

## NOTE

## Feeding of captive, tropical carcharhinid sharks from the Embley River estuary, northern Australia

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**ABSTRACT:** Twenty carcharhinid sharks of 3 species were fed pilchards at different frequencies to examine feeding-growth relationships. These results are among the first in Australia on food intake and growth of wild-caught juvenile and sub-adult carcharhinids held in captivity. Mean consumption rates ( $\pm$ SE) for all feeding rations were 2.91% ( $\pm$ 0.28) body weight per day (BWD) for *Carcharhinus dussumieri*, 3.44% ( $\pm$ 0.40) BWD for *C. tilstoni* and 3.35% ( $\pm$ 0.34) BWD for *Negaprion acutidens*. *N. acutidens* had the highest consumption rate of 5.02% BWD at 2 feeds d<sup>-1</sup>. Highest mean growth rates were 0.78% ( $\pm$ 0.11) BWD for *C. dussumieri*, 1.34% BWD ( $\pm$ 0.54) for *C. tilstoni* and 1.12% (n = 1) BWD for *N. acutidens*. Maintenance ration estimates were 1.29% BWD for *C. dussumieri*, 1.31% BWD for *N. acutidens*, and 2.06% BWD for *C. tilstoni*. These are similar to literature estimates. High consumption rates did not always translate directly to high growth rates.

**KEY WORDS:** Sharks · Consumption · Growth · Feeding · *Carcharhinus* · *Negaprion*

The carcharhinid sharks of tropical Australia are major predators of commercially important penaeid prawns (Brewer et al. 1991, 1995, Salini et al. 1990, 1992). Four species—*Rhizoprionodon acutus* (Rüppell 1837), *Carcharhinus dussumieri* (Valenciennes 1839), *C. amblyrhynchos* (Bleeker 1856) and *Himantura toshi* (Whitley 1939)—are abundant in the prawn fishing grounds of Albatross Bay (northeastern Gulf of Carpentaria) and account for over 40% of the predation on commercial penaeids (Brewer et al. 1991). These predation estimates were arrived at by using species abundances (kg ha<sup>-1</sup>), proportion of prawns in the diets and a conservative daily ration value of 3% body weight per day (BWD) for all fish predators.

This daily ration value was derived from literature values for teleosts. It was followed by a series of

experiments on the main teleost penaeid predators in order to obtain realistic estimates of their daily consumption rates (Smith et al. 1991, 1992). The present study was aimed at confirming the consumption rate used for sharks in calculating levels of predation on prawns.

Few direct measures of shark consumption and growth have been reported. Cortés & Gruber (1994) have studied the effect of ration size on growth of the lemon shark *Negaprion brevirostris* a species closely related to *N. acutidens* used in our study. Medved (1985) studied gastric evacuation in the sandbar shark *Carcharhinus plumbeus* by feeding them known quantities of food and then sacrificing the sharks at intervals.

**Materials and methods. Seawater system:** Experiments were carried out at the CSIRO Marine Laboratories field station at Weipa (northeastern Gulf of Carpentaria, Australia) using 4 above-ground pools, 3.7 m diameter, 7000 l, under cover of double-layered, 95%-shading shade cloth and open to the environment. Seawater was fully exchanged every 2 d using water from the Embley estuary about 100 m away. Water was filtered through a domestic pool sand filter and water temperature and salinity were recorded daily. Nitrites and pH levels were monitored every 5 d during experiments and rarely differed by more than 10%. An ambient light regime was used.

**Capture of sharks:** All sharks were caught in waters near the field station using 2 longlines of up to 20 hooks each. Baited lines were checked hourly as sharks were quickly exhausted or stressed beyond recovery after only 10 to 20 min on the hook. Most sharks settled down to a stable swimming pattern within minutes of revival in the pools and accepted food within a few days of capture. They were used in experiments 1 wk after regular feeding commenced.

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**Feeding experiments:** Consumption and growth experiments lasted 10 d with weight and total length recorded before and 24 h after the experiments ceased. Sharks were not fed for 24 h before weighing and measuring. They were anaesthetized in a 25 l bath of 100 ppm MS-222 until motionless, quickly carried in the 'tonic immobility' posture (Gruber & Keyes 1981) to be weighed ( $\pm 1$  g) and measured (total length) to the nearest millimetre. No shark died as a consequence of anaesthesia during the experiments. Ten *Carcharhinus dussumieri* (664 to 780 mm TL, 1350 to 2170 g) were used in 12 experiments; 4 *Negaprion acutidens* (652 to 864 mm TL, 1250 to 1350 g) in 10 feeding experiments; and 4 *Carcharhinus tilstoni* (609 to 721 mm SL, 1150 to 2290 g) were used for 8 experiments.

The following feeding frequencies were used during the experiments:

(1) 2 meals  $d^{-1}$  (feeding frequency = 2.0); (2) 1 meal  $d^{-1}$  (1.0); (3) 1 meal every 2 d (0.5); (4) 1 meal every 3 d (0.33); (5) zero meals over 5 d (0); (6) 25 meals over 20 d (1.25).

Sharks were fed to satiation with pre-weighed, bite-sized portions (to prevent shredding) of frozen pilchards (*Sardinops neopilchardus* Steindachner), excluding viscera and heads, at each feeding. Daytime meals were between 08:00 and 09:00 h and, for those fed twice a day, between 16:00 and 17:00 h; all uneaten food was removed and weighed after 5 min. This allowed the calculation of food consumed for each feeding period.

**Data analysis:** The growth increment ( $G$ ), expressed as a percentage of body weight  $d^{-1}$  (% BWD) was calculated as the difference between pre- and post-experiment weights and was calculated from the formula

$$G = 100(W_N - W_0)/NW_0$$

where  $W_0$  is the mean shark weight on day 0,  $W_N$  is the mean shark weight (to account for variability between individuals) at the end of each experiment and  $N$  is the duration of the experiment, that is 10 d for feeding and 5 d for starvation experiments (Smith et al. 1991). Consumption rate ( $C$ , or the % body weight eaten  $d^{-1}$ , % BWD) was calculated from the formula

$$C = 100C_i/N_n(W_N + W_0)/2$$

where  $C_i$  is the total food ingested by all sharks in the experiment,  $n$  is the number of sharks and  $(W_N + W_0)/2$  is the mean shark weight (Smith et al. 1991).

Growth was regressed against consumption; a linear relationship of the form

$$G = g + hC$$

provided the best fit for each species. Parameters  $g$  and  $h$  represent starvation weight loss (resting metabolic rate when  $C = 0$  obtained during the 5 d starva-

tion experiments) and the slope of the line of best fit (or rate of change in growth with change in consumption) respectively. Maintenance ration ( $G = 0$ ) can be estimated using the above parameters from the least squares linear regression for Growth versus Consumption.

**Results. Physical environment:** Salinity varied between 19.0 and 32.0 parts per thousand (ppt) during the experiments due to seasonal rainfall. There was no apparent distress or change in behaviour of the sharks when in the lower salinities, probably because they are adapted to similar regular salinity changes in the estuary. Temperature was less variable with a range of 26.2 to 30.0°C, made up of about a 2°C diurnal variation and about a 2°C seasonal change in temperature of the incoming seawater over 4 mo.

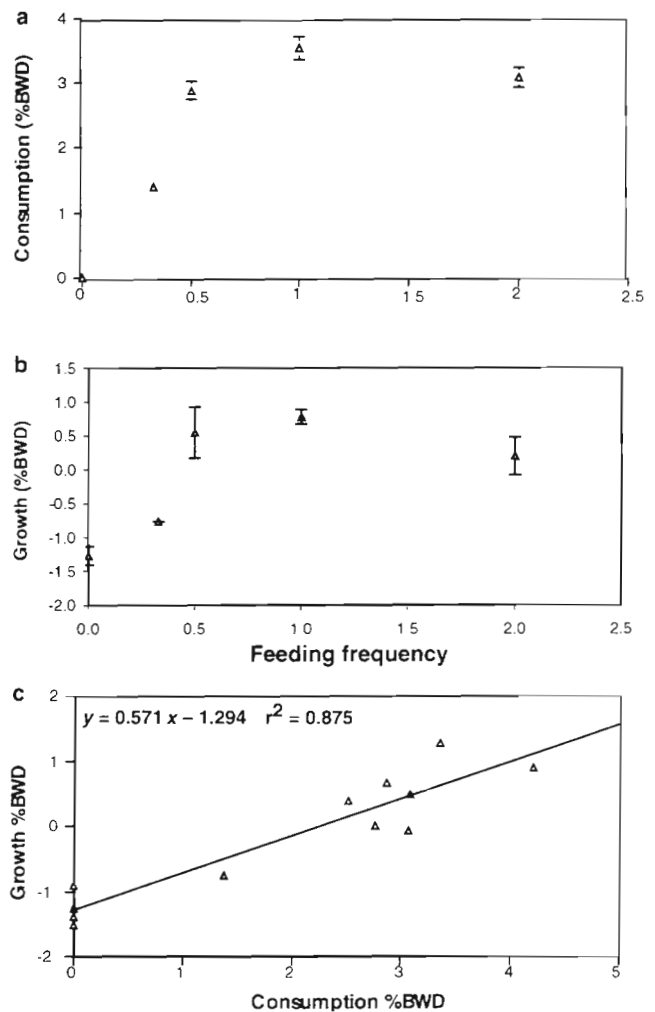


Fig. 1. *Carcharhinus dussumieri*. The relationship between feeding frequency (no. of meals  $d^{-1}$ ) and (a) consumption rate, (b) growth rate and (c) consumption regressed against growth. Consumption and growth rates are expressed as percentage of body weight  $d^{-1}$  (%BWD)

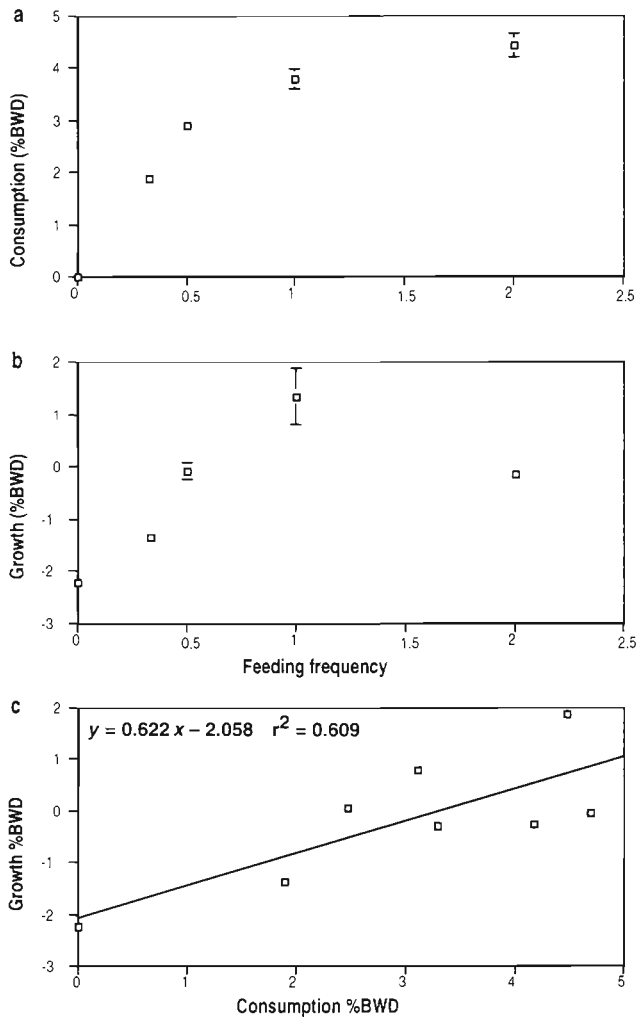


Fig. 2. *Carcharhinus tilstoni*. The relationship between feeding frequency (no. of meals  $d^{-1}$ ) and (a) consumption rate, (b) growth rate and (c) consumption regressed against growth. Consumption and growth rates are expressed as percentage of body weight  $d^{-1}$  (%BWD)

**Experiments:** *Carcharhinus dussumieri*: Average consumption ( $\pm$ SE) of pilchards by *C. dussumieri* was highest when the feeding frequency was once  $d^{-1}$  (3.5% BWD  $\pm$ 0.66), and second highest when it was twice  $d^{-1}$  (3.1% BWD  $\pm$ 0.01, Fig. 1a). Growth ( $\pm$ SE) showed a similar trend with a maximum value of around 0.8% BWD ( $\pm$ 0.11) when fed once  $d^{-1}$ , but feeding once every 2 d still gave a growth of 0.6% BWD ( $\pm$ 0.38) (Fig. 1b). Despite the levelling off of consumption and growth with increased meal frequency, there was a strong correlation between growth and consumption (Fig. 1c,  $r = 0.94$ ,  $p < 0.001$ ).

*Carcharhinus tilstoni*: Consumption ( $\pm$ SE) of pilchard by *C. tilstoni* was highest for 2 feeds  $d^{-1}$  (average of 2 experiments, 4.4% BWD  $\pm$ 0.26), with slightly

lower consumption for 1 feed  $d^{-1}$  (average of 2 experiments, 3.8% BWD  $\pm$ 0.69, Fig. 2a). Growth ( $\pm$ SE) was highest for 1 feed  $d^{-1}$  (average of 2 experiments, 1.3% BWD  $\pm$ 0.53). In contrast, the maximum feeding ration of 2 times  $d^{-1}$  produced an average weight loss of  $-0.2\%$  BWD  $\pm$ 0.12), suggesting disrupted digestion with little or no assimilation of the consumed pilchard (Fig. 2b). The correlation between growth and consumption is significant but had higher variability between replicate experiments than *C. dussumieri* (Fig. 2c,  $r = 0.78$ ,  $p < 0.01$ ).

*Negaprion acutidens*: Consumption rate was highest (5.0% BWD, single experiment only, Fig. 3a) when fed twice  $d^{-1}$  but was consistently relatively high even at 1 feed  $3 d^{-1}$ . The highest growth rate was 1.1% BWD for the 1.25 feeds  $d^{-1}$  (25 feeds during a single 20 d experiment, Fig. 3b). The highest consumption rate did

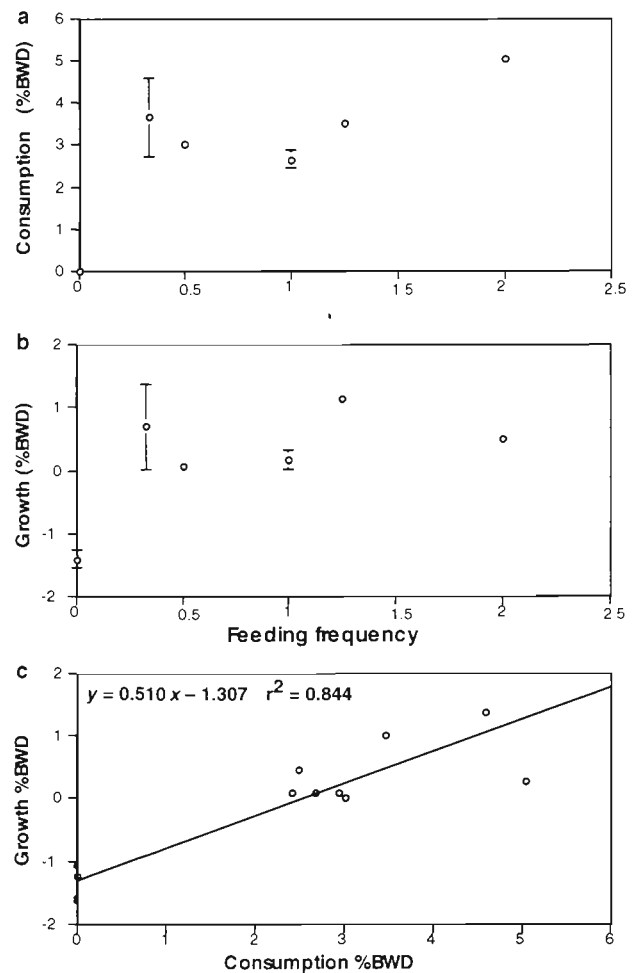


Fig. 3. *Negaprion acutidens*. The relationship between feeding frequency (no. of meals  $d^{-1}$ ) and (a) consumption rate, (b) growth rate and (c) consumption regressed against growth. Consumption and growth rates are expressed as percentage of body weight  $d^{-1}$  (%BWD)

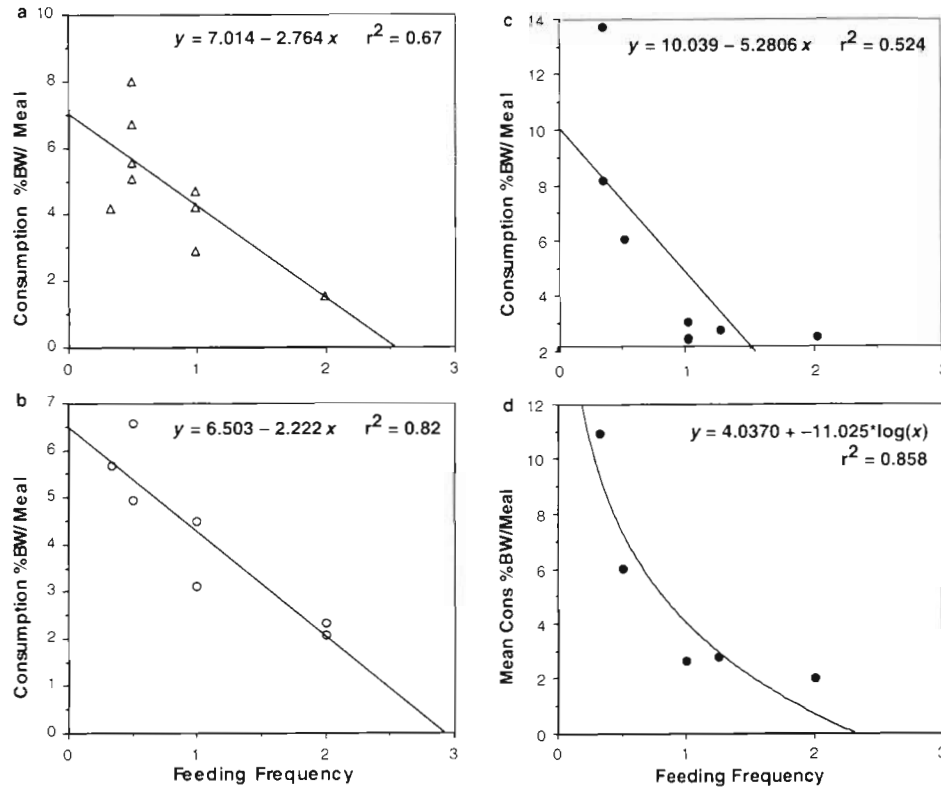


Fig. 4. The linear relationship between meal size (as %BW meal<sup>-1</sup>) and feeding frequency expressed as meals d<sup>-1</sup> for (a) *Carcharhinus dussumieri*, (b) *Carcharhinus tilstoni*, (c) *Negaprion acutidens*, and (d) the logarithmic relationship between meal size and feeding frequency for *Negaprion acutidens*

not produce the highest growth rate although there was a strong relationship between consumption and growth (Fig. 3c,  $r = 0.92$ ,  $p < 0.001$ ).

**Comparison between species:** Average consumption rates ( $\pm$ SE) for all feeding frequencies were 2.9% ( $\pm 0.28$ ) BWD for *Carcharhinus dussumieri*, 3.4% ( $\pm 0.40$ ) BWD for *C. tilstoni* and 3.4% ( $\pm 0.34$ ) BWD for *Negaprion acutidens* (Table 1). Maximum growth rate (mean) was 0.8% BWD ( $\pm 0.11$ ) for *C. dussumieri* fed once d<sup>-1</sup> and was the product of the highest mean consumption rate, 3.5% BWD ( $\pm 0.66$ ); 1.3% BWD ( $\pm 0.54$ ) for *C. tilstoni* fed daily, and 1.1% BWD (no replicate) for *N. acutidens* fed 4 d out of 5.

Values for starvation weight loss for *Carcharhinus dussumieri*, *C. tilstoni* and *Negaprion acutidens* were 1.3, 2.1 and 1.3% respectively. Maintenance ration at zero growth for *C. dussumieri*, *C. tilstoni* and *N. acutidens* was 2.3, 3.3 and 2.6% BWD respectively and was derived from the least squares linear regressions in Figs. 1c, 2c & 3c.

**Compensatory feeding behaviour:** *Carcharhinus dussumieri* showed some compensatory feeding ability due to reduced feeding frequency (Fig. 4a), to a maximum of about 7% BW meal<sup>-1</sup> (the  $y$ -intercept of the plot of single meal size as a percentage of body weight against ration). The single experiment for 1 meal every 3 d appears not to fit the trend (at ~4.1% BW meal<sup>-1</sup>) of increasingly larger meals with less frequent feeding.

*C. tilstoni* adjusts its food intake up to about 6.5% BWD (Fig. 4b) by increasing meal sizes for less frequent meals. *Negaprion acutidens* has the most developed compensatory feeding behaviour of all 3 species (Fig. 4c). The maximum meal size occurs for the least frequent feeding experiments (once every 3 d,  $y$ -intercept 10% BW meal<sup>-1</sup>). The relationship is not linear. A log relationship provides a more accurate fit of the data, but allows unrealistic meal sizes near starvation (Fig. 4d).

**Discussion.** The tropical sharks in this study had consumption rates that were below those reported for juvenile tropical teleosts (Smith et al. 1991, 1992), but above those reported for temperate sharks (Medved et al. 1988). Other studies have also reported that elasmobranchs generally have lower rates of consumption than teleosts (Wetherbee & Gruber 1990, Wetherbee et al. 1990). Our consumption rates were 5 to 6% BWD lower than in juvenile teleosts under 200 g wt (Smith et al. 1991, 1992).

Our sharks were able to increase consumption as feeding frequency increased to 2 meals d<sup>-1</sup> except for *Carcharhinus dussumieri*, which slightly decreased its consumption with 2 meals d<sup>-1</sup> (Fig. 1b). The highest consumption rate recorded (*Negaprion acutidens* when fed twice d<sup>-1</sup>), resulted in a relatively low growth rate of 0.5% BWD (Fig. 3a,b,c). Average consumption rates for all feeding frequencies decreased with less

Table 1. Summary of maintenance ration, growth and consumption estimates from studies on various captive shark and teleost species. Values for the current study are averages over all feeding frequencies with SE given in 'Results'

Species	Maintenance ration (% BWD)	Growth (% BWD)	Consumption (% BWD)	Source
<i>Carcharhinus dussumieri</i>	1.2	0.8	2.9	Present study
<i>C. tilstoni</i>	2.1	1.3	3.4	Present study
<i>Negaprion acutidens</i>	1.3	1.1	3.4	Present study
<i>N. brevirostris</i>		-0.34–0.61	0.6–2.73	Cortes & Gruber (1994)
<i>N. brevirostris</i>			1.7–4.3	Wetherbee & Gruber (1990)
<i>N. brevirostris</i>	1.6			Gruber (cited in Medved et al. 1988)
<i>Carcharhinus plumbeus</i>			1.0	Medved et al. (1985, 1988)
<i>C. plumbeus</i>			0.86	Stillwell & Kohler (1993)
<i>Carcharias taurus</i>			0.27	Schmid et al. (1990)
<i>C. plumbeus</i>			0.47	Schmid et al. (1990)
<i>C. leucas</i>			0.5	Schmid et al. (1990)
<i>Ginglymostoma cirratum</i>			0.31	Schmid et al. (1990)
<i>Caranx bucculentus</i>	2.7	1.3	8	Smith et al. (1992)
<i>Lutjanus russelli</i>	3.8	1.1	9	Smith et al. (1991)

frequent meals corresponding with a drop in growth, except in the case of *N. acutidens* which was able to consume larger meals infrequently (Fig. 4c,d). There was an obvious levelling off in daily consumption for each shark species with maximum values for individual replicates of 4.7% BWD for *C. dussumieri*, 4.7% BWD for *C. tilstoni* and 5.0% BWD for *N. acutidens*, although this limit was not tested with more than 2 meals  $d^{-1}$ . At 2 meals  $d^{-1}$ , all 3 species began to reject some of the second meal, hence no higher feeding frequencies were attempted. Variation in both consumption and growth within a feeding regime reflects the limited number of replicates attainable during the field work.

Few direct comparisons with other species are possible for tropical or subtropical sharks due to the paucity of published food intake and growth experiment results that are available. Consumption rates for a variety of carcharhinids reported in the literature ranged from 0.27 to 4.3% BWD (Table 1). The mean consumption rates demonstrated in the present study fall within this range of 2.1% BWD for *Carcharhinus dussumieri*, 3.4% BWD for *C. tilstoni* and 3.4% BWD for *Negaprion acutidens*. Most studies derived consumption rate estimates from diet studies of wild sharks and empirical calculations (Medved et al. 1985, 1988, Stillwell & Kohler 1993). *C. plumbeus* values were for adult sharks in commercial aquaria (Schmid et al. 1990).

Growth rates reported for *Negaprion brevirostris* ranged from -0.34 to 0.61% BWD under controlled conditions (Table 1). Our mean growth rate for *N. acutidens* was higher. Reported teleost growth rates were similar to those demonstrated for sharks in the present study, but the maintenance rations were about half those for juvenile *Lutjanus russelli* and juvenile

*Caranx bucculentus* (Smith et al. 1991, 1992, most fish were <200 g). Maintenance ration estimates for our sharks were comparable with those for *N. brevirostris* (Table 1). This supports the notion of sharks having generally lower energy requirements than teleosts (Gruber 1986, Wetherbee et al. 1990, Wetherbee & Gruber 1993). The higher maintenance ration for *Carcharhinus tilstoni* is supported by our observations of high activity relative to the other sharks. Similarly, Hussain (1991) found that *C. limbatus* (closely related to *C. tilstoni*) swam faster than *N. brevirostris* in experiments at Sea World, Orlando, Florida.

Average meal size for *Carcharhinus tilstoni* and *Negaprion acutidens* increased with decreasing meal frequency to about 6.5% BW for *C. tilstoni* and 13.5% BW for *N. acutidens*. This is well above the 6% BW meal $^{-1}$  limit found for the carangid *C. bucculentus* under similar experimental conditions (Smith et al. 1992) and suggests *N. acutidens* has considerable compensatory feeding ability.

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