecology 70:1943-1953.

Hyslop, E. J. 1980. Stomach contents analysis - a review of methods and their application. Journal of Fish Biology 17:411-429.

Ivantsoff, W. and Aarn. 1999. Detection of predation on Australia native fishes by *Gambusia holbrooki*. Marine and Freshwater Research 50:467-468.

Leiper, G. 1984. Honey blue-eyes - endangered? Fishes of Sahul 2:72.

Leiper, G. 1985. *Rhadinocentrus ornatus* - rare colour forms. Fishes of Sahul 2:82-83.

Mathur, D. 1977. Food habits and competitive relationships of the bandfin shiner in Halawakee Creek, Alabama. Amererican Midland Naturalist 97:89-100.

McDowall, R., Editor. 1996. Freshwater fishes of South-eastern Australia. A.H. and A.W. Reed, Sydney.

Meffe, G.K. 1985. Predation and species replacement in American southwestern fishes: a case study. Southwestern Naturalist 30:173-187.

Morisita, M. 1959. Measuring of interspecific association and similarity between communities. Memoirs of the Faculty of Science. Kyushu University Series E3:64-80.

Myers, G.S. 1965. Gambusia, the fish destroyer. Tropical Fish Hobbyist 13:31-54.

Penn, L.J. and I.C. Potter. 1991. Reproduction, growth and diet of *Gambusia holbrooki* (Girard) in a temperate Australian river. Aquatic Conservation and Marine Freshwat.er Ecosystems 1:159-172.

Pusey, B.P. 1992. Strategies for survival in freshwater fishes of south-western Australia. Ph.D Thesis, University of Western Australia, Perth, Western Australia.

Schlosser, I.J. and L.A. Toth. 1984. Niche relationships and population ecology of rainbow (*Ethesotoma caeruleum*) and fantail (*E. flabellare*) darters in a temporally variable environment. Oikos 42:229-238.

Shakuntala, K. 1977. Effect of feeding level on the rate and efficiency of food conversion in the cyprinodon fish *Gambusia affinis*. Ceylon Journal of Science 12:177-184.

Smith, E.P. 1985. Estimating reliability of diet overlap measures. Environmental Biology of Fishes 13:125-138.

Wager, R. and P.D. Jackson. 1993. The action plan for Australian freshwater fishes. Australian National Parks and Wildlife Service, Canberra.

Winemiller, K.O. 1989. Ontogenetic diet shifts and resource partitioning among piscivorous fishes in the Venezuelan ilanos. Environmental Biology of Fishes 26:177-199.

Manuscript recieved 27 March 1998; Accepted 02 October 1998.