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High biomass and production but low energy transfer efficiency of Caribbean parrotfish: implications for trophic models of coral reefs§

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Quantitative data are presented to assess the trophic role of scarids on the fringing coral reef of Bonaire (Netherlands Antilles), with particular emphasis on the stoplight parrotfish *Sparisoma viride*. Average herbivore biomass on the reef was 690 kg ha^{-1}, 22% of which was accounted for by *S. viride*. From data on relative gonad weights, daily spawning frequencies, and egg numbers obtained by stripping, with previous estimates of somatic growth and energy intake, a gross efficiency (GE: somatic plus gamete production/consumption) of 2·3% was obtained. This is a factor of five to seven lower than the GE suggested to be valid for most aquatic ecosystems, including coral reefs. To investigate one potential cause for our low estimate, overestimation of food intake, our intake estimates were compared with published values for other herbivorous coral reef fish. This yielded a relationship (daily C intake$=0{\cdot}0342 \times W^{0{\cdot}816}$; wet body mass W in g) with high correlation ($r^2=94{\cdot}6\%$, $n=13$), which shows that the intake estimates agree well with other published data. Averaged over the year, primary production at 0–3 m depth was 17·2 kg C ha^{-1} day^{-1} while herbivore consumption was estimated at 17·4 kg C ha^{-1} day^{-1}, indicating an ecotrophic efficiency (EE, the fraction of total production at one trophic level that is consumed by all predators) of 100%. This suggests strongly that the food intake estimates are realistic, since no changes in algal biomass were observed over the study period. The two scarids for which food intake was actually measured in our own study area, were estimated to consume 55% of the algal production in the shallow reef (*S. viride*, 20%; *Scarus vetula*, 35%). This is lower than expected if consumption were proportional to biomass (*S. viride*, 22%; *S. vetula*, 40% of herbivore biomass in the shallow reef). Consequently, a minimum estimate of 88–91% can be inferred for the EE of these two species. Multiplied by GE, this yields a transfer efficiency (TE, the fraction of production passing from one trophic level to the next) of 2%. For coastal and coral systems the primary production required (PPR) to sustain fisheries was estimated to be 8·3%, which was based on a TE of 10%. The present estimates show that the TE of a major herbivore at our reef is at least a factor of five lower. Assuming that the estimate is representative for all scarids (comprising 70% of the herbivore standing stock), it can be concluded that the PPR to sustain coral reef fisheries may be as high as 40% of the total primary production. The low value reported before, might suggest that the effect of fishing mainly affects target populations but not the lowest trophic levels. It is argued that our estimate is more realistic for coral reefs supporting high scarid biomass and explains better the many reports of coral destruction due to algal overgrowth at exploited reefs.

Key words: *Sparisoma viride*; reproductive effort; primary production; food intake; density; gross conversion; ecotrophic efficency; ECOPATH; herbivory; Scaridae.

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INTRODUCTION

Pauly & Christensen (1995) estimated that the primary production required (PPR) to sustain all fisheries catches (including discarded bycatch) at coastal and coral reef systems amounts to 8·3% of the total primary production. This estimate is low compared to the 35–40% that has been reported for terrestrial ecosystems. It might lead to the conclusion that fishing activity at coral reefs is insufficient to alter any but the target populations (and closely interacting species) and does not affect the lowest trophic levels. This suggestion strongly conflicts with the many examples of coral reefs dramatically improverished due to overfishing. Such reefs are often heavily overgrown by benthic algae, even in case of relatively low fishing effort. This has led to the idea that coral reef fish are more vulnerable to overexploitation than the species targeted in northern high-latitude fisheries (Russ, 1991). One of the suggested reasons for this vulnerability is that the high productivity of coral reefs (' oases in nutrient deserts ') is highly dependent on rapid and tight recycling of nutrients (see Russ, 1991, for references). An increasing number of studies have confirmed the high primary productivity of coral reefs (Wanders, 1976; Lewis, 1977; Ruyter van Steveninck & Breeman, 1981; Vooren, 1981; Carpenter, 1985; Klumpp & McKinnon, 1989). However, few studies have quantified the fate of this production, leaving the tight recycling hypothesis untested.

Most attempts to estimate trophic flows in coral reef ecosystems are based on a modelling approach, known as ECOPATH (Polovina, 1984; Aliño *et al*., 1993; Opitz, 1993; Pauly *et al*., 1993). Based on the assumption that the system is in steady state, trophic flow is modelled as a system of simultaneous linear equations. For each trophic group (*i*) the model requires estimates of biomass, production/biomass (P/B) and consumption/biomass (Q/B) ratios, ecotrophic efficiency [EE, the total fraction of the production of (*i*) that is consumed by predators] and the fraction of prey (*i*) in the average diet of all predators (Pauly & Christensen, 1992). Usually, P/B and Q/B ratios can be estimated from empirical relationships, while biomass and diet composition of most trophic groups can be obtained relatively easily from surveys and stomach contents analyses. That explains why it has become an important tool in fisheries management (Christensen, 1991). The model can also be used to estimate EE and transfer efficiencies (TE, the fraction of production passing from one trophic group to the next, which is the product of EE and the P/Q ratio or cross efficiency, GE). This was done by Pauly & Christensen (1995), who obtained 140 TE estimates from 48 models of aquatic ecosytems on which their PPR estimates were based. They found an average ($\pm$ S.E.) TE of 10·1 ($\pm$ 0·5)% without apparent trend with trophic level. This justified their assumption of a constant TE of 10% for the transfer biomass between all trophic groups in six major aquatic ecosystem types, including some coral reefs. Given the lack of other independent TE estimates, this approach yields at present the best possible estimate for the PPR to sustain coral reef fisheries.

This study presents a summary of quantitative data collected to assess the trophic role of scarids, particularly of the stoplight parrotfish *Sparisoma viride* Bonnaterre, 1788, on a fringing reef at Bonaire (Netherlands Antilles). They are the results of an 8-year project set up to test the hypothesis of efficient transfer of

nutrients and energy from primary producers to one of the most abundant herbivores. Two main objectives were addressed: to determine the GE for the entire *S. viride* population in our study area, and to estimate the EE for all herbivores in the shallow part of our reef.

It was not feasible to study all herbivores with the same level of detail. Therefore, the present study focused on one major scarid, *S. viride*, to obtain quantitative estimates of its production, taking into account differences between life phases, sexes, social categories and size classes. Measurements of its food intake and somatic production have been published (Bruggemann *et al.*, 1994*a*; Van Rooij *et al.*, 1995). Social organization and population structure are described in Van Rooij *et al.* (1996*b*). Our quantitative estimates of daily reproductive output are new, based on relative gonad weights, stripped egg numbers, daily spawning frequencies, and field collections of spawned eggs.

Besides for *S. viride*, uptake of algal food in our study was also measured in detail for the most prominent member of the *Scarus* genus, the queen parrotfish *Scarus vetula* Bloch & Schneider, 1801 (Bruggemann *et al.*, 1994*b*). Combined with published values for some acanthurids, pomacentrids and an echinoid, we have been able to estimate total herbivore consumption. This was done for the shallow part of the reef, where herbivore density is highest and where we also measured primary productivity. Thus an estimate of the EE for the entire herbivorous guild in the shallow reef zone was obtained.

To assess the relative role of *S. viride* and *S. vetula* compared to that of other scarids, acanthurids, pomacentrid and echinoids, we will also present biomass estimates for these major groups of herbivores. It is shown that the TE for *S. viride* is as low as 2% and that scarids play a prominent role as primary consumers at our reef. Assuming that our direct estimate for one major species is more representative for reef herbivores than the previously suggested 10%, which was mainly based on indirect estimates for other ecosystems with no scarids, it is concluded that the PPR for coral reefs should be adjusted to a value as high as 40%.

MATERIALS AND METHODS

STUDY AREA AND ANIMALS

The study was carried out on the fringing reef off Karpata Ecological Centre at Bonaire, Netherlands Antilles (12°13′ N, 68°21′ W) between May 1987 and January 1992. The entire reef of Bonaire is a marine park where spearfishing has been banned since 1971. Fishing pressure on herbivores is negligible and adult fish can be observed at close range, using SCUBA or snorkel gear. Reef profile and dominant growth forms at our study site are described by Bruggemann *et al.* (1994*c*) and Van Rooij *et al.* (1996*a*). A 100-m section of this reef, extending from the coast to a depth of 22 m (below which adult density dropped to zero), was demarcated and forms the study area.

Sparisoma viride and *S. vetula* are both prominent grazers on many Caribbean reefs attaining lengths up to 45 and 50 cm, respectively. They feed almost exclusively on epilithic algal turfs, crustose corallines and endolithic algae, which they scrape from dead coral substrates with their powerful, beaklike jaws. Apart from some differences in grazing mode and micro-habitat preferences between the two genera, all scarids graze largely on the same substrate types (Bruggemann *et al.*, 1994*c*; Van Rooij *et al.*, 1996*a*. These are also shared with the other major groups of herbivores, territoriality being directed mainly against conspecifics (Van Rooij *et al.*, 1996*a*). Parrotfish are protogynous

TABLE I. Wet body mass–length relationships of Scaridae caught in the study area. Parameters of the equation $W=a \times L_f^b$ were obtained by ordinary regression of ln body mass (W, g) on ln fork length (L_F, cm)

Species	a	b	r	n
Sparisoma viride	$9{\cdot}115 \times 10^{-6}$	3·140	0·999	386
Sparisoma aurofrenatum	$1{\cdot}899 \times 10^{-6}$	3·430	0·995	27
Sparisoma rubripinne (Valenciennes, 1839)	$24{\cdot}114 \times 10^{-6}$	2·956	0·989	11
Scarus vetula	$2{\cdot}887 \times 10^{-6}$	3·330	0·991	170
Scarus taeniopterus	$0{\cdot}785 \times 10^{-6}$	3·574	0·982	50
Scarus iserti	$5{\cdot}070 \times 10^{-6}$	3·229	0·994	22

The GM regression parameters [$b_{gm}=b/r$; $a_{gm}=\text{mean}(\ln W) - b_{gm} \times \text{mean}(\ln L_F)$] were used to obtain body mass predictions from fork length.

hermaphrodites, males being derived from females through sex change (Reinboth, 1968; Robertson & Warner, 1978). Two adult colour phases are distinguished in most species, drably coloured initial phase fish (IP) and brightly coloured terminal phase (TP) males.

Adult *S. viride* are defined as fish >15 cm fork length (L_F), the estimated size of the smallest fish that were observed to spawn. All IP *S. viride* adults proved to be females at our study site. Territorial adults live in groups of one to 14 females that share a common home range between 3 and 22 m depth with a single male. The latter defends its territory (240–820 m^2 in size) against conspecific TP males. Non-territorial fish, further referred to as group fish, reside mainly in the shallower parts (<4 m) of the reef where they form groups of up to 14 TP and 30 IP adults, all sharing a common home range. TP males could be recognized individually by the pattern of yellow spots at the base of tail and opercula. Females were tagged with anchor tags and/or small clips in the median fins for individual identification. A record was kept of the inhabitants of up to 17 territories and several group areas, allowing the verification of the social status of focal animals. Territorial fish form stable social units (observed residence times: median 17, maximum 42 months). The shallow reef zone is defined as the reef part shallower than 3 m and coincides with the non-territorial part of the reef. This zone comprises 30 m of the 88-m long reef profile. Further details on the social organization can be found in Van Rooij *et al.* (1996*b*).

BIOMASS OF *S. VIRIDE* CATEGORIES AND OTHER HERBIVORES

A total of 26 visual censuses was carried out between February 1989 and January 1992 in five permanent quadrats (15 × 15-m quadrats in the 2–4-, 6–12-, and 12–22-m depth ranges, 10 × 15-m quadrats in the 0–2- and 4–6-m range). The quadrats formed a 15 m wide transect perpendicular to the coast, covering 65 m of the 87-m long reef profile between the coast and 22 m depth. All scarids, acanthurids, echinoids and adult herbivorous pomacentrids were counted. Parrotfish were counted in 5 cm fork length classes, except for the smallest juveniles that were divided in a 0–2- and a 2–5-cm class. For surgeonfish a distinction was made between juveniles (<5 cm L_F), solitary adults and schooling adults. Numbers per quadrat were converted to fish ha^{-1}. Mean density over the entire reef was calculated as the average of all quadrats, weighted for the width of the reef zones they represented. The shallow reef was represented by the shallowest quadrat. Further details on the census procedure are given by Van Rooij *et al.* (1996*a*). Determination of the relative abundance of group and territorial *S. viride* males was somewhat complicated due to temporary invasions of the deeper reef by group TP. Density and size distribution of these two categories was therefore corrected as explained in Van Rooij & Videler (1997).

Sufficient numbers of all scarid species were caught and measured (see Van Rooij *et al.*, 1995, for procedures) to establish species-specific mass–length relationships (Table I). The GM regression versions (Ricker, 1984) of these were used to obtain predicted weights

TABLE II. Average fork length (L_F) and wet body mass (W) ± S.D. of adult acanthurids and pomacentrids caught in the study area

Species	L_F (cm)	W (g)	n
Acanthuridae			
Acanthurus bahianus Castelnau, 1855 (solitary/in group)	16·5 ± 1·7	112·8 ± 22·0	30
Acanthurus coeruleus Schneider, 1801 (foraging solitary)	22·7 ± 0·8	370·0 ± 43·4	6
A. coeruleus (foraging in group)	12·9 ± 2·8	147·6 ± 39·6	8
Pomacentridae			
Microspathodon chrysurus (Cuvier, 1830)	13·3 ± 1·5	84·3 ± 21·7	20
Stegastes fuscus (Cuvier, 1830)	9·4 ± 0·9	26·0 ± 7·7	14

for the mid-length of each length class (W_{mid}), which were multiplied by density to obtain biomass per size class. For acanthurid and pomacentrid species mean adult body mass was used (Table II). The biomass estimate for *Diadema antillarum* was based on an average of 40 g individual (ind)$^{-1}$ reported by Williams & Carpenter (1988).

For *S. viride* biomass was converted to ash free dry mass (AFDM) and energy equivalents (23·1–24·8 kJ g^{-1} AFDM) using data on biochemical composition and energy content of six size classes (Fig. 4 in Van Rooij *et al.*, 1995).

GAMETE PRODUCTION *S. VIRIDE*

In our study area *S. viride* spawned pelagic eggs daily (between 0700 and 0930 hours) and throughout the year, without seasonal or lunar variation in spawning frequency (Van Rooij *et al.*, 1996*b*). Three different methods were used to quantify the daily investment in reproductive products: collection of spawned eggs in the field, stripping eggs or sperm from anaesthetized fish, and dissection of gonads. Combined with daily spawning rates, these yielded estimates of daily gamete production.

A total of 345 h was spent on underwater observation of focal animals during the daily spawning period using scuba gear. Spawning rates (F_{90}) were calculated as averages, weighted for the observation time during the spawning period and converted to spawnings per 90 min (the maximum duration of the daily spawning period). F_{90} thus yields an estimate of the daily number of spawnings, which agrees well with the number counted for individuals that were observed throughout a daily spawning period (Van Rooij *et al.*, 1996*b*).

For field collections, a 4-l ' slurp-gun ' was used initially to suck up the whitish gamete cloud that can usually be seen right after a pair had spawned. Because the volume proved to be too small to collect all the rapidly dispersing eggs in the water column, we constructed a hoop-net. Two 75-cm diameter hoops were connected with nylon cloth to form a 1-m long cylinder (of *c.* 450 l). The lower hoop ended in a nylon funnel, with a 7·5-cm diameter PVC pipe with dismountable filter cap (0·25 mm mesh) at its end. Right after a spawning we swam quickly (with the hoop-net folded) to the spot of gamete release. The eggs were collected from below by releasing the lower hoop while slowly swimming upwards, thus enclosing the water containing the gamete cloud.

Eggs were transferred to the laboratory within 1 h after collection. Egg diameter of a sample of 25–50 eggs (or all if less were obtained) was measured (in sea water) under a dissecting microscope with micrometer at a magnification of 25 × . In smaller samples (<2000), all eggs were counted. For larger samples the volume of all eggs was measured to 0·1 ml, after removing adherent water using a filter. Division by the volume per egg (calculated as $4\pi r^3/3$, r being the average radius of the measured eggs) yielded an estimate of egg number. The eggs were dried at 60° C until their mass remained constant and then weighed to the nearest mg. Because the dried eggs contained visible salt encrustrations, some later samples were flushed briefly with distilled water before drying to remove salts

(eggs remained intact after this treatment, as checked under the microscope). Dry eggs were stored in sealed tubes at −20° C for later calorimetric determination.

For stripping, fish were caught at night and examined for the presence of gametes next morning around spawning time. By exerting mild pressure on the ventral side, eggs or sperm could be stripped and were collected. Determination of egg volume, number, diameter, and dry mass were as described above, except that eggs were never flushed with distilled water before drying. Because there was no adherent water in these samples, the wet mass of stripped eggs could be measured with reasonable precision, unlike that of eggs collected in the field.

The number of fish that were killed in our study was kept to a strict minimum. The gonads of those killed (for various purposes) were dissected out, and wet and dry mass were measured. A gonadosomatic index (I_G) was calculated as: gonad wet mass × 100/W. In one case hydrated eggs were present in the oviduct. These were counted and weighed separately and treated as stripped eggs.

The energy content of eggs and gonads were measured using bomb calorimetry. Triplicate sub-samples (1 g dry mass) of larger samples were combusted in an adiabatic bomb calorimeter (Gallenkamp Autobomb). For smaller samples, triplicate measurements were made using a non-adiabatic Phillipson microbomb (Centry Instruments Inc., described by Prus, 1975). Samples were also weighed after combustion to determine the ash fraction. Energy content was expressed in kJ g^{-1} AFDM.

TOTAL HERBIVORE CONSUMPTION

At our study site, energy and carbon intake were quantified in great detail for *S. viride* (Bruggemann *et al.*, 1994*c*) and for the queen parrotfish *S. vetula*, taking into account differences between life phases, size classes and reef zones (Bruggemann *et al.*, 1994*b*). For other herbivorous reef fish, data on carbon intake were taken or calculated from Chartok (1983); for *Acanthurus guttatus* (Bloch & Schneider, 1801), Montgomery *et al.* (1989); for *Acanthurus nigrofuscus* (Forsskål, 1775), Polunin (1988); for *Plectroglyphidodon lacrymatus* (Quoy & Gairnard), and from Klumpp & Polunin (1989); for *Stegaste apicalis* (de Vis). Plotting these against body mass (Fig. 1), gave:

$$\text{C intake} = 0{\cdot}0342 \times W^{0{\cdot}816} \quad (r^2 = 0{\cdot}946\%,\ n = 13). \tag{1}$$

This relationship was used to calculate the carbon intake per size class (as the product of W_{mid} and density) for all herbivorous reef fish on the shallow reef, other than *S. viride* and *S. vetula*.

With one exception, all data represent annual averages. Because all these fish were strictly diurnal foragers, daily food intake can be expected to vary with day length, as confirmed for the two scarids (Bruggemann *et al.*, 1994*b* and *c*). Therefore, relative day length was used as weighting factor to estimate seasonal fluctuations in food intake.

An average carbon intake of 0·22 g C ind^{-1} day^{-1} was calculated for *Diadema antillarum* as the mean of food intake reported by Hawkins & Lewis (1982); 0·7 g algal dry mass ind^{-1} day^{-1} and Carpenter (1988); 0·38 g algal dry mass ind^{-1} day^{-1}, and the carbon contents (40·5%) of algal food (Bruggemann *et al.*, 1994*a*).

PRIMARY PRODUCTION SHALLOW REEF

Productivity was measured for the four main algal food types that were distinguished (see Bruggemann *et al.*, 1994*a*,*b*,*c*): large algal turfs (fronds 3·5–15 mm in height), sparse turfs (fronds 0·1–3·5 mm) on substrates infested with endolithic algae, sparse turfs growing on substrates covered with crustose corallines, and bare coralline crusts. Species composition and relative abundance (corrected for substrate rugosity) on vertically and horizontally exposed substrates of these food types was determined by Bruggemann *et al.* (1994*c*). For each food type, net primary production was estimated by measuring changes in dissolved oxygen during incubations in two UV-transparent perspex respiration chambers (volume 3·15 l, modified from Carpenter, 1985). Substrate blocks with algae were incubated for consecutive 10–30-min periods (depending on photosynthetic

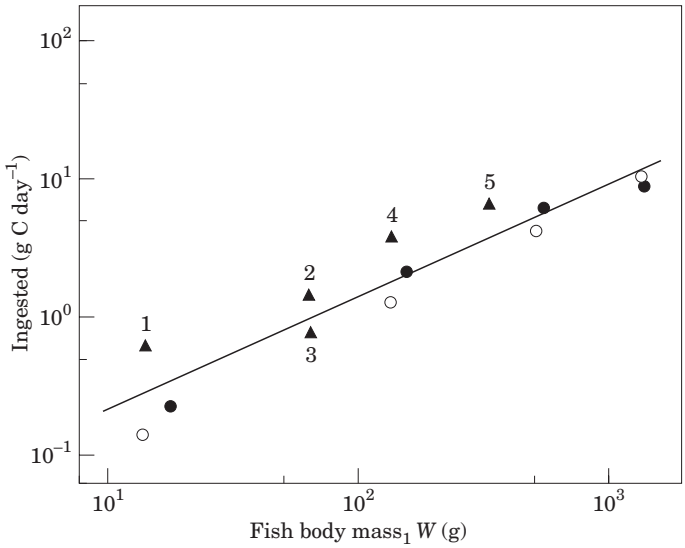

FIG. 1. Log–log plot of daily intake of algal carbon by herbivorous reef fish in relation to body mass. Circles: Values obtained from studies at our own study site. Triangles: Taken or calculated from published data for other coral reefs. Data for *Sparisoma viride* (●) from Bruggemann *et al.* (1994*c*), for *Scarus vetula* (○) from Bruggemann *et al.* (1994*b*), for *Plectroglyphidodon lacrymatus* (1) from Polunin (1988), for *Stegastes apicalis* (summer, 2; winter, 3) from Klumpp & Polunin (1989), for *Acanthurus nigrofuscus* (4) from Montgomery *et al.* (1989), for *Acanthurus guttatus* (5) from Chartok (1983). Line obtained by linear regression: $y=0{\cdot}0342W^{0{\cdot}816}$, $r^2=0{\cdot}946$, $n=13$.

rate), upon which the chambers were flushed with fresh sea water. A total of 27 incubations was performed in two seasons (March–April and November–December 1991) at *c.* 1 m depth in a back reef area that was partially protected from the surge. They commenced before dawn and were continued until solar zenith. Oxygen and temperature were measured with polarographic probes (YSI model 5750) connected to YSI model 58. The chambers were stirred by compressed air-driven stir bars and a surge driven paddle. Irradiance of photosynthetically active radiation (PAR) was recorded simultaneously with a flat quantum sensor (cosine corrected; LiCor model LI-192SA), connected to a datalogger (LiCor model LI-1000).

Dead coral substrates with a homogeneous algal vegetation cover, representative of the main food types, were collected from the reef and cut with a diamond rock saw while keeping them submerged in sea water. Prior to incubation, the algal vegetation was allowed to recover for 1–2 days in a cage at the site where productivity measurements were performed. All visible epifaunal and infaunal organisms were removed from the substrate blocks before incubation. After incubation, volume of the blocks was determined by water displacement to correct water volume in the incubation chambers. Surface area was measured as described by Bruggemann *et al.* (1994*a*) and algal biomass (in mg AFDM cm^{-2}) from replicate sub-samples ($n=4$) as described by Bruggemann *et al.* (1994*c*).

Rates of photosynthesis and respiration (in μg O_2 cm^{-2}) were obtained from the changes in [O_2] over each incubation period and plotted against average photon flux density. A hyperbolic tangent function (Jassby & Platt, 1976) was fitted using non-linear least-squares regression. Values for $P\text{net}_{\max}$, the initial slope of the curve (α), I_k (saturating irradiation of PAR), I_c (irradiation at compensation), and R (respiration) were calculated for each food type.

The relationship between sub-surface irradiance of PAR (I) and solar elevation (β) was determined empirically on 11 days in June and 15 days in November 1991, when I was recorded continuously with the sensor suspended horizontally in the water column at a depth of 0·3 m. Solar elevation was calculated from the time of day, solar declination and

latitude, using the equations given by Dring (1984). Linear regression was used to obtain the relationship between I and sin β. Attenuation of total PAR with depth for downward irradiance was calculated from the difference in I between two horizontally oriented sensors, a reference at 0·3 m (I_{ref}) and the second sensor at different depths (I_{depth}). These measurements were performed on 3 June and 18 August 1991. Attenuation on vertical surfaces was measured on 17 and 20 August 1991 by suspending the second sensor vertically at several depths. All measurements were carried out between 1200 and 1400 hours under normal weather conditions. The relationship between $\ln(100 \times I_{depth}/I_{ref})$ and depth was fitted by linear regression.

Integrated daily net production per surface area of substratum at 2-m depth (average depth of the shallow reef zone) was derived for each food type. It was calculated from the sum of the cumulative oxygen flux in 2-min intervals as estimated from α and $P\text{net}_{max}$, and the corresponding I. It was assumed that no differences occurred between the P–I curves in the morning and evening (Carpenter, 1985; Klumpp & McKinnon, 1989).

RESULTS

GAMETE PRODUCTION *S. VIRIDE*

Table III summarizes the weighted average spawning rates for different size classes for the four categories, based on our entire data set. Territorial males clearly attained the highest rates, group males only spawning incidentally, whereas most females >20 cm spawned once or twice a day. In all categories an increase in spawning rate with size is apparent.

Up to 1910 eggs were collected in a single spawning with the slurp gun, while the maximum yield of the hoop net was nearly five times higher (Table IV). Both methods yielded <50 eggs in more than 55% of the trials [Fig. 2(a)], thus resulting in highly variable estimates. In only 20 out of 63 field collections, the social status of the spawning females was known (territorial males spawn both with territorial and with group females). Consequently, the differences between group and territorial fish, although large, were not statistically significant (Kruskal–Wallis tests, see Table IV). Female length was estimated in 39 cases and no effect of size on the number of spawned eggs was detected.

Twenty-three territorial IP and 19 group IP were examined for the presence of ripe eggs, which were obtained in 65 and 58% of the cases. All eight territorial TP released sperm, compared to 75% of 134 group TP. From 16 females all eggs were stripped and counted, yielding averages of 41 600–50 900 eggs per female with no significant effect of social status (territorial IP, group IP, and females of unknown status) or size [Table IV, Fig. 2(b)]. The lowest number, stripped from a 24·6-cm female, was 9690 (0·55% of W), while the maximum amounted to 77 400 eggs (3·01% of W). All stripped eggs were identical in appearance to eggs collected in the field: spherical, transparent and containing a small yellowish oil droplet. Because of the small volumes and high water content, the sperm stripped from males could not be quantified.

Average egg diameter showed no correlation with fish size (field eggs: $r^2 = 5{\cdot}6\%$, $n = 8$, $P = 0{\cdot}570$; stripped eggs: $r^2 = 0{\cdot}1\%$, $n = 22$, $P = 0{\cdot}899$). Stripped eggs were significantly smaller than eggs collected in the field (0·678 *v.* 0·695 mm diameter; $F_{1,39} = 4{\cdot}35$, $P = 0{\cdot}044$) with no significant differences between group IP and territorial IP eggs (field eggs of territorial IP, group IP, and ?IP: 0·682, 0·697, and 0·694 mm, respectively, $F_{2,30} = 1{\cdot}79$, $P = 0{\cdot}185$).

TABLE III. Average daily number of spawnings (F_{90}: spawnings per 90 min) of *Sparisoma viride* adults, subdivided according to category (TIP, GIP, TTP and GTP denoting territorial and group IP and TP, respectively) and fork length (L_F) class; also shown are the number of individuals (n_{ind}) and the total observation time during spawning periods (min) on which the rates are based

L_F	TIP			GIP			TTP			GTP		
	F_{90}	n_{Ind}	Min	F_{90}	n_{Ind}	Min	F_{90}	n_{Ind}	Min	F_{90}	n_{Ind}	Min
15–20 cm				0·13	3	701						
20–25 cm	0·78	3	698	0·78	4	576						
25–30 cm	1·41	10	2226	1·29	9	1263				0·11	5	807
30–40 cm	1·50	3	1141				4·57	13	1693	0·23	10	798
34–38 cm							6·74	19	9972	1·32	8	817
Average	1·33	16	4065	0·85	16	2540	6·42	32	11 665	0·56	23	2422

Modified from Van Rooij *et al.* (1996*b*).

TABLE IV. Comparison of egg numbers collected in the field (using slurp gun or hoop net) with those obtained by stripping narcotized *Sparisoma viride* females (TIP, GIP and ?IP denote territorial and group females and a rest category of females of unknown status; L_F is fork length

Egg number	Slurp gun			Hoop net			Stripped		
	TIP	GIP	?IP	TIP	GIP	?IP	TIP	GIP	?IP
Range									
Min	12	1	0	1	0	0	32 290	24 900	9690
(L_F, cm)*	(31)	(28·5)	(30)	(27·3)	(29)	(26·3)	(24·5)	(31·2)	(24·6)
Max	1748	725	1910	5366	500	9180	67 710	77 400	67 861
(L_F, cm)*	(31)	(26)	(25)	(27·7)	(26)	(27)	(26·9)	(28·5)	(31·4)
Mean	880	191	224	1510	116	893	50 871	43 212	41 599
S.E.	868	178	92	768	79	491	5903	17 109	8461
n	2	4	24	8	6	19	6	3	7
Effect size (all IP pooled; model: $N_{Eg}=a \times W^b$)									
r^2 (*n*) *P*		0·003 (12) 0·878			0·076 (24) 0·193			0·036 (16) 0·480	
Effect status (Kruskal–Wallis)									
H (*n*) *P*		0·728 (30) 0·695			0·764 (33) 0·682			0·434 (16) 0·805	

*Lengths rounded to the cm were estimated visually, values with one decimal were actually measured.

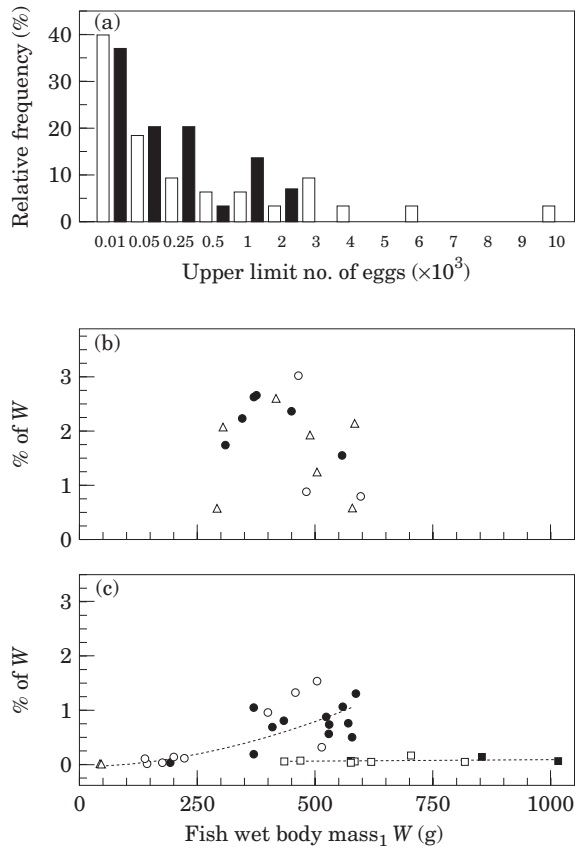

FIG. 2. *Sparisoma viride*. Comparison of (a) egg numbers ($\times 10^3$) collected with the hoop-net (□, $n=33$) and slurp gun (■, $n=30$) (b) relative egg mass of stripped females, and (c) gonadosomatic index of juvenile (JUV, △), territorial and group males [(TTP, ■ and GTP, □) and females (TIP, ● and GIP, ○; ?IP denotes females of unknown social status—shown as △ in (b)]). The lines plotted ln (c) are the predictions obtained with least squares regression; for Juv and females: $I_G=3{\cdot}178\times10^{-6}\times W^{1{\cdot}999}$ ($r^2=0{\cdot}871$, $n=21$, $P<0{\cdot}001$), for males: $I_G=8{\cdot}458\times10^{-3}\times W^{0{\cdot}303}$ ($r^2=0{\cdot}136$, $n=10$, $P>0{\cdot}20$).

The wet mass of dissected ovaries (W_{Ov}) varied from 0·1 to 7·6 g (0·04–1·54% of W) and was correlated with female size. Least-squares regression yielded the equation:

$$W_{Ov}=3{\cdot}178\times10^{-8}\times W^{2{\cdot}999}\ (r^2=0{\cdot}876,\ n=21,\ P<0{\cdot}001). \quad (2)$$

Analysis of covariance (ANCOVA) revealed no differences between territorial IP and group IP ovaries ($F_{1,18}=1{\cdot}08$, $P=0{\cdot}313$). Testes mass (W_{Tst}) ranged from 0·1 to 1·1 g (0·01–0·16% of W) and showed a much weaker relationship with male size:

$$W_{Tst}=8{\cdot}500\times10^{-5}\times W^{1{\cdot}303}\ (r^2=0{\cdot}257,\ n=10,\ P=0{\cdot}130). \quad (3)$$

Again, no difference between the two social categories was detected [analysis of variance (ANOVA): $F_{1,8}=1{\cdot}07$, $P=0{\cdot}331$].

No energy contents were determined for eggs contaminated with salt. The average energy content of flushed field eggs was significantly higher than that of stripped eggs ($F_{1,9}=19{\cdot}5$, $P=0{\cdot}002$), whereas their ash content was lower ($F_{1,9}=23{\cdot}5$, $P<0{\cdot}001$) (Table V). Flushed eggs appeared to swell slightly, indicating that they were not impermeable to water, so their higher energy content might be an artefact. The dry mass of stripped eggs (W_{DryEg} in mg) proved to be correlated with egg diameter (d in mm), regression yielding the equation:

$$W_{\mathrm{DryEg}}=0{\cdot}02835 \times d^{3{\cdot}685} \ (r^2=0{\cdot}763\%,\ n=11,\ P<0{\cdot}001). \qquad (4)$$

Compared to ovaries, stripped eggs contained five times more water (as reflected in their wet : dry mass ratio, Table V), confirming their hydrated state. Per mg AFDM, their energy content was significantly higher than that of ovaries, testes taking an intermediate position ($F_{2,17}=4{\cdot}67$, $P=0{\cdot}024$; Tukey HSD: $P<0{\cdot}005$ for eggs *v.* ovaries).

Because of the large variability in egg numbers collected in the field, no reliable estimate of daily egg production can be given. A minimum and a maximum estimate were estimated. The minimum estimate for females assumed that they all release 901 eggs spawning^{-1}, 0·695 mm in diameter [i.e. the average number of eggs collected with the hoop net (S.E.=340, $n=33$), and the mean diameter of all field eggs (S.E.=0·0036, $n=33$)]. Average dry mass per egg was estimated at 7·40 mg [from equation (4)], which converts to 6·35 mg AFDM [$7{\cdot}4 \times (1-0{\cdot}142$, the average ash fraction of stripped eggs)]. Using the energy content of stripped eggs (24·88 J mg^{-1} AFDM) as the most accurate estimate, a caloric value of 0·158 J egg^{-1} was obtained. Multiplication by 901 eggs spawning^{-1} and by the female spawning rates for the smallest and largest size classes (from Table III), yielded the minimum estimates presented in Table VI. These correspond with 120–700 eggs day^{-1} for 20-cm (group, respectively, territorial) females and 1160–1350 eggs day^{-1} for 30-cm fish.

Our maximum estimates for females assume a daily release that is equivalent to 50% of the total energy content of their ovaries, i.e. 50% of predicted ovary wet mass [from equation (2)] divided by the average wet : dry mass ratio (4·55) and multiplied by (1 − 0·0892, ash fraction) and by the average energy content of ovaries (23·19 J mg^{-1} AFDM). The resulting values in Table VI correspond with a daily production of 1660 eggs for 20-cm females and 75 980 eggs for 30-cm females.

The only data available to estimate daily sperm production by males were their spawning rates and testes mass and energy content. It was assumed that, at maximum, males release the total energy equivalent of their testes per spawning. The minimum estimate assumed a 10-fold lower sperm release. The five to 40 times higher estimated sperm production of territorial TP compared to group TP (Table VI) reflects their higher spawning rate (F_{90} in Table III).

GROSS EFFICIENCY *S. VIRIDE*

Figure 3(a) summarizes our maximum estimates for daily energy investment (in kJ ha^{-1} day^{-1}) in gamete production (E_{Gamete}) and somatic growth (E_{Growth}), together with the intake (E_{Intake}) estimates for the major *S. viride*

TABLE V. Comparison of wet : dry mass ratios, ash, and energy content (per mg AFDM) of eggs (field collections *v.* stripped) and gonads of *Sparisoma viride* adults

	Wet : dry mass			Ash (% dry mass)			Energy (J mg^{-1} AFDM)		
	Mean	(S.E.)	*n*	Mean	(S.E.)	*n*	Mean	(S.E.)	*n*
Eggs									
Field*		n.d.		9·26	(0·67)	3	26·92	(1·18)	3
Stripped	22·51	(1·20)	9	14·20	(0·56)	8	24·88	(0·30)	8
Gonads									
Ovaries	4·55	(0·19)	12	8·92	(0·38)	7	23·19	(0·52)	7
Testes	6·63	(0·07)	7	10·86	(1·35)	5	23·60	(0·48)	5

*Flushed with aqua dest before drying.

TABLE VI. Minimum and maximum estimates of the daily energy invested in gamete production by *Sparisoma viride* adults [territorial and group IP of 20 and 30 cm fork length (153 and 547 g wet body mass), territorial and group TP: 30 and 40 cm (547 and 1350 g)]

Gamete production (E_{Gamete}) Min–max (J day^{-1})	Females		Males	
	20 cm	30 cm	20 cm	30 cm
Territorial	111–263	214–12 004	454–4543	2173–21 734
Group	19–263	184–12 004	11–109	426–4257

The minimum estimates for females are based on 901 eggs released per spawning, and for males on a sperm production equivalent to 0·1 × the energy content of their testes per spawning. The maximum estimates for males assume a production equivalent to 1 × energy content of the testes per spawning. These were multiplied with spawning rate (Table III) to obtain the daily estimates. Maximum female egg production based on a daily production equivalent to 50% of the energy content of the ovaries.

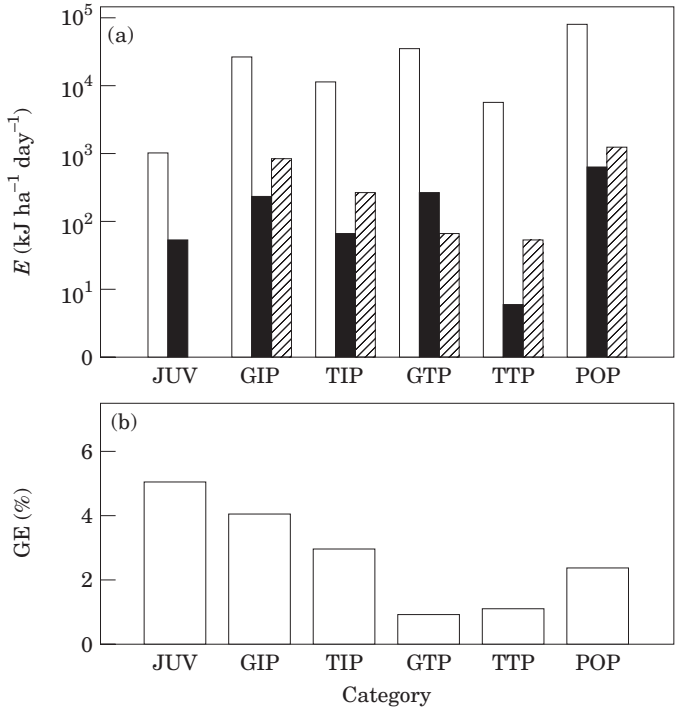

FIG. 3. *Sparisoma viride*. Comparison of energy expenditures, intake and efficiencies of juveniles (JUV), territorial and group females (TIP and GIP) and males (TTP and GTP), and the population total (POP). (a) Daily energy intake (E_{Intake}, □) and investment in somatic growth (E_{Growth}, ■) and gamete production (E_{Gamete}, ▨; maximum estimates). (b) Gross efficiency [GE = 100% × (E_{Growth} + E_{Gamete})/E_{Intake}]. Investment in growth from Van Rooij *et al.* (1995). Note the logarithmic scale of the *y*-axes in (a).

categories. It reveals the relatively high investment in growth of juveniles and the high gamete production of females (77·8–79·3% of total production for group and territorial IP, respectively). Whereas territorial males invest 90% of their

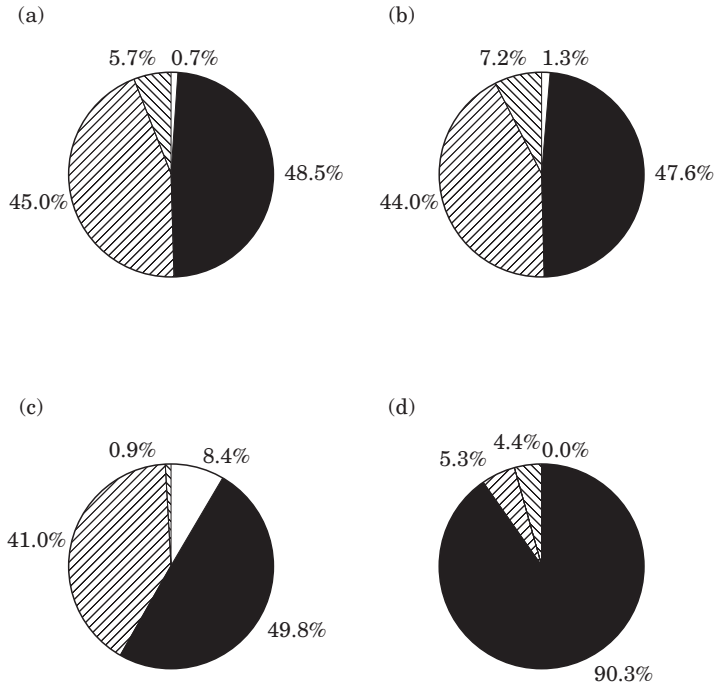

FIG. 4. *Sparisoma viride*. Relative contribution of juveniles (JUV, □), females (territorial and group IP pooled, ■), group and territorial males (GTP, ▨ and TTP, ▧) to total population biomass, food intake, somatic growth and gamete production (maximum estimates). All expressed in energy equivalents. Intake estimates from Bruggemann *et al.* (1994*a*,*c*). Somatic growth from Van Rooij *et al.* (1995). (a) Biomass (612 089 kJ ha^{-1}), (b) intake (79 259 kJ ha^{-1} day^{-1}), (c) growth (624 kJ ha^{-1}), (d) gametes (1232 kJ ha^{-1} day^{-1}).

production in sperm production, group males invest 79·5% in somatic growth. Mean gross efficiency [GE = 100% × (E_{Growth} + E_{Gamete})/E_{Intake}] for the population is estimated at 2·3%, ranging from 0·9% for group males to 5·1% for juveniles [Fig. 3(b)].

RELATIVE IMPORTANCE *S. VIRIDE* CATEGORIES

The relative contribution of juveniles, females, group TP and territorial TP males to total biomass, energy intake and production of the population is shown in Fig. 4. The data are based on average densities over the entire study period. Territorial and group females were pooled because they hardly differed in size-adjusted growth and egg production. Due to their low biomass, the juvenile contribution to population production is low, despite their high specific growth rates (Van Rooij *et al.*, 1995). They account for 8% of the somatic growth, compared to 50% for females and 41% for non-territorial males. Using our maximum estimates, the gamete production of the population is estimated to be twice its somatic production, female egg production accounting for 90% of total reproductive output. Based on our minimum estimates, total gamete production would be no more than 43 kJ ha^{-1} day^{-1} (IP, 70%; group TP, 15%; territorial TP, 13%), which is only 7% of the somatic production.

PRIMARY PRODUCTION SHALLOW REEF

The following relationship between sub-surface irradiance of PAR (I) and solar elevation (β) was obtained:

$$I = 112 + 2330 \times \sin \beta \ (r^2 = 0{\cdot}718\%,\ n = 912,\ P < 0{\cdot}001) \qquad (10)$$

This equation was used to calculate I for each month of the year.

The vertical attenuation coefficients (mean ± S.D.) measured for horizontally ($0{\cdot}093 \pm 0{\cdot}007$) and vertically ($0{\cdot}076 \pm 0{\cdot}020$) exposed surfaces are typical for oceanic waters (Kirk, 1983 and do not differ significantly (ANCOVA homogeneity of slopes test: $F_{1,27} = 0{\cdot}56$, $P = 0{\cdot}463$). This means that irradiance of PAR on a vertical surface equals that on a horizontal surface, multiplied by a constant shading factor of 0·185.

The irradiance at which algal food types approach maximum productivity (I_k in μmol m^{-2} s^{-1}) ranged from 443 ± 134 for algal turfs on vertical surfaces to 733 ± 101 for sparse turfs on endolithic algae. Irradiance at compensation (I_c in μmol m^{-2} s^{-1}) varied between 21 ± 10 and 47 ± 6, the extremes being for the same two food types. The initial slope of the P–I curve [a in μg O_2 cm^{-2} h^{-1} (μmol m^{-2} s^{-1})$^{-1}$] was highest for vertically exposed turfs ($0{\cdot}163 \pm 0{\cdot}040$) and lowest for sparse turfs on endolithic algae ($0{\cdot}099 \pm 0{\cdot}015$). $P\text{net}_{max}$ (in μg O_2 cm^{-2} h^{-1}) ranged from $61{\cdot}44 \pm 2{\cdot}28$ for crutose corallines to $72{\cdot}87 \pm 4{\cdot}09$ μg O_2 cm^{-2} h^{-1} for sparse turfs on endolithic algae. R (in μg O_2 cm^{-2} h^{-1}) ranged from $8{\cdot}04 \pm 4{\cdot}86$ for turfs on vertical surfaces to $11{\cdot}25 \pm 2{\cdot}03$ for crustose corallines.

From these parameters annual mean integrated daily production under prevailing light conditions was estimated, ranging from 0·64 g C m^{-2} day^{-1} for vertically exposed turfs to 2·00 g C m^{-2} day^{-1} for large algal turfs on horizontal substrates. Total algal production per planar area and averaged over the year amounts to 1·72 g C m^{-2} day^{-1} with a winter minimum and summer maximum of 1·46 and 1·86 g C m^{-2} day^{-1}, respectively.

RELATIVE IMPORTANCE *S. VIRIDE* AND OTHER HERBIVORES

Averaged over the entire reef, *S. viride* accounted for 32% of the biomass of all scarids and for 22% of the total herbivore stock [690 kg wet mass ha^{-1}, Fig. 5(a)]. Scarids clearly represent the most prominent herbivore family, comprising 70% of the total herbivore standing stock. In the shallow reef zone, herbivore density was much higher [1460 kg ha^{-1}, Fig. 5(b)], but the relative contribution of *S. viride* and scarids to biomass was virtually the same as for the whole reef. The only species with a deviating vertical distribution were *Scarus taeniopterus* (Desmarest, 1831) and *Sparisoma aurofrenatum* (Valenciennes, 1839), which were distributed relatively evenly over the depth profile (Van Rooij *et al.*, 1996*a*). As a result, their contribution to biomass was lower on the shallow reef. The two dominant grazers here were clearly *Scarus vetula* and *S. viride*, accounting for 40% and 22% of total herbivore biomass [Fig. 5(b)] and for 35% and 20% of the total carbon intake [Fig. 5(c)].

ECOTROPHIC EFFICIENCY HERBIVORES IN THE SHALLOW REEF

Mean (± S.D.) annual consumption of algal carbon on the shallow reef amounted to 17·4 (± 2·6) kg C ha^{-1} day^{-1} with a winter minimum and summer

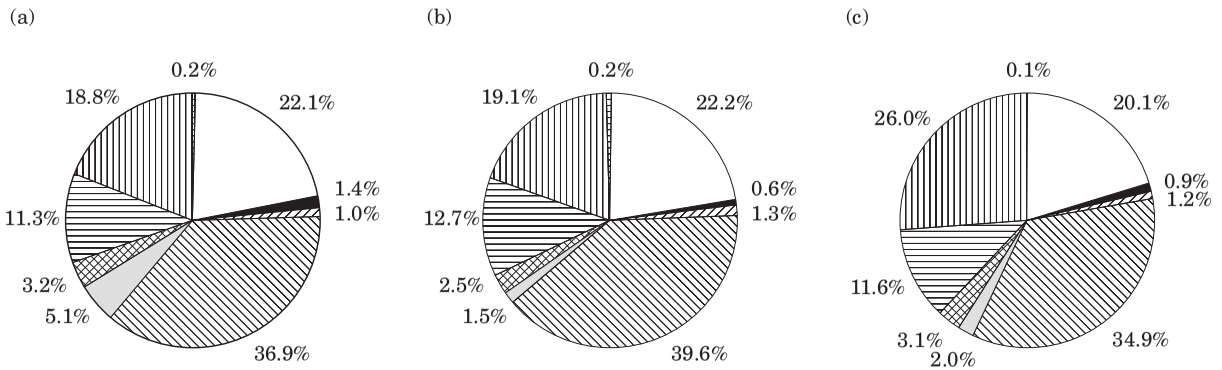

FIG. 5. Relative contribution of all parrotfish (genus *Sparisoma*: *S. viride, S. aurofrenatum, S. rubripinne*+*S. chrysopterum* pooled; genus *Scarus*: *S. vetula, S. taeniopterus, S. iserti*), surgeon fish (*Acanthurus bahianus*+*A. coeruleus* pooled), herbivorous damselfish (*Microspathodon chrysururs*+*Stegastes partitus*+*S. planifrons*+other *Stegastes* spp. pooled), and sea urchins (mainly *Diadema antillarum*) to: (a) total herbivore biomass on the entire reef (0–22 m depth, 690 kg ha^{-1}), (b) herbivore biomass on the shallow reef (0–4 m, 1460 kg ha^{-1}), and (c) carbon intake by all herbivores on the shallow reef (0–4 m, 17·4 ha^{-1} day^{-1}). (□), *S. viride*; (■), *S. aurofrenatum*; (▨), *Sparisoma* other; (▧), *S. vetula*; (⬚), *S. taeniopterus*; (▩), *S. iserti*; (▤), Acanthurids; (▥), Pomacentrids; (▦), Diadema.

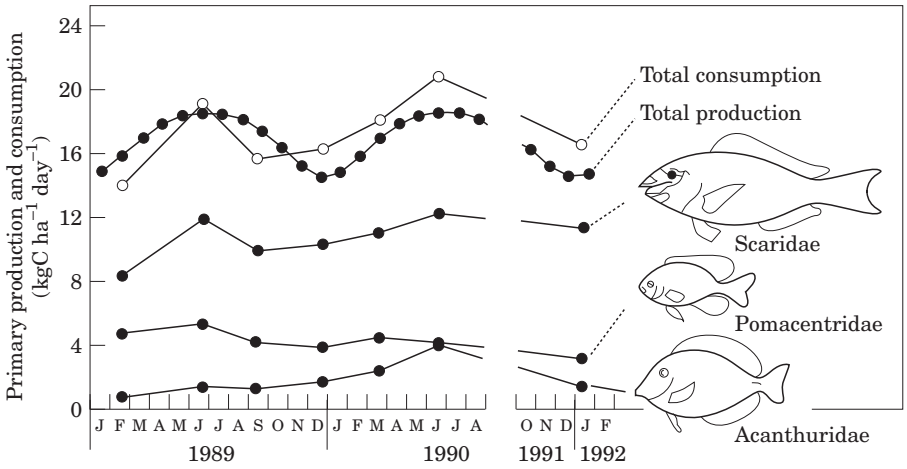

FIG. 6. Temporal pattern of primary production (●) and consumption (○) on the shallow reef throughout the study period. Consumption also shown separately for the three main families of herbivorous fish. Consumption by the seaurchin *Diadema antillarum* is not shown for figure clarity, but is included in a total consumption.

maximum of 15·7 (± 1·8) and 20·0 (± 1·9) kg C ha^{-1} day^{-1}. These averages were slightly above those for primary productivity, but the temporal patterns matched remarkably well (Fig. 6). Apparently, all algal production was consumed by the herbivores, from which it follows that their EE was as high as 100%.

Based on its relative biomass, *S. viride* would be expected to consume 22% the algal production. However, its consumption was estimated to be 20%, which is 91% of its expected share. Likewise, *S. vetula* consumed (35/40=) 88% of its expected share. These proportions can be regarded to represent a conservative estimate of their EE.

DISCUSSION

This study obtained a direct estimate for the gross efficiency of a major grazer on the coral reef of Bonaire, which was as low as 2·3%. Multiplied by our low and high estimate of ecotrophic efficiency (88–100%), this yields a transfer efficiency of 2·0–2·3% for our *S. viride* population. Given that this efficiency is based on our maximum estimate for gamete production, a TE of 2% will be considered to represent our best estimate. This is a factor of five lower than the value suggested by Pauly & Christensen (1995). Therefore it can be argued that the estimate of PPR to sustain coral reef fisheries should also be adjusted to a value as high as 40% of the primary production. This conclusion requires a number of assumptions, however, that need to be addressed before considering the implications of such a high PPR.

VALIDITY GE, EE AND TE ESTIMATES

A first question to be addressed is to what extent our GE estimate for *S. viride* is representative for other herbivores. The high r^2 of equation (1) shows that our food intake estimates for *S. viride* and *S. vetula* fall well in line with

those for damselfish and surgeonfish obtained in other studies. Moreover, the estimated intake of all herbivores in the shallow reef matched the (seasonal variation in) primary production closely. This is as expected, since no changes in biomass of the reef algae have been observed throughout the study period. The validity of our food intake estimates therefore seems well justified. That of the GE estimate depends on the validity of our growth and gamete production estimates.

Van Rooij *et al.* (1995) compared the growth rates of *S. viride* with those of other reef fish and found their estimates to agree well with the scarce published data for other herbivorous reef fish (Munro & Williams, 1985; Russ & St John, 1988). Our low estimates of E_{Growth} for the largest adults agree well with those reported for adult damselfish in two other studies (Polunin & Brothers, 1988; Polunin & Klumpp, 1992). Low adult growth rates can be expected for any species showing a von Bertalanffy growth pattern, simply because the fish have approached their maximum size.

We know of no other quantitative estimates of daily gamete production for reef herbivores. There are obvious differences in spawning mode (pelagic *v.* demersal eggs, pair *v.* group spawning) and frequency (daily *v.* biweekly) between the three families (Thresher, 1984; Robertson *et al.*, 1990). Consequently, our estimates of gamete production are not likely to be representative for the other families. More important in the present context, however, is whether our maximum estimate could be too low. Our maximum estimate suggests that 66% of the total population production is in the form of gamete release. In most trophic models of aquatic ecosystems, the production estimates are entirely based on the parameters of the von Bertalanffy growth equation, i.e. on the somatic growth of the smaller stages. Therefore, our maximum estimate for gamete production seems to be too high.

The only other coral reef fish for which we found published data on daily numbers of spawned eggs is *Thalassoma bifasciatum* (Bloch, 1791). In this small but common labrid, females of 6–6·8 cm spawned an average of 3719 eggs (0·54 mm diameter) per spawning (Shapiro *et al.*, 1994). By combining these findings with data on spawning rates (0·67 day^{-1}), with a mass–length relationship to convert lengths (both in Shulz & Warner, 1991), and with relative gonad weights (2·5–3·0% of *W* for 5·5–6·5 cm females; Warner *et al.*, 1975), and by assuming the same energy content and wet : dry mass ratios as measured here (Table V), it was estimated that *T. bifasciatum* females attain a daily egg production that is equivalent to 5·5–6·7% of their wet body mass or 48–58% of the energy content of their ovaries. This is close to our maximum estimate for *S. viride* females. Strikingly, the largest number of eggs that we stripped from any female (77 400, Table IV) is close to the number that was equivalent to our maximum estimate for 30-cm females (75 980). The uniform diameter and hydrated state of the stripped eggs suggest that these might actually represent the clutch for a single day. Hoffman & Grau (1989) provide evidence that vitellogenesis occurs throughout the day in the Hawaiian wrasse *Thalassoma duperrey*. Therefore, a daily egg production as high as half the energy equivalent of the ovaries may actually be more realistic than initially assumed. Nevertheless, it seems unlikely that our maximum estimate for egg production is too low.

Because primary production was measured only in the shallow reef, EE could be estimated only in this zone, so its validity can also be questioned. Although the relative abundance of large algal turfs was higher in the territorial part of the reef (Bruggemann *et al.* 1994*c*), algal biomass appeared to be just as constant as in the shallow reef, suggesting that all production is actually consumed there as well. Important to note is that this study has considered only the production of the main algal food types here. An important proportion of total reef productivity is produced by the endosymbiotic zooxanthellae in scleractinian corals, which are not grazed to any extent by reef herbivores (Bruggemann *et al.*, 1994*c*; van Rooij *et al.*, 1996*a*). If this production would be added to that of the epi- and endolithic algal community, our estimate of EE would have been considerably lower, especially for the deeper reef where live coral formations cover up to 50% of the bottom substrate. However, the production by zooxanthellae takes place largely in a closed compartment that communicates only indirectly with the rest of the reef via the few fish (mainly chaetodontids) that forage on live coral tissue (Larkum, 1983). It therefore seems best to place corals plus their zooxanthellae in a separate trophic group.

More research could certainly yield more accurate direct estimates for the GE of other herbivores, especially for acanthurids and pomacentrids. However, given the dominance of scarids on our reef and the fact that our production estimates for *S. viride* are the best available for any scarid, our TE estimate should be a reasonable approximation for the entire herbivorous guild. To what extent it can be extrapolated to other reefs will depend on the relative abundance of scarids on those reefs. Russ & St Johns (1988) present standing stock estimates of scarids for three heavily fished Philippine reefs that range from 34 to 92 kg ha^{-1}. Munro & Williams (1985) report a scarid biomass of 106–130 kg ha^{-1} with a somatic production of 36–76 kg ha^{-1} $year^{-1}$ for central Great Barrier reefs, where they comprised 19–21% of the herbivorous fish biomass. Compared to these reefs, scarid biomass (480 kg ha^{-1}) and somatic production (57 kg ha^{-1} $year^{-1}$ for *S. viride* alone) is clearly very large at our reef. This will be due partly to the low fishing pressure on Bonaire.

TE ESTIMATES FROM ECOPATH

Pauly & Christensen (1995) based their PPR estimate for coastal/reef systems (8·3%) on a TE of 10%, the average of 140 values for 48 ECOPATH models of aquatic ecosystems. In the first attempt to model a coral reef, the French Frigate Shoals at Hawaii, all reef fish and octopuses were treated as a single trophic group, for which a Q/B ratio (of 2%) had to be ' borrowed ' from published data for salmon (Polovina, 1984). This illustrates the paucity of quantitative data for coral reef fish at that time. Some more detailed information was available for the only two coral reef systems that were included in the 48 models mentioned above. Pauly *et al.* (1993) reported a Q/B ratio of 13·1% day^{-1} for *Siganus spinus* (Linnaeus), an up to 20-cm long herbivore on the Bolinaeo reef (Philippines). Their estimate was based on parameters of the von Bertalanffy growth equation and on daily food intake data and is remarkably close to our estimate of 12·9% day^{-1} for *S. viride* (see Fig. 4). In the ECOPATH model of this reef, Aliño *et al.* (1993) used similar Q/B ratios, but still assumed transfer efficiencies of 15–19% for most herbivorous fish. Their estimate of EE is not

quite as high as ours (76–95%), so it cannot explain their seven to 10 times higher TE estimate. The discrepancy must be caused largely by their high estimate for the P/B ratio (0·8–3·8% day^{-1}, compared to our estimate of 0·3% day^{-1}). If we use our minimum estimate of gamete production we obtain a P/B ratio of 0·12 day^{-1} for *S. viride*, so our low and high estimates are indeed a factor of seven and 12 lower. Finally, Opitz (1993) modelled the trophodynamics of the reefs fringing the Virgin Islands. She distinguished small (e.g. *Sparisoma radians*) and large (e.g. *S. vetula*) herbivorous reef fish for which TE was estimated to be around 4%. This corresponds well with our estimate, considering that her estimates of both P/B and Q/B were calculated from general empirical relationships based on von Bertalanffy parameters, temperature and aspect ratio (as a measure of fish activity; Pauly, 1980; Palomares & Pauly, 1989).

In conclusion, the mean TE of 10% that Pauly & Christensen (1995) assumed to be valid for all trophic groups on coral reefs is not well supported for herbivorous fish in the two coral reef studies that were included in their analysis. This suggests that coral reefs cannot be compared with other aquatic ecosystems. They contain a unqiue trophic group of herbivorous fish that exploit a benthic algal food source. In most other aquatic systems, macroherbivores are much less abundant and the main primary food source is phytoplankton (Horn, 1989; Choat, 1991). Therefore, our present estimate of 2% appears to be more representative for scarids at least, and perhaps also for all other reef herbivores exploiting the epi- and endolithic algae, than the 10% estimate that was based mainly on indirect estimates for other ecosystems without any scarids.

EXPLANATIONS AND IMPLICATIONS OF LOW TE

There are many sad examples of reefs that have deteriorated due to human activities, and also in cases where fisheries effort appeared to be low (Russ, 1991). At first glance, the tight recycling hypothesis that has been put forward to explain this sensitivity to overexploitation seems to be contradicted by our low GE and TE estimate. However, this is not necessarily so and depends on the underlying cause. Four explanations can be envisaged for the low GE of *S. viride*: sloppy feeding, low digestion efficiency, a high energy release in metabolism, and/or a high nitrogenous excretion.

Food intake was estimated from the amount of material removed from grazing substrates and not from the amount actually ingested. Fish were observed occasionally to expel fine particles from their gills and to spit out substrate fragments, which were apparently too large to be handled. These observations point to sloppy feeding. The spilled fraction was not quantified and may partly explain why energy intake has been overestimated.

Perhaps more important is the low nitrogen content of algal food and the presence of cellulose cell walls, which the fish can not digest (Horn, 1989; Choat, 1991). Given the high protein content of fish (87–96% of their AFDM; Van Rooij *et al.*, 1995) and the low nitrogen content of their food (Bruggemann *et al.*, 1994*c*), parrotfish can be expected to feed to meet their nitrogen, rather than their energy demand. There is no lack of (solar) energy on coral reefs, nor of carbon, so no need for efficient retention of carbon in the system. Indeed, our estimates of gross conversion efficiency for nitrogen are much higher than for

energy or carbon (Bruggemann *et al.*, 1994*a*; Van Rooij *et al.*, 1995). This means that much of the organic material leaves the fish undigested with the faeces. This undigested fraction of organic carbon was probably underestimated in the absorption efficiency experiments in Bruggemann *et al.* (1994*a*) due to the difficulties associated with biochemical determination of faeces, containing >90% inorganic carbon.

The organic fraction of excavated food that is lost for the fish (as spilled food or as faeces) is not necessarily lost for the reef. A large proportion of the food of *S. viride* consists of endolithic and crustose coralline algae, which are very difficult to harvest for smaller organisms. It may well be that the spilled and undigested fraction of this food forms an important resource for micrograzers and/or microbial organisms. This would mean that average food chain length is much shorter in coral reef systems than generally assumed. This could be seen as an efficient way to ensure fast and tight recycling of organic matter.

Given the low nitrogen content of its food, it seems unlikely that the nitrogenous excretion by *S. viride* is higher than 4–15% of E_{Intake}, the maximum range found for most fish (Jobling, 1994). However, even if its excretion would be high, the ammonia might be taken up rapidly by benthic algae (e.g. at night when the fish sleep on the bottom) or by phytoplankton. If the low GE would have to be ascribed to high active metabolic rates, the dissipated energy and the carbon dioxide formed would represent real losses from the system. Therefore, this remains an important expenditure to be quantified (Van Rooij & Videler, unpubl.).

If it is accepted that 2% is a better estimate for the transfer efficiency of herbivorous reef fish than the 10% used by Pauly & Christensen (1995), this may have great implications for coral reef management. Many coral reefs are found in the developing world where there is often a shortage of protein sources. Fisheries effort is relatively low compared to northern high latitude areas (Russ, 1991), whereas primary productivity and fish biomass on reefs can be very high. Local authorities may thus be tempted to promote more intense exploitation of coral reefs. They might be further encouraged if they are told that fishing at higher trophic levels has little effect on the corals themselves. That is exactly what a PPR estimate as low as 8% might suggest. Therefore an adjustment of the PPR that is used to model coral reefs is required. A value of 40% is not only more realistic but also more conservative when used to guide reef fisheries management. Note that it is not suggested that the TE between all trophic groups on coral reefs is as low. The prominent trophodynamic role of reef herbivores has been long recognized (e.g. Ogden & Lobel, 1978; Hatcher, 1983; Horn, 1989; Choat, 1991), so a low efficiency for this group would implicate a lower carrying capacity for organisms at higher trophic levels. To what extent that is true will depend on the fate of the material spilled by parrotfish and other macrograzers. It may well be that the small food web plays a more important role on coral reefs than traditionally assumed.

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