The success of the Gobiidae in tropical Pacific insular streams

P. A. RYAN*

Biology Department School of Pure and Applied Sciences University of the South Pacific P.O. Box 1168, Suva, Fiji

*Present address: c/- West Coast Regional Council, P.O. Box 66, Greymouth, New Zealand

Abstract The high islands of the tropical Pacific possess a sparse native fish fauna dominated by the family Gobiidae. Evidence of this domination is presented, together with possible reasons for the success of the Gobiidae. Factors which may have contributed include a marine larval stage, euryhalinity, small size, an excellent climbing ability, a range of trophic level from carnivory through omnivory to herbivory, frequent lack of a gas bladder, and an associated bottom-living life style. The evolution of streams in the high islands of the tropical Pacific is relatively recent, thus there has been little time for colonisation to occur. Furthermore, estuaries in many islands are poorly developed, thereby placing euryhaline estuarine species at a competitive disadvantage.

Keywords Gobiidae; evolution; freshwater; distribution; colonisation; Pacific; islands; reproductive strategies; euryhalinity

INTRODUCTION

Native primary and secondary freshwater fish are absent from the tropical Pacific (Herre 1940; Myers 1953; Berra 1981) and although the faunal biomass

of insular inland waters may be similar to those of comparable continental waters, the species diversity is much lower (Maciolek 1984). Of the larger islands in the tropical Pacific, Fiji has been one of the best studied. The group was visited by Wilkes and the United States Exploring Expedition of 1838–1842, by the "Challenger" Expedition in 1874 and by Gardiner (in Boulenger 1897).

Publications on fish collections from the group have been made by Nutting (1924), Whitley (1927), Fowler (1928, 1929, 1959), and Herre (1936). More recently there have been visits from the Royal Ontario Museum (1983) and the Smithsonian Institution (1982, 1985). In the latter visits most of the sampling effort was directed at marine habitats. Ryan (1980)* published a checklist of Fiji's brackish and freshwater fish and some new records (1981*). Information is also available from the Samoas (Jordan & Seale 1906; Schultz 1943; Wass 1984)*, Vanuatu (Baker 1929*; Ryan 1986*; and author's collections), Palau (Bright & June 1981*), the Cook Islands (author's observations and Jellyman in press*). For comparison with a continental landmass, information on a collection of fishes by Allen & Hoese (1980*), from the Jardine River, Cape York Peninsula, Australia, is also included. Unfortunately, no checklists could be obtained from north east Queensland which would have provided a more meaningful comparison with the tropical Pacific. Information from asterisked authors is summarised in Table 1. Many workers (following Springer 1983; Hoese 1984) split gobioid fishes into the Eleotridae and the Gobiidae but for the purposes of this paper I have followed Miller (1973) as the argument's apply equally well to both electrids and gobiids. For other families I have followed the classification used by Masuda et al. (1984).

RESULTS

The carnivorous sicydiine Sicyopus zosterophorum, not previously reported from Fiji, was collected by the author on Vitilevu, Vanualevu, and Taveuni. The presence of the ophichthid eel, Achirophichthys

Table 1 Families and numbers of species represented in some selected tropical insular streams. Cape York, Australia, is included for comparison. Percentage representation of each family is given in brackets.

	P3	= 7		Cook	-	Cape
	Fiji	Vanuatu	Samoa	Islands	Palau	York
CLASS Chondrichthye Order Lamniformes						
Family Carcharhinidae	1 (1.3)					
Order Rajiformes Family Dasyatidae	1 (1.3)				- -	
CLASS Osteichthyes Order Elopiformes						
Family Elopidae	2 (2.5)		2 (4.1)		1 (2.5)	1 (3.3)
Family Albulidae	1 (1.3)		ì (2)		1 (2.5)	<u> </u>
Order Anguilliformes						
Family Anguillidae	4 (5.0)	3 (10.3)	3 (6.1)	3 (30)	2 (5.0)	1 (3.3)
Family Moringuidae	1 (1.3)		1 (2)		1 (2.5)	- -
Family Muraenidae	1 (1.3)		1 (2)		1 (2.5)	- -
Family Muraenesocidae Family Ophichthidae	1 (1.3) 3 (3.8)	1 (3.4)	1 (2)		_ _	
Order Osteoglossiforme		1 (3.4)	1 (2)			
Family Osteoglossidae						1 (3.3)
Order Gonorhynchiforn			1 (0)	1 (10)		
Family Chanidae	1 (1.3)		1 (2)	1 (10)		
Order Siluriformes						
Family Ariidae Family Plotosidae	2 (2.5)		1 (2)			1 (3.3)
•	2 (2.3)		1 (2)			4 (13.3)
Order Beloniformes						1 (2.2)
Family Belonidae Family Hemiramphidae	1 (1.3)		1 (2)			1 (3.3)
			1 (2)	- -		
Order Syngnathiformes Family Syngnathidae	6 (7.5)	2 (6.9)	4 (8.2)		4 (10)	
Order Lophiiformes						
Family Antennariidae					1 (2.5)	
Order Perciformes						
Family Atherinidae						1 (3.3)
Family Melanotaeniidae Family Mugilidae	3 (3.8)	3 (10.3)	1 (2)	1 (10)	1 (2.5)	6 (20) ?
Family Centropomidae	J (J.6)	3 (10.3)	1 (2) 	1 (10)	1 (2.3) 	1 (3.3)
Family Ambassidae	1 (1.3)	1 (3.4)	1 (2)		1 (2.5)	3 (10)
Family Serranidae	1 (1.3)					- -
Family Kuhliidae	4 (5.0)	3 (10.3)	2 (4.1)	?	2 (5.0)	
Family Apogonidae	1 (1.3)		ì (2)		<u> </u>	1 (3.3)
Family Carangidae	1 (1.3)	1 (3.4)	2 (4.1)			
Family Leiognathidae	1 (1.3)					
Family Gerreidae	2 (2.5)	1 (3.4)	3 (6.10)			
Family Monodactylidae	1 (1.3)	1 /2 /)	1(2)		- -	
Family Lutjanidae	1 (1.3)	1 (3.4)	1(2)			2(66)
Family Teraponidae Family Scatophagidae	2 (2.5) 1 (1.3)	1 (3.4) 1 (3.4)	1 (2)		1 (2.5)	2 (6.6)
Family Toxotidae		1 (J. 4)			1 (2.3) 	1 (3.3)
Family Siganidae Family Gobiidae	1 (1.3) 33 (41.3)	10 (34.5)	18 (36.7)	5 (50)	23 (57.5)	
•		10 (34.3)	10 (30.1)	5 (50)	23 (31.3)	5 (16.6)
Order Tetraodontiformes Family Tetraodontidae 2 (2.5) 2 (4.1)						
Order Synbranchiform			- \/			
Family Synbranchidae	- -				1 (2.5)	1 (3.3)
Total species	80	29	49	10	40	30
a vani species		2)	77	10	-1 0	

kampeni, predicted to be found in Fiji (Ryan 1980), was confirmed from electro-fished specimens caught in Vitilevu by the Fisheries Department during 1987 and identified by the author. Dawson (1984), added the syngnathids Microphis brevidorsalis, Microphis argulus, and Microphis brachyurus to the Fijian, Samoan, and Vanuatuan fauna, respectively. These additions have been incorporated in the families represented in Tables 1 and 2. A checklist of the freshwater fish of the Cook Islands is given in Table 3.

DISCUSSION

Despite Fiji's distance from centres of origin (probably the Philippines), Fiji has a substantial fresh and brackish water fish fauna of at least 80 species, represented by 28 families (Ryan 1980). This diversity is much greater than the 30 species reported from the Cape York Peninsula, Australia, by Allen & Hoese (1980), the 40 species from Palau (Bright & June 1981), or the 29 species reported from Vanuatu (Baker 1929; this paper). This may just indicate the intensity with which Fiji has been studied or could be a reflection of the nearly four degrees of latitude covered by the group which has enhanced the chances of marine tolerant, or freshwater species with marine larval stages, reaching the islands. Vitilevu is at least 40×10^6 years old (Kroenke 1984) which has given

ample time for both colonisation and speciation. Despite this, with the one obvious exception of the family Gobiidae, little speciation has occurred. Gobiids account for 41% of the native Fijian stream fish fauna and fill a wide variety of niches. There are at least 4 endemics out of the 33 brackish and freshwater species and a number still remain undescribed. It is likely that there are 10 or more endemic gobies accounting for around 30% of the total gobiid fauna and around 12.5% of the total brackish/freshwater fauna.

Information from other tropical Pacific islands is sparse. In Palau over half of the freshwater fish fauna is composed of gobiids although there are only two known endemic species (Bright & June 1981). Of the 29 species known from Vanuatu, 10 (35%) are gobiids. At least one gobiid is endemic (Ryan 1986). Samoan gobiids make up 37% of the freshwater fishes (18 out of 49 species). In the Cook Islands, gobies make up 50% of a depauperate stream fauna (including one yet to be described species of *Stiphodon* in author's collection). In Cape York, the gobiid component of the fauna represents only 16% of the total species, a contribution less than half that of any of the island groups considered.

The question arises as to why there has not been more speciation amongst the other families on oceanic islands? (*Mesopristes kneri*, an endemic Fijian

Table 2 Brackish and freshwater fish species reported from Vanuatu. "*" denotes observed or collected by the author; "+" indicates information from Baker (1929). Dawson (1984).

Species Family Anguillidae Anguilla megastoma+ Anguilla marmorata+ Anguilla obscura+

Family Ophichthidae Ophichthus polyophthalmus+

Family Syngnathidae Microphis leiaspis* Microphis retzii* Microphus brachyurus¹

Family Muglidae Liza macrolepis+* Crenimugil crenilabis+ Cestraeus plicatilis+

Family Ambassidae Ambassis urotaenia+

Family Kuhliidae Kuhlia repustris+* Kuhlia bilunulata+ Kuhlia marginata+ Family Carangidae Caranx sexfasciatus+

Framily Gerreidae Gerres filamentosus+

Family Lutjanidae Lutjanus argentimaculatus+*

Family Teraponidae Mesopristes argenteus+*

Family Scatophagidae Scatophagus argus+

Family Gobiidae
Guavina gyrinoides+
Ophiocara porocephala+
Ophiocara macrolepidota+
Ophioeleotris aporos+
Gobius sp.+
Awaous ocellaris+*
Stenogobius genivittatus+*
Sicyopterus micrurus+*

Stiphodon "elegans" *

Stiphodon astilbos*

teraponid, is the only one of which I am aware). A reasonable hypothesis is that non-gobiids have been outcompeted by the gobies to the extent that speciation has not been able to take place. This competition takes place on a variety of fronts. In many gobiids the adults breed in freshwater, only the eggs or fry making the journey to the sea (Miller 1984). This passive transport requires little energy expenditure. By contrast, most, if not all, of the other families encountered in tropical Pacific insular streams (TPIS) require the return of reproductively mature adults to the sea or estuaries for breeding to occur. A number of metabolic changes take place before the migration and as a result of this journey, less energy is available for reproduction (Miller 1984). In those long-lived species which breed each year, energy must also be expended in the return upstream. Probable examples of this type of strategy would include the various Kuhlia species (Lewis & Hogan 1987). In energy terms, goby reproductive strategies may be more efficient than their competitors.

In Fijian freshwater gobies, most would appear to be r selected in marked contrast to the many k selected marine species. Female gobiids of the genera Stiphodon and Sicyopterus produce large numbers of tiny eggs and Fijians harvest the upriver migration of young larvae. Elsewhere, Maciolek (in McDowall 1988) considers that the sicydiine genera Lentipes, Sicydium, Sicyopterus, Sicyopus, and Stiphodon all lay eggs in freshwater with the young being swept to the sea and migrating back up rivers as larvae. I have collected a small upstream migrating school of transparent gobiid larvae in the lower reaches of Fiji's Rewa river (although it is not known where the adults spawn.) Tank reared, they were identified as Hypseleotris guntheri.

McDowall (1988) summarises our current knowledge of the breeding biology of a number of freshwater gobiids. Amphidromy (Myers 1949) seems to be the rule, rather than the exception, amongst gobiids inhabiting TPIS.

Species diversity increases in estuaries and lagoons and with this increase in diversity there are more predators, thus increasing the hazards of a catadromous life style. There is a relative lack of midwater predators in TPIS (author's unpublished data), so larvae drifting in streams face little predation although they are exposed to a full gamut of predators upon arrival in the estuary. At this point they are no more at risk than those r selected species which breed in estuaries (although they may be smaller). However, the adult breeding stock has not been exposed to the additional risks faced by downstream migration.

The largest gobiid encountered in TPIS is Ophioeleotris aporos which can reach 30 cm. Most gobiids are considerably smaller than this. Small size confers the ability to penetrate streamlets and utilise niches unavailable to marine families with relatively larger euryhaline representatives such as the Carangidae, Lutjanidae, or Serranidae. Smallness is also an advantage if food is in short supply, which would be the situation in depauperate streams on newly-formed islands. This does not explain why small specimens of predominantly marine species cannot compete for niche space with the TPIS Gobiidae. Estuarine species are usually capable of short forays into freshwater. When they do move upstream, large size confers an osmotic advantage over smaller individuals. The effect of size on oxygen demand can be described by the power function: $y = ax^{b}$ where y = oxygen uptake x = body weight

The exponent b for most fish has an average value of 0.86 (Brett & Groves 1979). Most gas exchange is through the gills (Hughes 1980) and so is ionic regulation (Evans 1980). The implication is that larger fishes require proportionately less oxygen than small fish. Hence, the branchial epithelium and rate of ionic exchange should also be proportionately smaller. Large grouper (Epinephelus spp.) are frequently found in the lower reaches of freshwater streams (author's observations and P. Kailola, pers. comm.) but are too big to find an adequate food supply or physically to enter many streams. Small specimens, which seem ideally suited to such habitats, do not occur there, perhaps because of the osmotic stress that they would encounter.

Another possible reason for the lack of speciation amongst the non-gobiid component of TPIS stems from the difference between oceanic islands and continental islands and continents. Most Pacific islands are geologically young. The Fijian island of Taveuni ($< 1 \times 10^6$ years old) provides a graphic example of what many of these islands may have been like. On the east coast of Taveuni there is an almost constant slope of 15° stemming from a 1200 m mountain chain. There are few estuaries. In most instances, the water changes from fully fresh to fully salt in the matter of a few metres. Under these conditions, species that breed in freshwater and have a marine larval stage are favoured, as are those such as the Anguillidae which actually breed in the sea. Anguillids are the second most successful colonisers of TPIS (in terms of species diversity). Estuarine breeders will be at a great, if not impossible disadvantage. Weathering will eventually cause estuaries to form, but by then the majority of niches in freshwater will have already been colonised.

Streams on the east coast of Taveuni are characterised by large numbers of waterfalls. Gobies, because their pelvic fins are modified as a sucking disc, are at an advantage in colonising headwaters. Even young electridines, without a suctorial disc may still use their pelvic fins to aid in climbing. I have seen the gobiine Parioglossus sp. (which lacks a suctorial disc) climbing the glass walls of aquaria in this manner. Young streams often lack gravel and sand substrates simply because there has not been enough weathering to form them. This limits food supplies and reduces relief from the current. On Taveuni, with its 15° slope, fish without low energy anchoring devices must swim the entire time just to keep station. Again, this places them at a competitive disadvantage in comparison with the gobiids.

Most, if not all, TPIS gobiids are negatively buoyant. After collection with rotenone or quinaldine, few species float to the surface. Most gobies also lack a gas bladder, in marked contrast to the majority of nongobiid estuarine species. The end result is that even in the absence of a suctorial disc, gobiids expend less energy keeping station than gas bladder equipped species.

Another advantage possessed by the Gobiidae is trophic. They cover a full spectrum of feeding strategies from herbivory through omnivory to carnivory. Many TPIS gobiids are herbivores or omnivores. In the Cook Islands for instance, three of the five gobiids recorded by the author (Table 3) were herbivorous. The other two were carnivores

Table 3 The trophic status of fresh and brackish water species reported from the Cook Islands. "*" denotes collected by author, "+" denotes Jellyman pers. comm.

Species	Trophic status		
Family Anguillidae			
Anguilla megastoma+	carnivore		
Anguilla marmorata+	carnivore		
Anguilla obscura+	carnivore		
Family Chanidae Chanos chanos+1	herbivore		
Family Mugilidae Mugil cephalus*	herbivore		
Family Gobiidae			
Awaous ocellaris*	carnivore		
Stiphodon "elegans"*	herbivore		
Stiphodon "stevensoni" *	herbivore		
Sicyopterus "micrurus" *	herbivore		
Eleotris fuscus*	carnivore		

¹Farmed in Lake Terotonue, Mitiaro. Juveniles or adults may ascend a short distance up some streams on Rarotonga.

with omnivorous tendencies (*Eleotris fuscus* and *Awaous ocellaris*). With such a suite of choices resident within the family, it is hardly surprising that some species are able to colonise the virgin habitat a recently formed stream offers. Once present, selection ensures that the resident gobies become better adapted to the environment.

The three herbivorous gobies (Stiphodon "elegans", Stiphodon "stevensoni", and Sicyopterus "micrurus") are sympatric algal grazers and may reach very high densities in some streams. It is not known how they partition the algal resource. The same pattern of two Stiphodon and sometimes two Sicyopterus spp. is repeated in many other TPIS. In French Polynesia and on Vanualevu in Fiji I have observed interactions between four algal-grazing sicydine species. The situation is made even more complicated by competition from algal-grazing molluscs!

The ideas presented above require further development, particularly the comments on goby reproductive strategies. However there is little doubt that the gobies are TPIS colonisers par excellence. Once the occupation has occurred it may be difficult for them to be displaced.

Genetic isolation between different stream populations and the original colonisers will favour speciation. The relative importance of the different contributory factors is unknown, but this could be a fruitful field of study for evolutionary biologists.

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