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Age, growth and reproduction of the lane snapper *Lutjanus synagris* (Pisces: Lutjanidae) at Bermuda

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ABSTRACT: The sagittal otoliths of 300 lane snapper *Lutjanus synagris* (Linnaeus) with a size range of 18 to 37 cm fork length were analyzed to estimate age. Transverse sections of embedded sagittae were prepared for microstructural analysis. All specimens presented clear annular increments that were readily counted by 3 independent readers. Marginal increment analysis and OTC (oxytetracycline)-injected specimens held in captivity validated that 1 increment was formed annually. The results enabled us to estimate von Bertalanffy growth parameters (growth coefficient, K = 0.395, asymptotic length, L_∞ = 33.09, t_0 = –1.95). Ninety percent of L_∞ is reached in 4 yr and first sexual maturity is attained in the 1+ yr class. There was no significant difference in the growth-parameter estimates between males and females. The high correlation between otolith weight (OW) and age permits the use of OW as a proxy for age in future stock assessments. The maximum age of 19 yr determined in this study is the oldest age recorded for this species in the western Atlantic Ocean.

KEY WORDS: Lane snapper · Age · Growth · Otoliths · Reproduction · Fisheries management

INTRODUCTION

The lane snapper *Lutjanus synagris* (Linnaeus) is considered amongst the most important species of lutjanids caught in the greater Caribbean region. It has been reported from a variety of habitats ranging from coral reefs to muddy brackish water and is known from the sub-tropical waters of Bermuda in the north to southern Brazil (Allen 1985). It is taken by a variety of gear types in the fisheries of the region, where it is often a significant component of the landings from directed demersal fisheries as well as comprising a portion of the by-catch from shrimp trawlers along the coast of Venezuela (Luckhurst pers. obs.). Aspects of the biology (age and growth, reproduction) and fisheries for lane snapper have been extensively studied in: Brazil (Alegria & de Ferreira 1970), Cuba (Claro & Reshetnikov 1981, Claro 1994), Jamaica (Thompson & Munro 1983), United States (Manooch & Mason 1984), Trinidad (Manickchand-Dass 1987), Puerto Rico (Acosta & Appeldoorn 1992) and Mexico (Rivera-Arriaga et al. 1996).

In Bermuda, Bardach et al. (1958) conducted tagging studies and examined aspects of lane snapper biology including feeding and movement patterns. No further research was conducted on this species in Bermuda until the present study. The rapid expansion of the line fishery following changes in the fishery regulations in 1990 (fish-pot ban), and the lack of information about the basic biology of lane snapper necessary to formulate fishery management measures, provided the impetus for this study. As Bermuda is a high-latitude (32° N) coral reef ecosystem with sub-tropical oceanographic conditions, and as it represents the northern extent of the range of this species, there was uncertainty concerning the use of existing growth parameter values for lane snapper from more tropical locations (listed in Pauly & Binohlan 1996). This uncertainty was based on Pauly's (1980) hypothesis that cooler water temperatures, such as those found in Bermuda during the winter months (18°C), would promote slower growth and produce longer-lived fishes than those in the Caribbean.

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Luckhurst (1996) provided commercial landings figures for lane snapper for the period 1975 to 1992 and discussed the effect of the fish-pot (Antillian fish trap) ban of 1990 on subsequent landings. Before the ban, reported landings showed a general increase through the mid-1980s with 80 to 90% of landings derived from fish-pots. Landings reached a peak of 15165 kg in 1987. In an effort to maintain catch levels, there was an expansion of the commercial line fishery, with landings increasing to 20000 kg in the 2 yr following the fish-pot ban. Anecdotal information suggested that an increase in recreational fishing effort occurred during this same time period but no documentation is available. Commercial landings stabilized at approximately 16000 kg for the next 4 yr, followed by a significant decline in 1997 to under 10000 kg. It is unknown if this decline was effort-related.

As a result of these developments in the fishery, there was a need to assess the status of the lane snapper population. Because of the paucity of biological information available, the following objectives of our study were determined: (1) to describe the growth pattern of lane snapper and to estimate the von Bertalanffy growth parameters by direct age estimation using the sagittal otoliths, (2) to determine the maximum age and the relationship between otolith weight and age as a technique for age estimation, and (3) to define the reproductive life span and seasonality at Bermuda's high-latitude coral reef system. In addition, an analysis was made of the age structure of the population and these results were evaluated in relation to the fishery management implications for the stock.

MATERIALS AND METHODS

Hook-and-line fishing by the senior author and Bermuda Fisheries staff (mostly between 19:30 and 22:00 h) collected specimens of *Lutjanus synagris* (Linnaeus) on the Bermuda reef platform. However, cooperative fishers provided the majority of specimens, most of which were processed carcasses, which precluded obtaining weights. All specimens were measured (fork length [FL] to the nearest 1 mm), and whenever possible, sex was determined. Gonads were staged macroscopically at the time of sampling, using the 7 stage system developed by Munro (1983). Both sagittal otoliths were removed by cutting through the cranium with a small saw and extracting the sagittae with forceps. Otoliths were washed in fresh water, air-dried and stored in envelopes until processing. Individual otoliths were weighed to the nearest 0.0001 g on a Mettler balance.

The otoliths were processed following the methodology of Secor et al. (1991). One otolith from each pair was embedded in Araldite epoxy resin (Ciba-Geigy Corp.) and allowed to cure for 24 h. A transverse section including the core area was cut using a Isomet low-speed saw (Buehler), and the section was mounted on a microscope slide with Crystal Bond (Aremco Products Inc.). Each preparation was hand-polished until the annuli were clearly defined. Marginal increment analysis and OTC marking validated the formation of the annulus. Each otolith was read independently by each of the authors and the results were compared at the completion of the readings. Any counts which did not match were read again. A final value for different readings of the same otolith was reached through discussion and consensus. None of the 300 preparations were rejected as unreadable.

Measurements of various dimensions of the sagittae were made using an image-analysis system (Optimas Imaging software). We validated the formation of the annulus by marginal increment analysis. We measured the distance from the edge to the last presumed annulus (D1) and the distance between the last and previous annulus (D2) in 2 yr old fish on a monthly basis. The marginal increment was defined as D1/D2 × 100%. Four older specimens (Ages 3 to 5) were substituted in months when 2 yr old fish were unavailable.

Fish for the age-validation protocol were caught by hook and line in October (after the spawning season) and were held in an open seawater system at the Bermuda Division of Fisheries at ambient water temperature. They were fed cut squid on a daily basis and were injected with Bio-Mycin (oxytetracycline HCl) intraperitoneally in the lower abdominal area at an approximate dosage of 0.1 cm^3 100 g^{-1} wet body weight. A total of 22 specimens were injected (1 d after equilibration to the tank) in 2 equal batches with a 2 wk interval between batches. The injected specimens were held in a 1000 l fiberglass tank. A fungal infection spread amongst the fish causing progressive mortality over the weeks following injection. Only 3 specimens survived longer than 4 wk. The last fish died 19 wk post-injection. The sagittae from the 3 longest-surviving fish were prepared for analysis as described above. They were examined under the microscope using ultra-violet light to detect the presence of the OTC mark in order to measure the post-injection growth increment.

RESULTS

Population size structure

The size structure of the *Lutjanus synagris* population was determined by examining the size-frequency

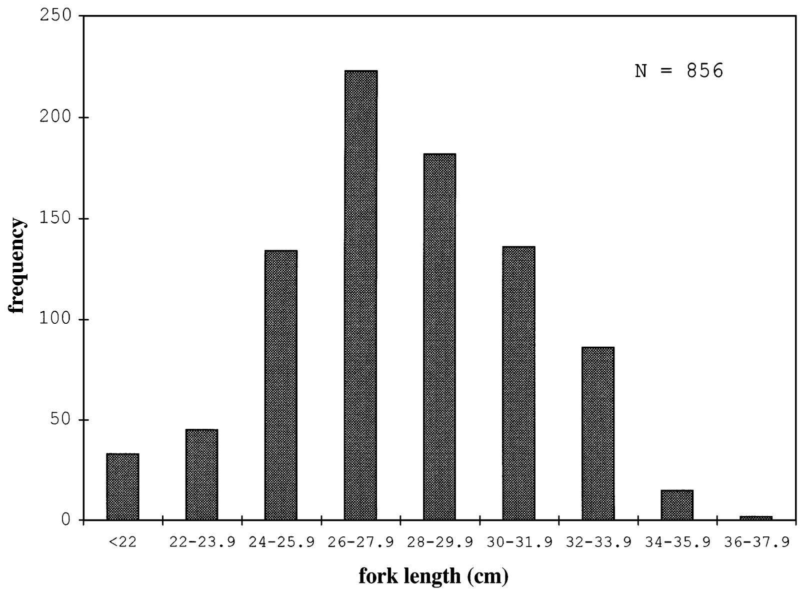

Fig. 1. *Lutjanus synagris.* Size-frequency distribution of lane snapper taken by hook-and-line fishery in Bermuda. Data from 1992 to 1996 were pooled

data from each calendar year from 1992 to 1996. Sample sizes in excess of 300 specimens a year were available only for 1993 and 1994; 1992 and 1995 had <100 specimens, while 1996 had 134 specimens. The size structure of the population during the study was generated by pooling samples from all years (Fig. 1). The modal values for the largest samples (1993, 1994 and 1996) were identical (26.0 to 27.9 cm FL). The mean sizes for the samples for these same years were 27.7, 28.4 and 26.6 cm FL, respectively. There was a significant difference between these mean sizes (ANOVA, $F = 15.47$, $p < 0.0001$). Further analysis indicated that this difference was due primarily to the 1996 sample (Scheffe's *F*-test, $p < 0.0001$) which was the smallest sample. An examination of all of the size data indicated that lane snapper recruit to the hook and line fishery at approximately 18 cm FL while the largest specimen examined was 38 cm FL.

The sex ratio in a subsample (n = 262) of the pooled sample was examined by size category. Four size categories (<25, 25 to 28.9, 29 to 33, and >33 cm FL) were established and tested for deviations from a 1:1 sex ratio. The only size category which exhibited a significant difference was the largest category (chi-square = 8.76, $p > 0.01$), which was male-biased.

Age validation

A marginal increment analysis was conducted using the available data from each month; however, due to the difficulty of obtaining 2-yr-old specimens in some months, there are 3 mo (January, July, November) without data. The marginal increment was at a minimum in April to June (Fig. 2), indicating that this was the period of annulus formation and that only 1 annulus is formed per calendar year. Claro (1994) found the marginal increment was at a minimum in May to July in Cuba.

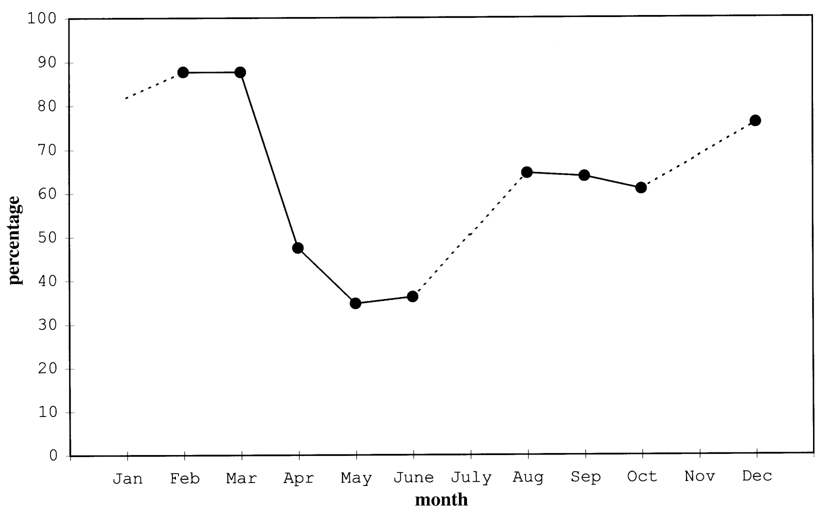

Fig. 2. *Lutjanus synagris.* Marginal increment analysis indicating period of annulus formation (April–June). No data were available for January, July and November

Further confirmation of the annulus was derived from the OTC-injected specimens. The OTC mark was clearly observed in all 3 specimens that had survived in the age-validation experiment. Despite the relatively short duration of the OTC experiment, measurements of the post-injection growth increment on the sagittae of these 3 specimens were consistent with the results of the marginal increment analysis and permitted the further validation of the annulus.

Von Bertalanffy growth model

A total of 300 otoliths over the range of collected sizes were prepared for age analysis. Ages ranged from young

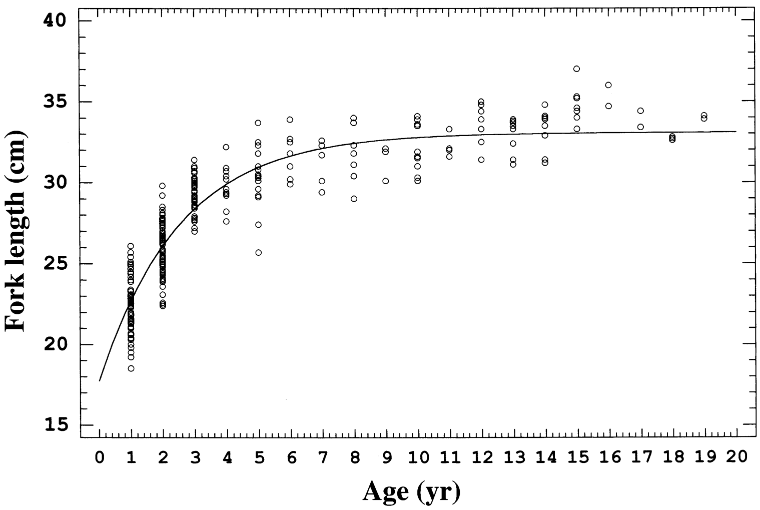

Fig. 3. *Lutjanus synagris.* Von Bertalanffy growth curve. See 'Results' for equation and values

of the year (Age 0+) to 19 yr. A length-at-age-by-sex analysis on a subset (n = 288) of the data indicated no significant difference between the sexes (ANOVA, F = 1.03, p = 0.312); therefore the data for sexes were pooled.

The von Bertalanffy parameters were estimated by non-linear regression analysis fitting the von Bertalanffy growth model: $L(t) = L_\infty \times \{1 - \exp[-K \times (t - t_0)]\}$. The following parameter values (± SE) were obtained: L_∞ = 33.09 ± 0.22 SE, K = 0.395 ± 0.026 SE, t_0 = –1.95 ± 0.20 SE (Fig. 3).

Relationships between age, otolith weight and fish length

There was no significant difference between the weight of the left and right sagittal otoliths and, as a result, we selected the left sagitta for further analysis. The regression analysis of the relationship between age and otolith weight (OW) indicated a square-root model (OW = –41.1 + 168.2 × √age) provided the best fit, explaining 94.4% of the variability in OW (Fig. 4). It should be noted that the model might not describe the relationship between OW and age in young-of-the-year fish accurately.

Due to the nature of the length/age relationship, it is more difficult to accurately estimate the age of older fish based on the fork length. A regression analysis of fork length-at-age excluding Age 0 fish, yielded a relatively high correlation (adjusted R = 83.1%) for the following equation/model: size (cm FL) = 23.3 + 4.124 × ln(age). The relationship between OW and age (Fig. 4) had a higher correlation than that between fork length and age, so the OW for this population can be used to estimate age with greater accuracy.

Mean size-at-age 1 is 23.3 cm FL, indicating that lane snapper grow rapidly in the first year. Growth slows markedly in the second year, as indicated by the mean size-at-age 2 (26.2 cm FL). Growth stanzas become progressively smaller each year until reaching virtually asymptotic values at approximately Age 9. The 2 oldest specimens (aged 19 yr) were only 34 cm FL.

Reproductive life span and seasonality

A total of 1034 specimens were sexed and the gonads evaluated macroscopically during this study. These data defined the seasonality of reproduction and the size at first sexual maturity. Data were not available for 2 mo during the late fall-winter period due to the difficulty in obtaining specimens. Reproductive seasonality was defined by the presence of females which were either ripe or in spawning condition (Munro 1983; Gonad Stages 5 or 6). The pattern was further confirmed by the presence of ripe-running males collected with females in the same sampling period. The proportion of ripe females and males in each monthly sample indicates that spawning nor-

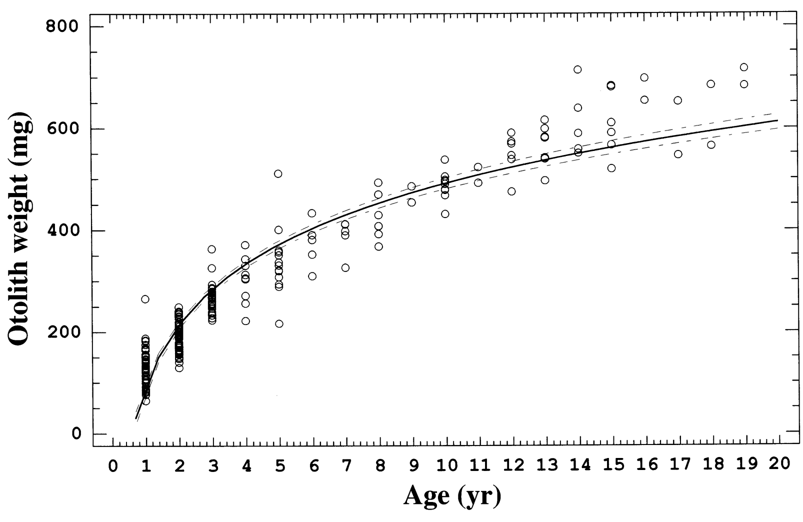

Fig. 4. *Lutjanus synagris.* Regression analysis of relationship between fish age and otolith weight. See 'Results' for regression equation

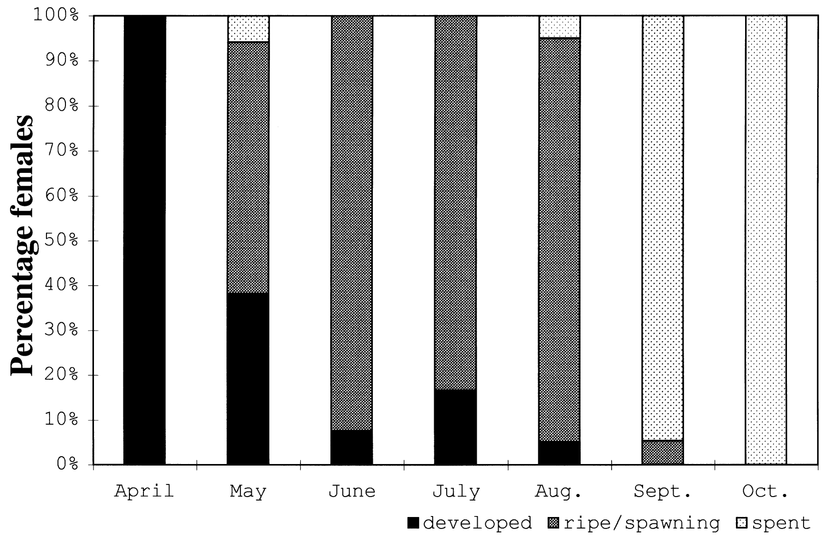

Fig. 5. *Lutjanus synagris.* Spawning seasonality as indicated by reproductive condition of females. Peak spawning season is June to August

mally occurs from late May until early September (Fig. 5). However, a large majority of the fish appear to have finished spawning by the end of August, and thus the peak spawning period is apparently confined to 3 mo (June to August). The water temperature range during this period is approximately 24 to 28°C. The smallest ripe female examined was 23.5 cm FL (Age 1) and the smallest ripe-running male was 21.4 cm FL (Age 0). The size at 50% maturity was estimated at 24.5 and 23.5 cm FL for females and males, respectively. We conclude from the data analysis that males reach sexual maturity at a slightly smaller size than females.

DISCUSSION

Size of fish in the population

The modal size (mid-point = 27.0 cm FL) in our *Lutjanus synagris* samples remained unchanged from 1993 to 1996. This suggests that fishing mortality had not reached a level which would significantly decrease the modal size during this time period. In particular, the larger size classes were still well represented in the most recent years of sampling. Modal sizes in other regional fisheries where lane snapper is heavily exploited were considerably smaller; in Cuba, the modal size was approximately 20 cm FL (Claro 1994) the same as in Puerto Rico (Acosta & Appeldoorn 1992) while Jamaica had a modal size of 21 cm FL (Thompson & Munro 1983). These size differences are considered to be mainly fishery-related, but the influence of different temperature regimes on growth rates and size distributions must also be taken into account.

The finding of a male-biased sex ratio in the largest size category departs from the expectation for a gonochoristic species where the population sex ratio approximates 1:1 (Polovina & Ralston 1987). It is unclear why the sex ratio was male-biased only in the largest size category (>33 cm FL). Possible explanations may be that the largest males are more aggressive than females in bait competition or differential movement patterns by sex on the fishing grounds, either daily or seasonally. There are insufficient detailed data to resolve this issue.

Bermuda implemented fishery-management measures for lane snapper in 1996 which included a minimum legal size of 25 cm FL for all fishers and a recreational bag limit of 30 fish per boat per day. Although lane snapper recruit to the line fishery at approx. 18 cm FL, the mean sizes for samples obtained from 1993, 1994 and 1996 ranged from 26.6 to 28.4 cm FL. Thus mean size-at-capture was 1.6 to 3.4 cm FL higher than the minimum legal size before implementation of the regulation. An examination of the pooled size distribution (Fig. 1) indicated that the proportion of the catch below 25 cm FL was relatively small, comprising less than 20% of the total catch (no. of fish). These data indicate that spawning stock biomass can probably be maintained at an adequate level for sustainable harvest with the present management measures, assuming a similar level of fishing effort.

Age characteristics of the population

The maximum age of 19 yr exceeds reported values from locations in the Caribbean by a considerable margin (Cuba, 10 yr, Claro & Reshetnikov 1981; Trinidad, 7 yr, Manickchand-Dass 1987). This may be related to the colder water temperatures in Bermuda during the winter months which may produce slower growth and longer-lived fishes, as was speculated by Pauly (1980). Alternatively, it could be the result of a healthier stock with a larger mean size and more long-lived individual fish. The presence of older year-classes in the population over the period of this study suggests that the exploitation rate in the Bermuda fishery is not yet sufficiently high to have removed them at the present level of fishing mortality. The mean size-at-capture from 1993 to 1996 of 27.5 cm FL indicated that the fishery was harvesting fish with a mean age of approximately 3 yr, while the older age classes (10+ yr) were still represented, although not in large numbers.

Relationships with otolith weight

The fact that otolith weight was more highly correlated with age than length can be of considerable practical use, as an analysis of the age structure of the Bermuda lane snapper population in future studies can be accomplished by the collection of otoliths (whole specimens are not necessary) and age estimates can be derived from otolith weights. An age-frequency distribution can then be constructed from these otolith weight data, after direct age estimation has been done to establish a growth curve, without the need to prepare otoliths for microscopic age estimation. Such an approach is predicated on the assumption that this otolith weight-age relationship will not change significantly over a number of generations.

Von Bertalanffy growth equation

The von Bertalanffy growth parameters reported in this study are broadly consistent with values derived from studies conducted in the Caribbean region. The growth coefficient (K) of 0.395 is higher than the majority of reported values, which generally range from 0.20 to 0.30 (Pauly & Binohlan 1996), but appears to be consistent with the early growth rate of lane snapper in Bermuda. The asymptotic length (L_∞) of 33.09 cm is amongst the lowest reported from the region (Pauly & Binohlan 1996), although the largest specimens sampled were approximately 5 cm larger than this calculated value. Due to rapid early growth, 90% of L_∞ is achieved by Age 5.

Reproductive seasonality

These data indicate that lane snapper are summer spawners, with the spawning season extending from late May until early September, although peak spawning appears to be confined to 3 mo (June to August). The water temperature range on the fishing grounds during the spawning season is approximately 22 to 28°C. Other species of lutjanids appear to have a similar summer spawning period in Bermuda (Luckhurst unpubl. data). Spawning periods of lane snapper may be more extensive (6+ mo) in the Caribbean, where extended spawning periods are common in many fish taxa (Thresher 1984). For example, the spawning period in Cuba is reported to be from March to September (Claro 1994).

The smallest ripe specimens were 21.4 and 23.5 cm FL for males and females, respectively. Claro (1994) also found that males reached sexual maturity at a slightly smaller size than females. With the minimum legal size established at 25 cm FL and a size at 50% maturity of 23.5 and 24.5 cm FL for males and females, respectively, an adequate proportion of the population should be able to spawn before being taken by the fishery. This minimum legal size is comprised of fish that are Age 1+ yr. The mean size of fish taken in the fishery during this study was approximately 27.5 cm FL (Age 3), which should provide an opportunity for fish to contribute to an average of 2 spawning seasons before being available to the fishery.

Fishery management implications

At present, the commercial-line fishery of Bermuda is highly regulated, while recreational fishers are not required to be licensed and must only comply with 2 existing fisheries regulations regarding lane snapper, i.e. a minimum legal size and a bag limit. As the submission of statistics for recreational fishers is not compulsory, it is difficult to ascertain the level of landings produced by the recreational sector. The lane snapper is one of the principal target species of the recreational fishery, as the fishing grounds are readily accessible by small vessels and catchability is high during the summer months. Given the difficulty of obtaining catch-and-effort data from the recreational sector, it is not possible to estimate the level of fishing mortality they produce with reliability.

Lane snapper are generally available on the fishing grounds on the reef platform beginning in April as the water temperature starts to rise from a winter minimum of approximately 18°C. They are most abundant during the summer months, while numbers decline dramatically by the end of October. Bardach et al. (1958) remarked on the phenomenon of reduced abundance in the winter months but did not suggest an explanation. It is not known whether lane snapper undertake a seasonal migration to a different habitat over the winter months or change their feeding behavior, but it appears from landings figures and anecdotal information from fishers that abundance during the winter months is much reduced. As a consequence, most fishers direct their efforts at different species during the winter. Our results provide an effective means of broadly assessing and monitoring the status of the Bermuda lane snapper population.

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