

DIETS, GROWTH RATES AND SECONDARY PRODUCTION OF HERBIVOROUS
CORAL REEF FISHES

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ABSTRACT

Literature on diets, growth rates and secondary production of herbivorous coral reef fishes was reviewed. The gut contents of the vast majority of species were dominated by algal turfs or turfs and detritus mixed with large amounts of inorganic material. Macroalgae and seagrasses dominated gut contents rarely. Limited growth data suggest that scarids may grow more quickly than acanthurids of similar size. Far more data on site-specific growth rates are needed before generalizations can be made. Few data exist to calculate the rate of secondary production of herbivorous coral reef fishes. The percentage contribution of herbivores to total yields of fishes from coral reefs range from 4 to 16%. Total yields of herbivorous fishes per unit area of coral reef range from 0.05-2.89 metric tons/km²/yr and provide a guide to maximum potential harvests. Estimates of yields of scarids from three Philippine reefs range from 9% to 38% of the standing crop per year. Estimates of secondary production of scarids from these three reefs ranged from 3.56 to 7.64 metric tons/km²/yr. This represents secondary production in the range of .05-0.3% of net primary production. Yield values are lower than for tropical fish ponds but comparable to those of tropical lakes and reservoirs.

INTRODUCTION

Coral reefs have some of the highest rates of primary organic production of any marine ecosystem and the low biomass, filamentous algal turfs account for the majority of this production (Carpenter, 1985; Gladfelter and Kinsey, 1985). Unlike other ecosystems, a very high proportion of the primary production is consumed directly by grazers (Hatcher, 1981; Carpenter, 1986; Russ, 1987). Fishes are the dominant large grazers on Indo-Pacific coral reefs (Hatcher, 1983; Russ, 1984a) and are a major component of the grazers in the Caribbean (Hay, 1984; Carpenter, 1986). Thus, secondary production of herbivorous fishes on coral reefs is potentially high. This contention is supported by evidence that assimilation efficiencies of herbivorous fishes may be much higher than suspected (e.g. Edwards and Horn, 1982). Furthermore, the standing stock of herbivorous fishes on coral reefs is often very large. Williams and Hatcher (1983) recorded that the standing stock of herbivorous fishes on three unfished reefs of the Great Barrier Reef ranged from 8.3 to 45 metric tons/km² (9 to 29% of the total biomass of reef fishes).

These characteristics of herbivory on coral reefs led to the following questions:

1. Are the highly productive algal turfs the major food source of herbivorous fishes on coral reefs?

2. What levels of secondary production of herbivorous fishes occur on coral reefs?

A review of the literature revealed a large amount of information on diet but limited information on secondary production. Secondary production is a function of population size and fish growth. Population size is determined by rates of recruitment and mortality. Even though standing stock estimates are available for many species of herbivorous coral reef fishes, there is restricted information on recruitment (Doherty and Williams, 1988) and even less data on rates of mortality. All of the estimates of natural mortality of herbivorous fishes in the review by Munro and Williams (1985) were derived from Pauly's (1980a) empirical formula and probably have wide confidence limits. There was insufficient data (on density, recruitment and age-specific growth and mortality rates) to calculate an estimate of secondary production of any species of herbivorous coral reef fish. In order to provide a guide to maximum potential production and harvests, the data on yields of herbivorous fishes per unit area of coral reefs were reviewed.

Diets

Table 1 summarizes data on gut contents of 91 species of herbivorous coral reef fishes (57 Indo-Pacific species and 34 Caribbean species). Algae were designated as 'turfs' or 'macroalgae' in Table 1 using Table 1a of Steneck (1988).

In 51% of species, the gut contents were dominated by filamentous algal turfs. This category includes 52% of the herbivorous acanthurids and the majority of herbivorous pomacentrids and siganids. Also, algal turfs were the major organic component of the gut contents of scarids (documented in detail by Randall 1967).

In a further 34% of species, gut contents were dominated by inorganic material (mainly sand in acanthurids and calcareous material in scarids and blennies) admixed with algal turfs and detritus.

Macroalgae, detritus or seagrasses were seldom the dominant component in guts of the species reviewed. Macroalgae dominated gut contents in 14% of the herbivorous acanthurids, all of which were in the genus *Naso*. Detritus was the dominant component of gut contents in 33% of blennies. Only one species, the scarid *Sparisoma radians*, fed principally on seagrass. Seagrass was a component in the gut contents of eight other species of scarids in the Caribbean and represented a mean volume of 7% (SE = 2.3).

The results in Table 1 suggest strongly that algal turfs constitute the main food of the majority of herbivorous fishes on coral reefs. These dietary studies are consistent also with studies reporting high rates of consumption of turfs by herbivorous fishes on coral reefs (Hatcher, 1981; Carpenter, 1985; 1986; Russ, 1987; Scott and Russ, 1987).

Table 1. Percentage of species of herbivorous coral reef fishes in which the main component of gut contents are those shown. Of the total number of species reviewed within each family, the numbers in brackets are Indo-Pacific species; the remainder are Atlantic species.

Main Component of Gut Contents	Acanthuridae	Scaridae	Siganidae	Pomacentridae	Blennidae	All Five Families
Algal Turfs	52%	-	100%	96%	27%	51%
Turfs, Detritus and Inorganic material	28%	94%	-	-	33%	34%
Macroalgae	14%	-	-	4%	7%	7%
Detritus	7%	-	-	-	33%	8%
Seagrass	-	6%	-	-	-	1%
Number of Species	29(26)	19(8)	4(4)	24(18)	15(11)	91(57)
Major Sources	1. Hiatt and Strasburg (1960) 5. Jones (1968) 2. Randall (1967) 6. Robertson (1984), Robertson and Gaines (1986) 3. Hobson (1974) 7. Montgomery (1980), Montgomery <i>et al.</i> (1980) 4. Sano <i>et al.</i> (1984) 8. Lobel (1980)					

Table 2: Estimates of the asymptotic length (L_{∞}) in cm., the coefficient of growth K (\pm 95% CL) and the growth performance index (ϕ) of herbivorous coral reef fishes. FL = fork length, SL = standard length, TL = total length.

Family and Species	Location	L_{∞}	K	ϕ	Method	Source
SCARIDAE						
<i>Bolbometapon muricatus</i>	Kavieng, PNG	105.0 FL	.104		Petersen	1
<i>B. muricatus</i>	Kavieng, PNG	102.0 FL	.130		ELEFAN	1
<i>Hipposcarus longiceps</i>	Kavieng, PNG	52.0 FL	.30		Petersen	1
<i>Scarus coeruleus</i>	St. John	46.0 FL	.403(+ .097)	2.01	Tag-Recapture	2
<i>S. vetula</i>	St. John	39.0 FL	.937(+ .082)	2.00	Tag-Recapture	2
<i>Sparisoma rubripinne</i>	St. John	45.5 FL	.430(+ .150)	1.74	Tag-Recapture	2
<i>Sp. viride</i>	St. John	29.0 FL	.963(+ .095)	1.82	Tag-Recapture	2
<i>Sp. chrysopterus</i>	St. John	35.2 FL	.927(+1.257)	1.93	Tag-Recapture	2
<i>Scarus frenatus</i>	Great Barrier Reef	38.0 TL	.38	1.61	Direct Observ ⁿ .	3
<i>S. niger</i>	Great Barrier Reef	34.0 TL	.38	1.53	Direct Observ ⁿ .	3
				$\bar{x}=1.81$		
				SE=.06	n=7	
ACANTHURIDAE						
<i>Acanthurus bahianus</i>	St. John	19.3 FL	.448(+ .145)	1.15	Tag-Recapture	2
<i>A. chirurgus</i>	St. John	31.6 FL	.141(+ .036)	1.13	Tag-Recapture	2
<i>A. coeruleus</i>	St. John	36.9 FL	.112(+ .105)	1.18	Tag-Recapture	2
<i>A. nigricauda</i>	Kavieng, PNG	28.4 FL	.402	1.41	Modal Progression	4
<i>A. nigricauda</i>	Kavieng, PNG	24.3 FL	.62	1.47	Daily otoliths	4
<i>A. xanthopterus</i>	Kavieng, PNG	48.0 FL	.21	1.61	Tag-Recapture	5
<i>A. triostegus</i>	Oahu, Hawaii	17.5 SL	.160(+ .044)	.81	Tag-Recapture	6
<i>A. triostegus</i>	Oahu, Hawaii	21.7 TL	.350	1.14	Tag-Recapture	6,7
<i>Ctenochaetus striatus</i>	Moorea	27.73 TL	.445	1.31	Modal Progression	8
<i>C. striatus</i>	Amer. Samoa	24.0 FL	.475		Daily otoliths	9
				$\bar{x}=1.28$		
				SE=.07	n = 7	
SIGANIDAE						
<i>Siganus vermiculatus</i>	Fiji	45.0 TL	.38	1.86	Direct Observ ⁿ .	10
<i>S. canaliculatus</i>	Tanzania	27.8 TL	1.73(+ .399)		Direct Observ ⁿ .	11
<i>S. canaliculatus</i>	Philippines	25.2 TL	1.87	1.83	Direct Observ ⁿ .	12
<i>S. spinus</i>	Philippines	24.4 TL	3.32	2.11	Direct Observ ⁿ .	13
POMACENTRIDAE						
<i>Stegastes planifrons</i> (m)	Jamaica	10.2 SL	.58	.80	ELEFAN	14
<i>S. planifrons</i> (f)	Jamaica	11.6 SL	.33	.55	ELEFAN	14
<i>S. nigricans</i>	Moorea	17.5 TL	.58	1.17	Modal Progression	8
BLENNIDAE						
<i>Salarias fasciatus</i>	Great Barrier Reef	14.4 TL	.73	.84	Direct Observ ⁿ .	15
<i>S. fasciatus</i>	Great Barrier Reef	13.8 TL	.72	.84	ELEFAN (visual census)	15

Sources: 1. Wright, A., P. Dalzell & A. Richards, Kavieng Lab., PNG Fisheries, unpublished.
 2. Randall (1962). 3. Bellwood (in prep). 4. P. Dalzell (in prep). 5. A. Wright (in prep)
 6. Randall (1961). 7. Pauly (1980b). 8. Galzin (1977). 9. Itano (1988). 10. Gunderman *et al.* (1983). 11. Bwathondi (1982). 12. Carumbana & Luchavez (1979). 13. Horstmann (1975).
 14. Pauly & Ingles (1982). 15. Russ & St. John (in prep).

Growth Rates

Growth rate data for 22 species of herbivorous coral reef fishes are summarized in Table 2 (see Munro and Williams (1985) for an extensive review of growth rates of coral reef fishes). The asymptotic length (L_{∞}) and the growth coefficient (K) in Table 2 are parameter estimates of the von Bertalanffy growth function. Asymptotic size and K are interdependent because small animals tend to have higher K values than related larger ones. A partial solution to this problem is the growth performance index (ϕ) of Munro and Pauly (1983) which relates both K and asymptotic size in a single index (see Munro and Williams, 1985).

The information in Table 2 provides few generalizations. Growth performance indices of the seven species of scarids were significantly higher than those of the seven species of acanthurids in Table 2 ($t_{12} = 5.25, p < 0.001$). This suggests that scarids may grow more quickly than acanthurids of similar asymptotic size. The growth performance indices of scarids in Table 2 were compared with those of other reef fish of similar asymptotic size ($L_{\infty} = 29.0$ to 46.0 cm FL) contained in Table 2 of Munro and Williams (1985). Growth performance indices of the 7 species of scarid were compared with those of 3 species of serranid, 3 species of haemulid and one species of lutjanid, balistid and siganid. Acanthurids were excluded from the comparison. The growth performance indices of scarids were higher ($\bar{x} = 1.81, 95\% \text{ CL} = .147$), although not significantly higher, than those of reef fish of similar asymptotic size ($\bar{x} = 1.53, 95\% \text{ CL} = .235; t_{14} = 2.12, p > 0.05$). Similarly, the growth performance indices of acanthurids in Table 2 were compared with those of other reef fish of similar asymptotic size ($L_{\infty} = 19.3$ to 48.0 cm FL) contained in Table 2 of Munro and Williams (1985). The growth performance indices of the 7 species of acanthurid were compared with those of 3 species of serranid, haemulid and siganid, 2 species of nemipterid and one species of lutjanid and balistid. Scarids were excluded from the comparison. The growth performance indices of acanthurids ($\bar{x} = 1.28, 95\% \text{ CL} = 0.171$) were significantly lower than those of reef fish of similar asymptotic size ($\bar{x} = 1.58, 95\% \text{ CL} = 0.192; t_{18} = 2.26, p < 0.05$).

These comparisons of growth performance indices are based on limited data and must be viewed as preliminary. For example, data for 5 of the 7 species of scarid used in the comparisons derive from tagging studies at St. John, U.S. Virgin Islands (Randall, 1962). An extensive review of growth rates of acanthurids by Dalzell (in prep) does not indicate that acanthurids grow more slowly than other reef fish of similar asymptotic size.

The small amount of information on growth rates of herbivorous siganids, pomacentrids and blennies (Table 2) does not provide any generalizations. The growth data for the three species of siganid are from culture conditions. All three species have high ϕ values and *Siganus spinus* and *S. canaliculatus* have exceptionally high K values. These data are included here to indicate that natural growth rates of siganids may be more similar to those of scarids than acanthurids. Far more data on site-specific growth rates of herbivorous coral reef fishes are needed before generalizations can be made.

Yields of Herbivorous Fishes from Coral Reefs

Herbivorous fishes constitute between 4 and 16% of the total yield of certain reef fisheries (Table 3). In absolute terms, yields of herbivorous fishes range from 0.05 metric tons/km²/yr from the lightly fished reefs of PNG to 2.89 mt/km²/yr. on heavily fished reefs of American Samoa (Table 3). All of the Philippine reefs in Table 3 can be considered to be heavily fished and the yields have been sustained over 5 years (Apo Island) and 8 years (Sumilon Island). Table 3 suggests that sustainable yields of herbivorous reef fishes from heavily fished small areas of pure coral reef may be in the order of 1-3 mt/km²/yr. This compares favourably with yields of all fish from large fishing grounds in the North Sea and Western Greenland ($\bar{x} = 2.53$ mt/km²/yr., see Table 2 in Russ 1984b).

The most extensive information on the magnitude and dynamics of yields of herbivorous fishes from coral reefs is available for the family Scaridae.

Table 3: Total yields of reef fish (metric tons/km²/yr.) and contribution of herbivorous fishes to yields on coral reefs.

Location	Total Yield	Approximate Yield of Herbivores	Herbivores as % of Yield	Source
Sumilon Is., Philippines	36.9	1.59	4.25%	1
Apo Is., Philippines	16.8	0.86	5.1%	2
Apo Is., Philippines	24.9	2.10	8.4%	3
Apo Is., Philippines	22.1	2.56	11.6%	4
Pamilacan Is., Philippines	10.7	1.52	14.2%	4
American Samoa	18.3	2.89	15.75%	5
Tigak Is., PNG	0.42	0.05	11.7%	6
Port Moresby, PNG	5.0	0.705	14.1%	7

Sources: 1. Alcala (1988). 2. Alcala & Luchavez (1981). 3. Bellwood (1988). 4. Savina & White (1986). 5. Wass (1982). 6. Wright & Richards (1985). 7. Lock, (1986).

Table 4: Yields of scarids (metric tons/km²/yr.) from coral reefs. Estimates of standing crop of scarids (metric tons/km²) are available for 3 reefs in the Philippines. For these reefs yield is expressed as the estimated percentage of the standing crop removed per year.

Location	Yield of Scarids	Estimated Standing Crop of Scarids	Yield as % of Standing Crop	Source
Sumilon Is., Philippines	0.83	7.9-9.2 (Source 8)	9-10.5%	1
Apo Is., Philippines	0.46	4-5.5 (Source 9)	8-11%	2
Apo Is., Philippines	0.82	4-5.5 (Source 9)	15-20%	3
Apo Is., Philippines	0.88	4-5.5 (Source 9)	16-22%	4
Pamilacan Is., Philippines	1.28	3.4-4.6 (Sources 4,9)	28-38%	4
American Samoa	0.915	-	-	5
Tigak Is, PNG	0.034	-	-	6
Port Moresby, PNG	0.25	-	-	7

Sources: 1. Alcala (1988). 2. Alcala & Luchavez (1981). 3. Bellwood (1988). 4. Savina & White (1986). 5. Wass (1982). 6. Wright & Richards (1985). 7. Lock (1986). 8. Russ (1985). 9. Bellwood & Alcala (1988).

Yields of scarids from coral reefs range from 0.03 to 1.28 mt/km²/yr. (Table 4). Both standing crop and yield estimates are available for three reefs in the Philippines. These data suggest that annual yields of scarids, expressed as a percentage of standing crop may range from 9-10.5% at Sumilon Island, 8-22% at Apo Island and 28-38% at Pamilacan Island. These estimates of yield can be expressed as rates of fishing mortality (in terms of biomass) and range from approximately 0.1 to 0.4.

Estimates of biomass, yield and fishing mortality for scarids on the three Philippine reefs were used to make very approximate estimates of secondary production in two ways.

(a) Assuming a P/B Ratio of 0.6-0.83

The only published Production/Biomass (P/B) ratios for herbivorous and detritivorous coral reef fishes are those of Galzin (1987). Galzin estimated a P/B ratio of 0.72 for the herbivorous pomacentrid Stegastes nigricans (average age 4 years, maximum weight approximately 100g) and 0.69 for the detritivorous acanthurid Ctenochaetus striatus (average age 6 years, maximum weight

approximately 250g.) In addition, in a review of P/B ratios of a large number of temperate, freshwater fishes Chapman (1978) concluded that species with 7 or more age groups may commonly have P/B ratios less than 1.0.

Using the relationships
 $P/B = Z$
 and $Z = M + F$
 where P = Production
 B = Biomass
 Z = Total Mortality
 M = Natural Mortality
 F = Fishing Mortality

and arbitrarily assuming a P/B ratio for Philippine scarids of 0.6-0.90, an estimate of mean $M = 0.5$ was obtained. Using this figure and the various estimates of F from Table 4 gave a mean estimate of secondary production (P) of scarids on the three Philippine reefs of 3.56 metric tons/km²/year (SE = 0.40) or approximately .001 g organic carbon/m²/day. Assuming a net primary production of 1-2 gC/m²/day gives an estimate of scarid secondary production of 0.05-0.1% of net primary production (Table 5).

Table 5. Estimates of secondary production of herbivorous coral reef fishes. Estimates for Scaridae derived from yield data assuming a P/B ratio of 0.6-0.83 or $M = 1.26$ (see text for further details). Estimates for Stegastes and Ctenochaetus from Galzin (1987). Estimates from temperate freshwaters from Chapman (1978).

TAXON	LOCATION	SECONDARY PRODUCTION gC/SQ.m/DAY	BIOMASS gC/SQ.m	SECONDARY PRODUCTION AS % NET PRIMARY PRODUCTION
1. Scaridae (P/B = .6-.83)	Philippines	.001	.69	.05 - .1%
2. Scaridae (M = 1.26)	Philippines	.003	.69	.15 - .3%
3. <u>Stegastes nigricans</u>	Moorea	.018	9.2	.9 - 1.8%
4. <u>Ctenochaetus striatus</u>	Moorea	.005	2.76	.25 - .5%
5. 69 SPP.	Temperate Freshwaters	.003	.79	-

(b) From an Independent Estimate of M

The empirical relationship of Pauly (1980a) was used to estimate rates of natural mortality of a variety of medium-sized scarids in Table 2 of Munro and Williams (1985). A mean estimate of $M=1.26$ was derived from this table and assumed to apply to scarids at the three Philippine reefs. Note that this estimate is much higher than the estimate in the previous section. Assuming $M=1.26$ and $F=0.1$ to 0.4 , Total Mortality (and thus P/B) ranged from $1.36-1.59$ with a mean secondary production of $7.64 \text{ mt/km}^2/\text{yr.}$ ($SE = 1.00$) or $0.003 \text{ gC/m}^2/\text{day.}$ This represents $.15-0.3\%$ of assumed net primary production (Table 5).

These two estimates for scarids are considerably lower than the estimates of Galzin (1987) for Stegastes and Ctenochaetus in French Polynesia (Table 5). Galzin did record a very high standing crop for both species, however. The estimates of secondary production for scarids are remarkably similar to those of 69 species of temperate freshwater fishes from Chapman (1978) (Table 5).

A final piece of speculation relates to the efficiency of transfer of net primary production to yield of all herbivorous coral reef fishes. Table 6 compares yields of herbivorous coral reef fishes with those derived from intensively managed, tropical tilapia ponds (with fertilization but without food supplements) and from tropical lakes and reservoirs. Tilapia ponds are known to be highly efficient at converting net primary production to yield (Marten and Polovina, 1982). Herbivorous, coral reef fishes do not appear to be as efficient at converting net primary production into secondary production as tilapia in ponds but the upper range of the estimates made here are very close to total yields gained from tropical lakes and reservoirs.

Table 6: Comparison of yields of herbivorous coral reef fishes with yields from tropical tilapia ponds and from tropical lakes and reservoirs. Data on tilapia ponds and lakes and reservoirs from Marten and Polovina (1982).

	YIELD AS % OF NET PRIMARY PRODUCTION	ABSOLUTE YIELD (METRIC TONS/ KM ² /YEAR)
Tilapia Ponds	.14 - .22%	6 - 20
Lakes & Reservoirs	.09 - .10%	1 - 15
Herbivorous Coral Reef Fishes	.01 - .09%	1 - 3

CONCLUSIONS

1. Algal turfs are likely to constitute the main food of the majority of herbivorous fishes on coral reefs.
2. Far more data is required on site and age-specific growth and mortality rates of herbivorous reef fishes.

3. Preliminary estimates of secondary production of herbivorous coral reef fishes based on yield data tend to indicate that the efficiency of conversion of net primary production into secondary production may not be exceptionally high. Nevertheless, the estimates of yield of $1-3 \text{ metric tons/km}^2/\text{year}$ come from low standing stocks ($4-10 \text{ mt/km}^2/\text{yr.}$). Higher levels of yield could be expected from unfished reefs with standing stocks up to $45 \text{ metric tons/km}^2$ and production studies on such systems are required.

ACKNOWLEDGEMENTS

We thank D. Bellwood, P. Dalzell and A. Wright for providing unpublished data on growth rates. Thanks to A.I. Robertson for helpful discussions and to Bev Gordy for typing the manuscript.

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