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Occurrence and life history characteristics of tropical flatfishes at the coral reefs of Curaçao, Dutch Caribbean

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ABSTRACT

In this paper, life history characteristics of tropical flatfishes occurring at the fringing reefs of Curaçao to a depth of 20 m were studied. In total four flatfish species were caught, three common Bothidae species: the eyed flounder *Bothus ocellatus*, the mottled or maculated flounder *B. maculiferus* and the peacock flounder *B. lunatus*, and –in small numbers- the channel flounder *Syacium micrurum*. *B. ocellatus* and *S. micrurum* only occurred in sandy moats on the shallow reef terrace and fore reef and between coral patches on the terrace and fore reef slope. The other species could also be found on coral patches. The depth distribution of the various species overlapped: all species were caught over a depth range from a few meters up to 20 m. All *Bothus* species were carnivores, preying on a variety of mobile benthic animals such as fishes and crustaceans. Reproduction seemed to occur year round in all three *Bothus* species. Growth between the species varied considerably with a maximum age found in *B. maculiferus* and *B. lunatus* of a little over 1 year, and in *B. ocellatus* of about 2 years. Growth was lowest in *B. ocellatus* and highest in *B. lunatus*: after one year *B. ocellatus* was about 10 cm in size, *B. maculiferus* 25 cm and *B. lunatus* about 35 cm. After correction for differences in water temperature, the *Bothus* species showed a similar variability and range in growth rate as some temperate and subtropical flatfish species. These observations do not fit the hypothesis postulated by Pauly (1994) of an increasing importance of food-limitation in juvenile flatfish with decreasing latitude, despite the low densities and biomass of benthic

in- and epifauna in the soft sediments in mangroves, seagrass beds and the reefs of Curaçao.

Keywords: coral reef, flatfish, life history, *Bothus* spec., Curaçao

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1. Introduction

Temperate coastal systems are often characterized by a substantial benthic community and especially for opportunistic (epi)benthic feeders such as juvenile (flat)fishes and crustaceans, food appear to be ample available (see for instance Beukema et al., 1996). Indeed, various juvenile flatfishes such as European plaice, flounder and sole, showed fast growth rates (Zijlstra et al., 1982; van der Veer 1986) and for a long time these rates were thought to represent the maximum possible rates under the prevailing temperature conditions, summarized by the ‘maximum growth-optimal food condition hypothesis’ (van der Veer & Witte, 1993). However, on the other hand, growth variability within individuals and among groups was found in a variety of European coastal areas suggesting that in addition to food quantity also food quality is of importance (van der Veer & Witte, 1993; Ciotti et al., 2013a,b, 2014). Even within various nursery areas, also seasonal variations in growth rate were observed, especially indications of some summer growth reduction (van der Veer et al., 2010, 2016; Freitas et al., 2012; Cardoso et al., 2016). A recent analysis also illustrated the importance of environmental variability (water temperature), non-genetic irreversible adaptation and especially sex in inducing variability in growth and hence in sizes (van der Veer et al., 2016). Overall, growth conditions in temperate flatfish species appear to be in the order of 0.5 – 1.0 mm d^{-1} and observations about stunted growth or starvation are lacking (for review see Ciotti et al., 2014).

It is thought that there is a general trend in food availability with low but relatively constant and uniform productivity at low latitude (Gross et al., 1988). The consideration that flatfishes in general might be overadapted to feeding on zoobenthic in- and epifauna led Pauly (1994) to the expectation that due to the decreasing importance of the benthic system towards the tropics, this would potentially result in increasing food limitation. So this would imply that reduced growth would become a more general phenomenon towards low latitudes and maybe year round in tropical systems. So far, this suggestion has not been studied and tested in more detail. Few laboratory studies (Reichert & van der Veer, 1991) and field studies (van der Veer et al., 1994, 1995) on juvenile flatfish growth and Von Bertalanffy growth parameters for some commercial flatfish species (Pauly, 1994) both even suggest that growth rates of subtropical flatfishes on soft sediments can be of the same order (between 0.5 - 1.0 mm d^{-1}) as that of temperate flatfish species.

Coral reef ecosystems are commonly found in tropical regions. Reef fish communities are composed of a variety of different taxa and species, often with complex life cycles, at least partly associated to the coral reef habitat (see for instance Sale, 2002). Among these reef fishes, also some flatfish species can be found, however, densities are often low, which might at least partly for epibenthic flatfish species due to the small amount of suitable habitat in the form of soft sediment (van Duyl, 1985). Apart from a general description of species composition and some information on feeding habits, ecological information about tropical flatfish species on coral reefs is scarce. Based on numerous studies in temperate and subtropical areas (a.o. Kuipers, 1977; Zijlstra, 1972), flatfish species are, except from seasonal migrations, in general considered as being rather sessile, especially during the juvenile stages. The condition and growth of these demersal species is often studied and considered to be an indicator for habitat quality of the benthic system (a.o. Ciotti et al., 2013ab, 2014; Freitas et al., 2016). However, it is unclear whether Pauly's hypothesis (Pauly, 1994) that tropical flatfishes are (year round) food limited is valid for these systems.

Often, various flatfish species occur in the same reef habitat with no basic information about their growth and reproduction, except for some observations about morphological differences. It is unclear to what extent the various species also differ in their performance despite occupying the same habitat. In this paper, basic population parameters such as abundance, distribution, length-weight, growth, reproductive effort etc. are collected for the common tropical flatfishes occurring on reefs environs in Curaçao, Dutch Caribbean, with the aim to estimate their growth and compare it with that in other systems. Some information is known about aspects of the social and reproductive behaviour of some flatfishes from a nearby island, Bonaire (Konstantinou & Shen, 1995).

2. Material and methods

2.1. Study area

The study was performed on the fringing reef along the SW coast of Curaçao (Dutch Caribbean), situated between 12°02′ and 12°23′ N and 68°12′ and 69°10′W. At Curaçao there is a prevailing trade wind from the north-easterly direction. Therefore, the south, southwest and west coasts are more sheltered than the northeast coast (van Duyl, 1985). Water temperature at the reef varies annually around 27 ± 1°C.

The atlas of the living reefs of Curaçao and Bonaire (van Duyl, 1985) was used to select suitable shallow sand flats for sampling on the reef terrace. At one station, Porto

Marie, a few flatfish were also caught at 20 m depth on a sand flat between the double reef. The dive sites are shown in Figure 1.

2.2. Sampling

Flatfishes were caught on sandy patches by scuba divers with nets. Two scuba divers swam next to each other carrying a small drift net of 270 cm in length, 75 cm in height and a mesh size of 1.25 * 1.25 cm with a tickler chain below the net and drifters on top. For small flatfish (1-2 cm) a small rectangular gauze net was used of 90 * 45 cm and a mesh size of 1.25 *1.25 cm with underneath a lead rope. In order to spot and catch small fishes the sediment was disturbed softly and the rectangular gauze net was placed over a detected fish. Large flatfish were detected by swimming 0.5 – 1 m above the bottom, and were caught by circling and closing the net around them. Subsequently the flatfish was taken out of the enclosure by hand and stored in a bag.

All flatfish were kept in a bag with a mesh size of 0.5 * 0.5 cm (Underwater Kenetics®) until the end of a dive. Fishes were put immediately on ice in a cooler, transported to the laboratory and stored individually in sealed plastic bags at -7°C until further analyses within a week. A subsample was weighted before storing at -7°C to determine weight loss due to freezing.

Flatfish were collected during the first two weeks of every month in 1995 and irregularly in 1996. Each day, two dives were made during daytime, randomly at various locations. On average, between 0 and 5 flatfishes were caught during each sampling dive on sandy patches on the reef. Diving continued until at least 20 specimens of each flatfish species were collected per monthly sampling period. In some months, fewer individuals were caught.

2.3. Data analysis

All analyses were done within a few days after collection of the fish. Before dissection, fish were defrosted in seawater. All flatfish were identified with the FAO sheets (FAO, 1978), Gutherz (1967) and Top & Hoff Jr (1972). After species identification, standard length (cm), total length (cm) and wet weight (g) was determined. Weight loss due to freezing was low between 1 and 2 %, therefore no correction was applied. Subsequently, the guts were removed and the gutted weight (g) was measured. Stomach content was analysed and weighted if possible. Also gonads (> 0.01 g) were weighted (g).

Age was determined by removing from each individual the sagittae otoliths and preparing transverse thin sections of 400 µm with a Buehler low-speed saw. Subsequently, each section was mounted on a microscope petrographic slide with thermoplastic glue and ground to the core in the sagittal plane with lapping film (30, 15, 9 and 3 µm). Otoliths were examined under an Olympus MX-51 transmitted light microscope at 400x at the National Marine Fisheries Services laboratory in Narragansett, Rhode Island, USA. Using Image-Pro image analysis software (Media Cybernetics 1998), increments were enumerated and increments widths along the anterior dorsal section of the otolith from the core to the outer edge following the standard protocol for reading and interpreting the otoliths (Searcy & Sponaugle, 2000, 2001). For reading, first, all unclear, abnormally shaped (nonlinear growth axis) sagittae were discarded. A sagitta from each specimen was read randomly twice independently by the same reader. If the increment counts were within 5% of each other, one measurement was randomly selected for analysis (Searcy & Sponaugle, 2000, 2001). If the increment counts differed by more than 5%, the otolith was read again. If the increment counts from the third reading differed from the other readings by more than 5%, the otolith was discarded. If the difference on the third count was less than 5% of one of the former readings, then one of these two measurements was randomly selected for analysis.

Growth curves were fitted to length-at-age data with the Von Bertalanffy growth model (VBGM) using the traditional version of the model developed by Von Bertalanffy with modifications by Beverton (1954) and Beverton & Holt (1957) in Cailliet et al. (2006):

$$L_t = L_\infty \times (1 - e^{-K\times(t-t_0)})$$

whereby L_∞ is the estimated maximum total length (cm), K is the growth rate constant (y^{-1}), t is age (y), t_0 is the age at length zero and L_t is the observed length at age t.

The investment in total body, somatic and gonadal mass was analysed by means of the body mass index (BMI), the somatic mass index (SMI) and the gonadal mass index (GMI) which are defined respectively as

$$BMI = 1000 * (\text{Total mass} / TL^3) \qquad (\text{g cm}^3)$$

$$SMI = 1000 * (\text{Somatic mass} / TL^3) \qquad (\text{g cm}^3)$$

$$GMI = 1000 * (\text{Gonad mass} / TL^3) \qquad (\text{g cm}^3)$$

whereby somatic mass was estimated as the gutted mass minus the gonad mass.

2.4. Statistical analysis

All data were stored in a database and all statistical analyses were performed in the R statistical package (R Development Core Team, 2018). Prior to the statistical analysis of the field data, a preliminary data exploration was carried out following the protocol described in Zuur et al. (2010). Potential outliers were checked using Cleveland dotplots, and multi-panel scatterplots using the xyplot function from the lattice package (Sarkar, 2008) were applied to identify the type of relationship (e.g. linear versus non-linear) between variables and the presence of collinearity. There was no collinearity between mass indices (BMI, SMI and GMI) and month or year for the three *Bothus* species (not shown).

The extent to which variability in total body, soma and gonad condition was accounted for by seasonal variability among each area was examined by fitting generalized additive models (GAMs) with Gaussian distribution errors. Two models were used:

Model 1: $\text{Mass index}_i = \alpha + f(\text{month}_i) + \epsilon_i$

Model 2: $\text{Mass index}_i = \alpha + f(\text{month}_i) + \text{factor}(\text{sex}_i) + \epsilon_i$

where α is an intercept, f is the smoothing function and ϵ_i is the residual. Model 1 assumed that males and females had the same monthly trend in mass index while Model 2 assumed that there were different trends between males and females. Differences in BMI, SMI and GMI between sexes were analysed by comparing the two models in terms of the Akaike Information Criterion (AIC), whereby the best model is the one with the lowest AIC.

In order to obtain normality, GMI data were transformed using the squared root transformation. Due to the fact that individuals with no gonadal development (< 0.01 g) were present the whole year and normality could not be obtained even after transformation, the gonad data were analysed in two ways: analysis of individuals with gonadal development (zeroes excluded) after squared root transformation (Gaussian distribution) and analysis of the presence and absence of gonadal development. For the last, the response variable (rank difference) was coded as a value from 0 to 1; therefore, a Gaussian distribution could not be used and instead a binomial distribution with a logistic link function was taken.

GAMs were developed and tested using the mgcv package (Wood, 2011) and Von Bertalanffy growth curves were analysed using the FSA and the nlstools packages (Baty et al., 2015; Ogle, 2017).

3. Results

3.1. Species composition

In total four flatfish species were caught. On the sandy moats between the coastline and the coral reef and on sandy patches in between the reef corals, three Bothidae species were found: the eyed flounder *Bothus ocellatus*, the mottled flounder *B. maculiferus* and the peacock flounder *B. lunatus*. *B. maculiferus* and *B. lunatus* could be distinguished by the dorsal profile of the head: *B. lunatus* has a notch above the nostril, while the dorsal profile of the head of *B. maculiferus* is not notched. Also the number of pectoral fin rays differs: between 9 (*B. lunatus)* and 11 (*B. maculiferus*). The eyed flounder and the mottled flounder could be distinguished by the blue spots of the mottled flounder. Male mottled flounder also had an extended pectoral fin almost reaching the base of the causal fin. Eyed flounders were smaller than mottled flounders, respectively 15 cm total length (TL) and 30 cm TL (Bohnsack & Harper, 1988).

The fourth species caught at the sand flats on the lower terrace near the drop off was the channel flounder *Syacium micrurum*. The channel flounder also belongs to the family of the Bothidae but it has an elongated body and lacks ocellated spots compared with the three other Bothidae species that were found. The channel flounder was also better camouflaged or covered with sand. Since only 12 individuals in size between 10 and 22 cm TL were caught, the species was excluded from further analysis.

3.2. Distribution

All three flounder species occurred on the sandy flat patches in between patch reefs and the occurrence of the eyed flounder *Bothus ocellatus* was restricted to these areas. *B. ocellatus* was always found on top of the sediment or even slightly buried. The two other species, the mottled flounder *B. maculiferus* and the peacock flounder *B. lunatus* were also found lying flat on top of the sediment but also sometimes curved upwards as if "sunbathing". These two species were incidentally also found lying curved upwards on top of hard substrates.

The three flounder species differed with respect to the size range caught (Fig. 2). *B. ocellatus* was caught from 2 to 14 cm TL, for *B. maculiferus* the size caught ranged from 2 to 26 cm and for *B. lunatus* no small specimens and only large individuals from 15 cm to 37 cm were caught.

The depth distribution of the various species overlapped (Fig. 3). *B. ocellatus* was caught over a depth range from 1 m up to 20 m (max. dive depth) and did not show a relationship between water depth and fish size. Also the two other species, *B. maculiferus* and *B. lunatus*, were found over the whole diving depth range from shallow waters to 20 m, whereby at least in *B. maculiferus*, there was a tendency of a positive relationship between fish size and water depth. For *B. lunatus* numbers caught were too low for such an analysis.

3.3. Feeding

All small *Bothus* species < 5 cm mainly consumed copepods (Fig. 4). With increasing size up to 10 – 15 cm the contribution of copepods decreased and *B. ocellatus* shifted to shrimps, crabs and fishes (Fig. 4).

B. maculiferus > 5 cm predated on shrimps, crabs and small fishes up to 4 cm, and with increasing fish size, the contribution of fishes increased (Fig. 4). One individual contained a full gut of fish larvae, a juvenile moray and a snake-eel. Another flatfish was observed foraging close to a school of yellow goat fish (*Mulloidichthys martinicus*) which disturbed the sand.

For *B. lunatus,* not enough fish with stomach contents were present to allow a detailed analysis for all size classes. The stomach content of *B. lunatus* > 5 cm comprised of crabs and mainly small fishes. Larger flatfish also consumed some small Cephalopods.

In all species, throughout the year, stomach content did not differ.

3.4. Age and growth

No significant differences in length-weight relationships were found between sexes (not shown), so data were treated together. Total length – total wet weight relationships in the form of $W = aL^3$, showed all species with similar relationships for *Bothus maculiferus* and *B. lunatus* ($a = 0.012$) with a slightly higher value for *B. ocellatus* ($a = 0.013$) (Fig. 5).

Age and growth between the three species varied considerably despite the similarity in body shape. Otolith reading indicated that the maximum age found for *B. maculiferus* and *B. lunatus* was slightly over 1 year, and for *B. ocellatus* around 2 years (Fig. 6). Growth was lowest in *B. ocellatus* and highest in *B. lunatus*: after one year *B. ocellatus* was about 10 cm in size, *B. maculiferus* 25 cm and *B. lunatus* about 35 cm (Fig. 6). Von Bertalanffy growth parameters differed between species (Table 1), however the estimates were based on scattered data and at least for *B. maculiferus* the estimate was unreliable due to the absence of large individuals in the samples.

For all species, body mass index (BMI) and somatic mass index (SMI) did not differ between males and females (similar AIC between models with and without separate sexes), therefore they were combined for further analysis. Significant differences in BMI and SMI along the year were found for both *B. ocellatus* and *B. maculiferus* (GAM; *B. ocellatus*: BMI $F=4.17$, $p<0.01$ and SMI $F=4.84$, $p<0.01$; *B. maculiferus*: BMI $F=7.71$, $p<0.01$ and SMI $F=8.23$, $p<0.01$). For *B. lunatus* no differences in BMI and SMI were found along the year (GAM; BMI $F=0.50$, $p=0.48$; SMI $F=0.69$, $p=0.41$) which could be due to the low number of observations in some months (Fig. 7). For *B. ocellatus*, highest values were found around June-July and for *B. maculiferus* highest values were found at the end of the year.

3.5. Reproductive effort

Gonadal mass (> 0.01 g) was found from a size of about 5 cm in *B. ocellatus*, 10 cm in *B. maculiferus* and 10-15 cm in *B. lunatus* (not shown). Differences in GMI between sexes showed that GMI significantly differed between males and females in *B. ocellatus* and *B. lunatus* (lowest AIC for the model including the factor sex), while in *B. maculiferus* differences between sexes were very small (similar AIC between models with and without the factor sexes). Therefore, GMI was treated separately between sexes in further analysis. In *B. ocellatus*, both females and males showed no significant differences in GMI along the year (GAM; females F=1.12, p=0.31; males F=0.75, p=0.46) (Fig. 8). This means that in both females and males there was no pattern during the course of the year but the absolute mean values differed with females showing a larger investment. In contrast, females of *B. maculiferus* showed significant differences in GMI along the year (GAM; F=3.73, $p<0.05$) suggesting low values in January/February which increase until about July, whereas males did not show differences along the year (GAM; F=2.26, p=0.10). For female *B. lunatus* no model prediction was possible due to the small number of individuals in some months. In males, the pattern in GMI along the year showed a borderline significant difference (GAM; F=2.09, p=0.04) with higher values around June and lower values in the beginning of the year. However, several months had only 1 observation, which could have influenced model results.

Seasonal patterns in reproductive effort can also be illustrated by estimating the proportion of fishes with gonads (weight >0.01 g) present over time (Fig. 9). No significant differences between sexes were found for the different species (similar AIC between models with and without separate sexes). In all species, no significant difference in the presence of gonads (weight >0.01 g) was found along the year (GAM, *B. ocellatus*: X^2=0, p=0.99; *B. maculiferus*: X^2=14.04, p=0.08; *B. lunatus*: X^2=5.97, p=0.13) (Fig. 9).

4. Discussion

4.1. Sampling and identification

The relatively low abundance of flatfishes as found in this study compared with other fish species in the area (Nagelkerken et al., 2000) makes the collection of the flatfishes at the fringing reefs of Curaçao demanding and time consuming. Also the taxonomic identification of these tropical flatfish species is difficult (Evseenko, 2008; Emery, 2016). In the beginning of this programme, only two *Bothus* species were identified: *B. ocellatus* and *B. lunatus*. However, after a few months it became clear from differences in the profile of the head and the number of pectoral fin rays, that *B. lunatus* consisted of a mixture of *B. maculifereus* and *B. lunatus* (van der Geest & Langevoort, 1995). Also the identification of *B. ocellatus* and *B. robinsi* was problematic at that time (FAO, 1978; Gutherz, 1967; Top & Hoff Jr, 1972) and still is (Carpenter, 2005; Richards, 2005; Evseenko, 2008; Emery, 2016). In Brasil, fisherman do not differentiate between these species and use the same generic name for both (Begossi et al., 2016). Based on dorsal, anal and pectoral fin ray counts a combination with the number of gillrakers, and the absence of two large dark spots on the caudal fin (Jutare, 1962) all individuals were identified as *B. ocellatus.* However, species verification by means of molecular techniques (DNA barcoding) would be useful (Weigt et al., 2012).

4.2. Life cycle

The life cycle of these *Bothus* species resembles that of other flatfish species: pelagic egg and larval stages followed by metamorphoses and a settlement into the demersal phase. This means that patchy populations on the isolated fringing reefs such as in the Caribbean are only connected by migration during the egg and larval stages. No information is available about egg and larval development time. The larvae of the different species appear to be very similar morphologically and their almost pigment-free body makes them almost invisible in the water column (Evseenko, 2008). All species are considered to belong to the nerito-oceanic group (according to Parin, 1968 in Evseenko, 2008) with a long pelagic development phase. As a consequence, *Bothus* larvae are widely distributed in the northern waters. This implies that they most likely will belong to a larger panmictic population with no clear structure (cf. Doherty & McB. Williams, 1988).

With increasing size, flatfish are found in deeper waters, especially in the case of *B. maculiferus* and *B. lunatus*. In *B. maculiferus,* it seems that the largest individuals were missed, maybe because they occur in waters deeper than 20 m (the max. dive depth). Most *B. ocellatus* were caught in shallow waters, buried in sandy patches, while the other species were more abundant on the sandy shallow terrace as well as the fore reef slope.

4.3. Seasonal patterns

The gonadal mass index does not show a clear seasonal pattern in reproduction for the three *Bothus* species, although in *B. maculiferus* and *B. lunatus* higher values seem to occur around July and low values in the beginning of the year. Jutare (1962) also observed an almost year-round spawning in *B. ocellatus* around Florida. Overall, this suggests some differences between species with a sequence in reproduction of *B. ocellatus*, followed by *B. maculiferus* and *B. lunatus*. However, more data are required to fully understand the reproductive cycle of these species, especially information about the seasonal pattern of the various egg development stages in mature adults. It is known that in *B. ocellatus*, mating occurs in groups, each consisting of a male and more females, whereby each female also has a distinct subunit within the male's territory (Konstantinou & Shen, 1995).

In contrast to the patterns in reproduction, significant although small seasonal differences in body mass and somatic mass index were found along the year in *B. ocellatus* and *B. maculiferus,* but not in *B. lunatus.* It is unclear whether these differences also occur in body composition. For *B. ocellatus* and *B. maculiferus* the observed maximum size in this study was larger than described in Fishbase (www.fishbase.org).

The lack of a clear seasonal pattern in reproduction also implies the absence of any pattern in settlement. For *B. ocellatus*, pigmented larvae were found from 17 mm onwards (Jutare, 1962), suggesting settlement around this size. For the other species, information is lacking, but settlement will be in the same size range. The size distribution of the individuals caught in the present study indicates that sampling was effective in collecting just-settled individuals, at least for *B. ocellatus* and *B. maculiferus.* However, for *B. lunatus* the smallest individual caught was 15 cm. For this species, either juveniles were overlooked or settlement occurred outside the sampling area: several small flatfishes have been observed with submarines (CuraSub) at Curaçao on sandy slopes below the reef >50m depth (van Duyl, pers. obs.). Juveniles of *B. ocellatus* and *B. maculiferus* were especially found in shallow areas. Under the assumption that age was determined correctly the maximum age found of *B. maculiferus* and *B. lunatus* was at least a little over 1 year, and for *B. ocellatus* around 2 years. This means that the population structure of the various *Bothus* species will consist of only a few age classes.

4.4. Trophic status

Bothus species are considered to be generalized carnivores, preying on a variety of mobile benthic animals such as crustaceans, worms, and small fishes (Randell, 1967, 1996). Stomach content analysis done in this study supports this view. Based on these prey items the trophic status of the studied *Bothus* species ranks from 3.7 in *B. maculiferus*, 3.8 in *B. ocellatus* to 4.5 in *B. lunatus* (www.fishbase.org). *Bothus* species can be considered as predators on reef systems focussing on relatively small epifaunal prey items. The low biomass of benthic infauna in the soft sediments at the reefs of Curaçao of around 0.2 g AFDW m^{-2} (Bremer, 1997) illustrates that these soft bottom sediments can only provide shelter but not food for these species and also that there is only a niche for epibenthic feeding carnivores such as *Bothus* species.

4.5. Are tropical flatfishes (year round) food limited?

Growth of the various species was analysed by counting otolith increments, under the assumption that these rings were deposited daily and that size-selective processes do not seriously bias the observations (Searcy & Sponaugle, 2000; 2001). The analysis suggested that growth between the three species varied considerably whereby growth was lowest in *B. ocellatus* and similar in the other two species.

An analysis of growth rates of juvenile flatfishes in relation to latitude require a general framework based on first principles in which the quantitative aspects of energy location in relation to temperature and food conditions are described in a coherent way. The theory of dynamic energy budgets (DEB) developed by Kooijman (1993, 2000) offers such a framework: differences between species can be captured in the same model using a different set of parameter values only (Kooijman, 2000; van der Veer et al., 2006). The problem is that so far parameter estimates are lacking for tropical flatfishes (https://www.bio.vu.nl/thb/deb/deblab/add_my_pet/species_list.html).

For all three species the length –weight relationship could be described by the "cube law" (b=3) (Ricker, 1973). This means that the body form maintains a constant proportion to the length and the fish grows isometrically. Furthermore, length-weight relationships were almost identical for the three Bothus species (a= 0.012 - 0.013). With almost identical shapes, this means from an energetic point of view, that the physiology (such as maintenance) of the various related *Bothus* species most likely will also correspond (Kooijman, 2000; van der Veer et al., 2006). According to the Dynamic energy budget theory (Kooijman, 1993, 2000), differences in growth will result in either differences in the so-called Kappa parameter describing the energy participation between growth and reproduction and/or in the food ingestion rate. The GSI is an indication for Kappa (van der Veer et al., 2001; 2006). Maximum values for the three *Bothus species* were around 0.4 suggesting no large differences in Kappa. Differences in food ingestion rate might be more likely since the maximum stomach content found, expressed as stomach mass index (=stomach weight/somatic weight), was larger in *B. maculiferus* (0.188) than in *B. ocellatus* (0.109). Unfortunalely, for *B. lunatus* not enough data were present.

An indirect approach is the estimate of growth based on length increase of the population during the juvenile stage. A preliminary comparison of the seasonal patterns in mean length of some juvenile temperate, subtropical and tropical flatfish species suggested a large variability in population growth (van der Veer et al., 1994). After correction for the differences in water temperature (assuming a Q_{10} of 2), there is no relationship between growth and latitude (Table 2). The *Bothus* species of this study fit with these observations: a large variability among species but no differences in growth range with temperate and subtropical species. The observed variability will partly be caused by environmental (a)biotic variability (temperature, food conditions) and by the fact that the various flatfishes show a taxonomic distinctness with different food preferences and maybe also physiological performance. Nevertheless, these observations do not support the hypothesis postulated by Pauly (1994) of an increasing importance of food-limitation in juvenile flatfish with decreasing latitude, despite the low densities and biomass of benthic in- and epifauna in the soft sediments in mangroves, seagrass beds and at the reefs of Curaçao (Bremer, 1997, Nagelkerken, 2000).

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Table 1 Von Bertalanffy parameters of the Bothus species at Curaçao, L_{inf}, K and t_0 with 95% confidence intervals (between brackets; this study), together with number of samples (N)

	N	L_{inf} (cm)	K (y^{-1})	t_0 (y)
B ocellatus	137	20.6 (16.5-31.9)	0.50 (0.27-0.72)	-0.06 (-0.15-0.00)
B. maculiferus	112	50.5 (36.3-94.5)	0.82 (0.36-1.36)	0.16 (0.11-0.20)
B. lunatus	53	38.6 (33.1-54.7)	2.92 (1.23-4.66)	0.17 (0.03-0.22)

Table 2. Comparison of length growth estimates (cm mo^{-1}) for various temperate, subtropical and tropical juvenile flatfish species in size around 10 cm after correction for temperature differences by applying a Q_{10} of 2.

Species type	Area	Temperature range (°C)	Species	Growth (cm.mo-1)	Growth after Q10 correction	Reference
Temperate	Wadden Sea, NL	4 -20	*Pleuronectes platessa*	1.5	1.5	van der Veer et al., 1994
		4 - 18	*Limanda limanda*	0.7	0.7	van der Veer et al., 1994
Subtropical	Georgia, U.S.A.	10 - 30	*Citharichthys spilopterus*	1.6	1.1	Reichert & van der Veer, 1991
		10 - 30	*Symphurus plagiusa*	1.2	0.8	Reichert & van der Veer, 1991
Tropical	Gulf of Mexico	± 27	*Cyclopsetta chittendeni*	2.3	1.0	Dawson, 1968 in Pauly, 1994
		± 27	*Citharichthys stampii*	3.4	1.4	van der Veer et al., 1994
	Curaçao	± 27	*Bothus ocellatus*	0.7	0.3	This study
		± 27	*Bothus maculiferus*	1.8	0.8	This study
		± 27	*Bothus lunatus*	4.3	1.8	This study

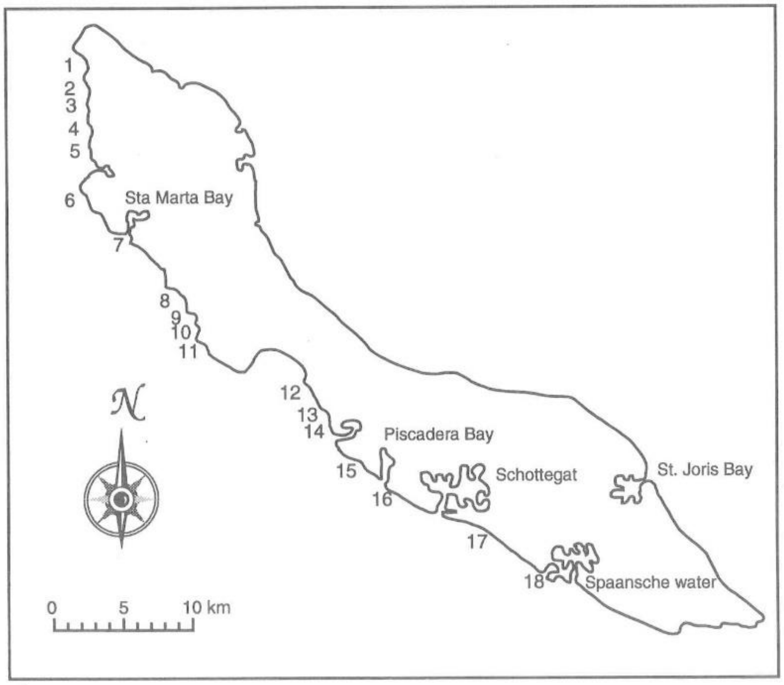

Figure 1 Map of Curaçao and the sampling stations. 1: Playa Kalki; 2: Grote Knip; 3: Kleine Knip; 4: Playa Jeremi; 5: Playa Legun; 6: Playa Manalina; 7: Coral cliff; 8: Cas Abao; 9: Porto Marie; 10: Daaibooibaai; 11: Rif St. Marie; 12: Pestbaai; 13: Varkensbaai; 14: Boca St. Michiel; 15: Blauwbaai; 16: Carmabi; 17: Sea aquarium/Jan Thiel; 18: Caracasbaai.

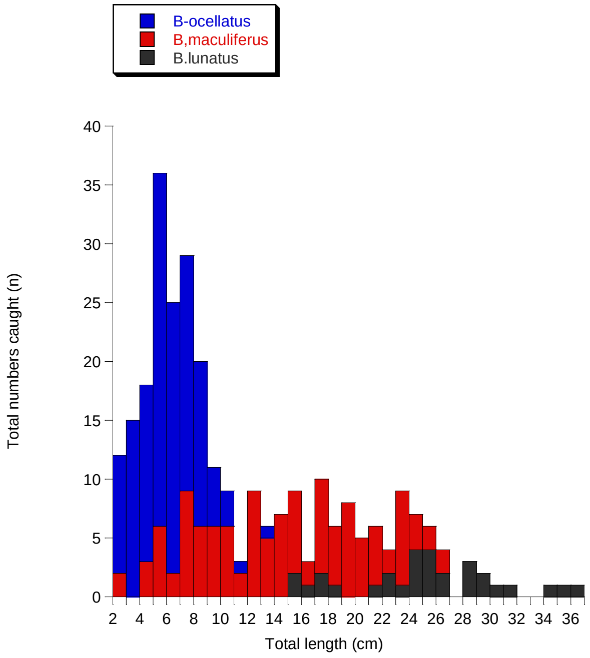

Figure 2. Size frequency distribution (n) of the various flatfish species caught at Curaçao, all data combined.

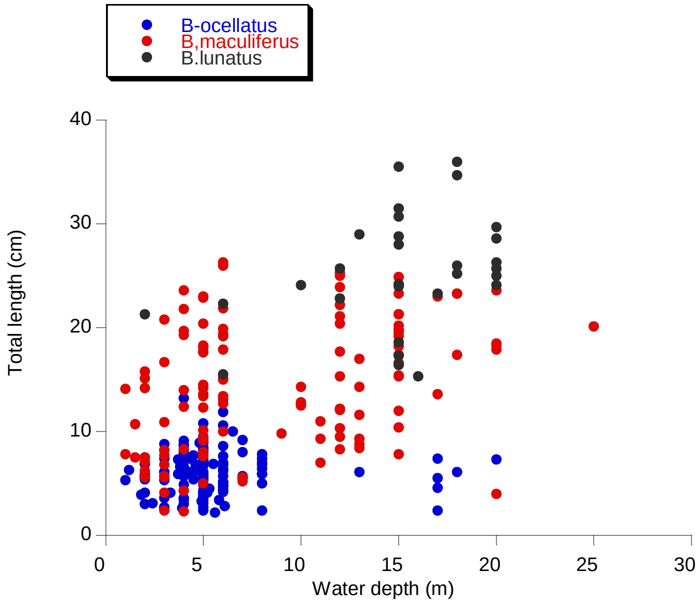

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Figure 3. Relationship between water depth of capture (m) and flatfish size (cm) for the various flatfish species at Curaçao, all data combined.

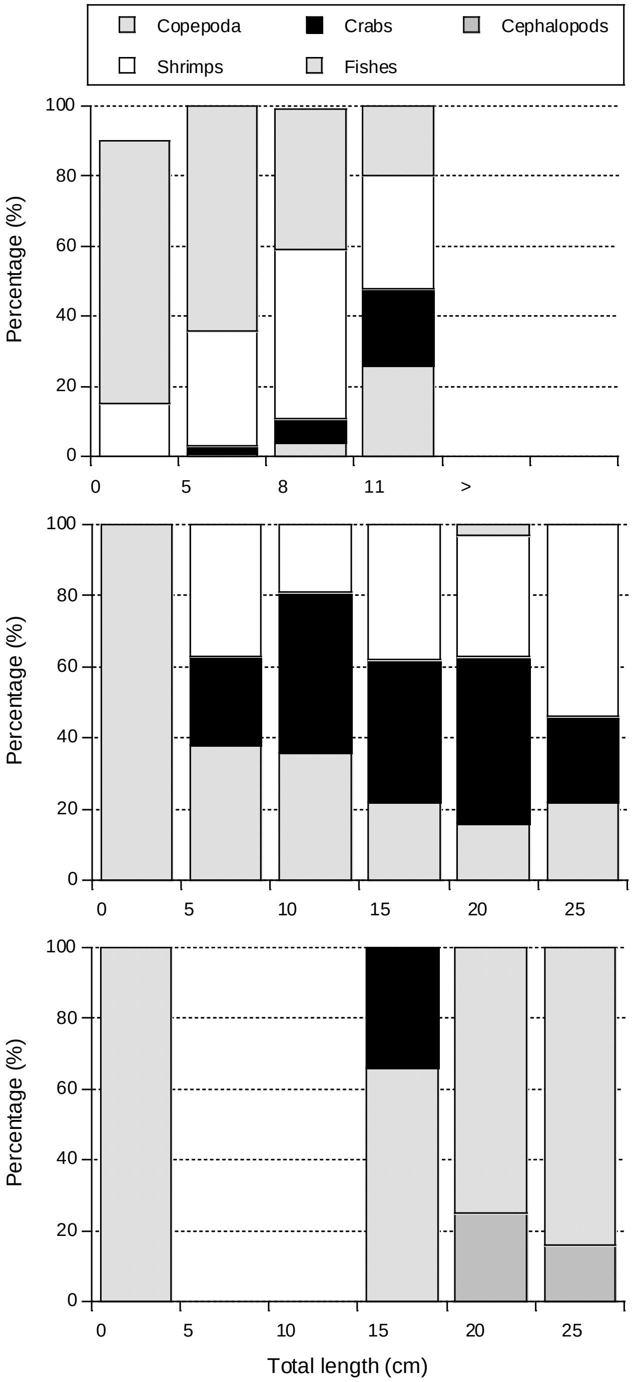

Figure 4. Percentage of different food types in the stomachs of *Bothus ocellatus* (top), *B. maculifeus* (middle) and *B. lunatus* (bottom) at different length classes at Curaçao in 1995.

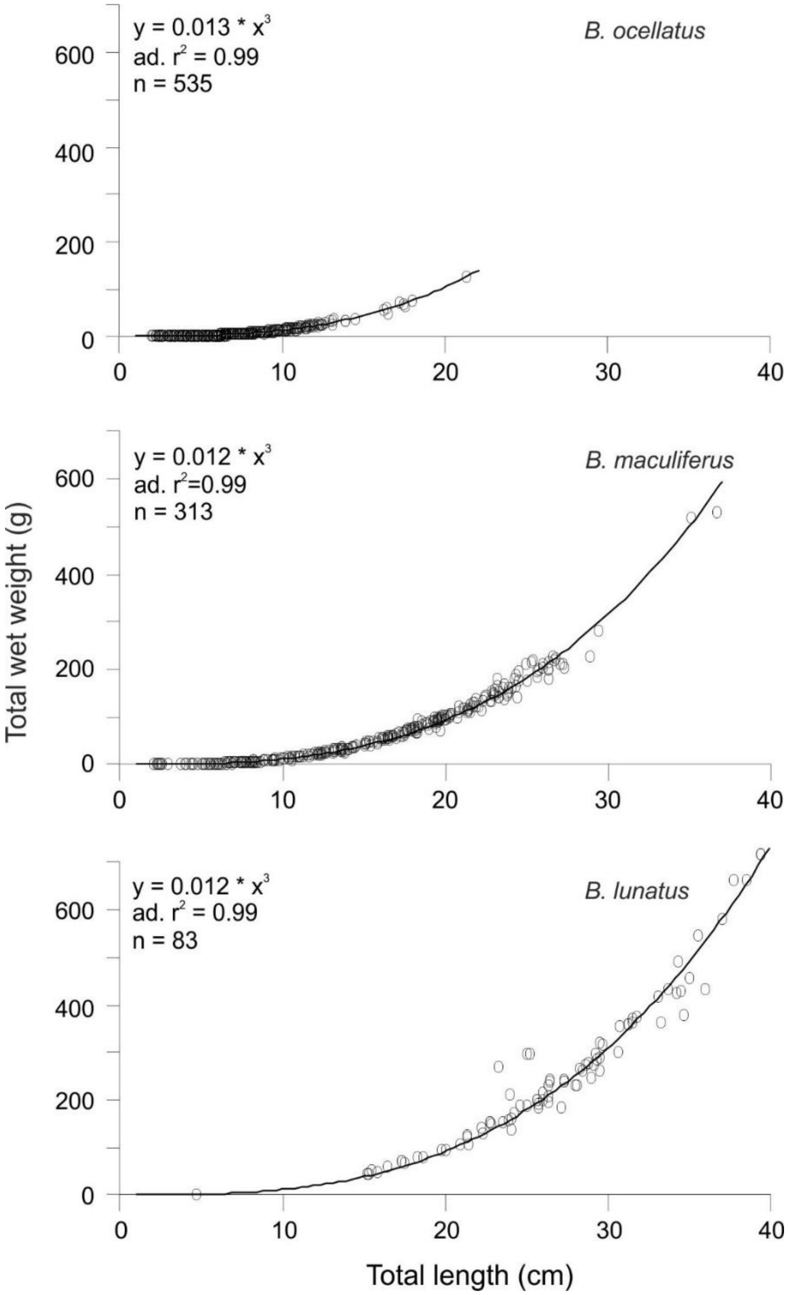

Figure 5. Total length (cm) - wet weight (g) relationships for *B. ocellatus*, *B. maculiferus* and *B. lunatus* at Curaçao in 1995.

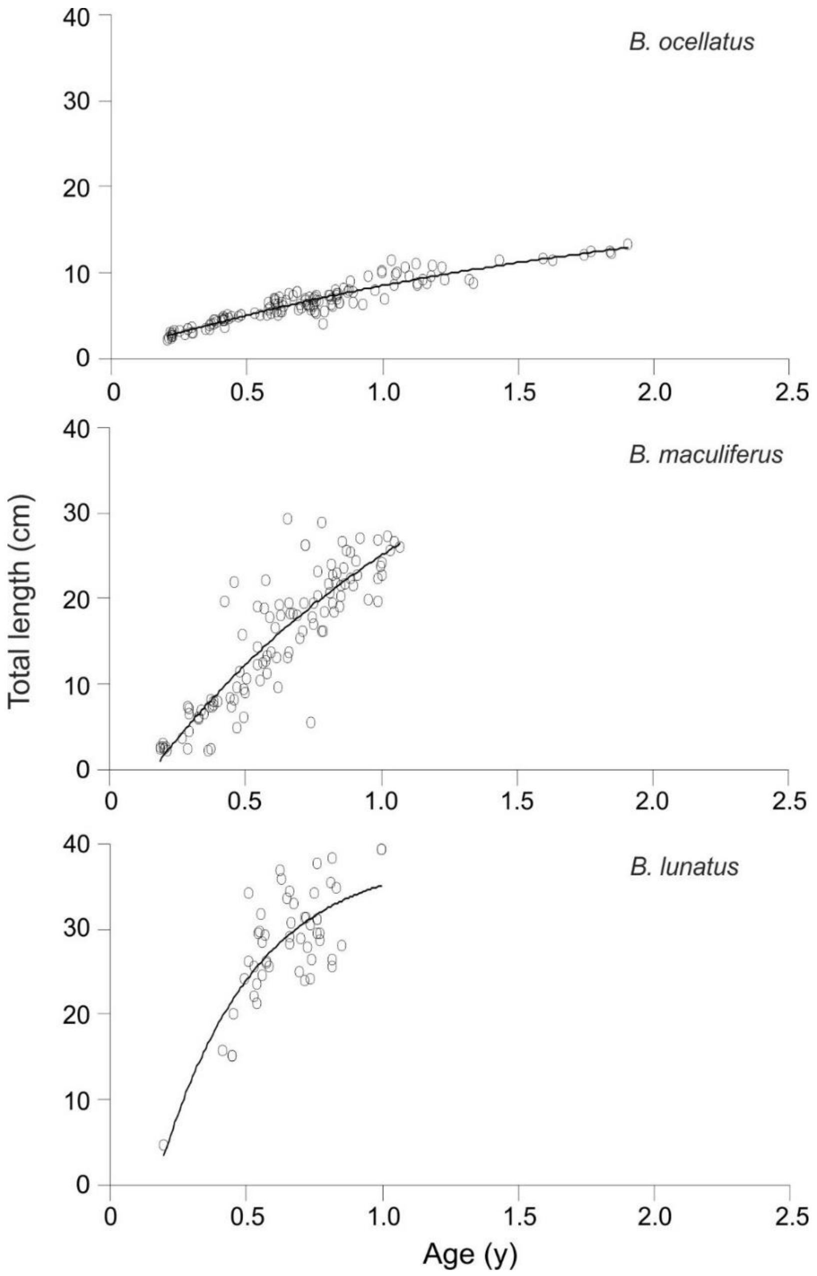

Figure 6. Von Bertalanffy growth curves for *Bothus ocellatus* (top), *B. maculiferus* (middle) and *B. lunatus* (bottom). For parameter, values see Table 1.

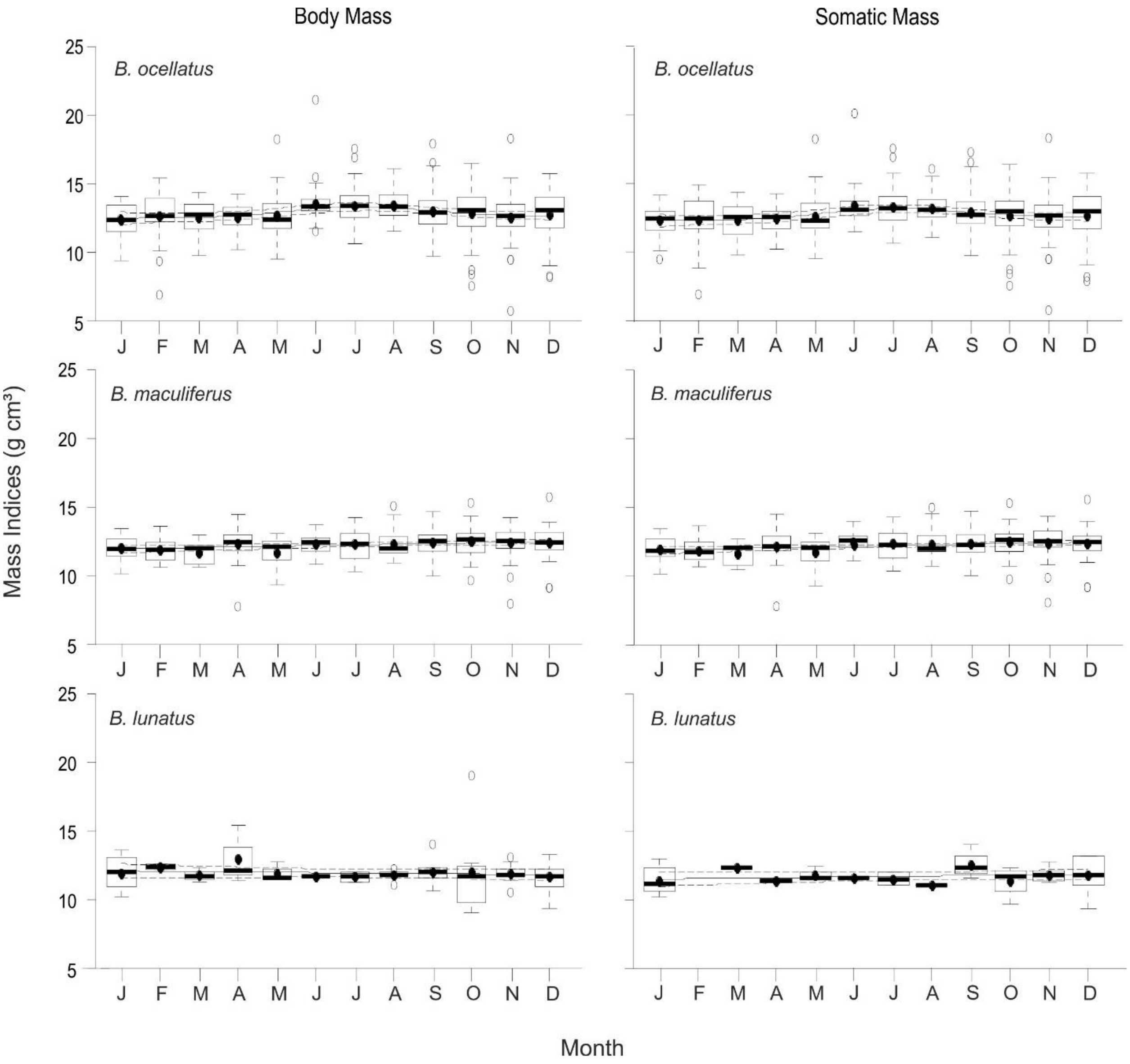

Figure 7. Seasonal pattern in body mass index (BMI; g cm^3) and somatic mass index (SMI; g cm^3) for *B. ocellatus*, *B. maculiferus* and *B. lunatus*, for both sexes and years combined. Curves are GAM model predictions and dotted lines represent the 95% confidence intervals. Boxplots: full dots and horizontal bars indicate mean and median values; boxes represent the range within which the central 50% of the values fall; bars represent the data range excluding outliers; outliers are observations more 1.5 times the box range and are represented by open circles.

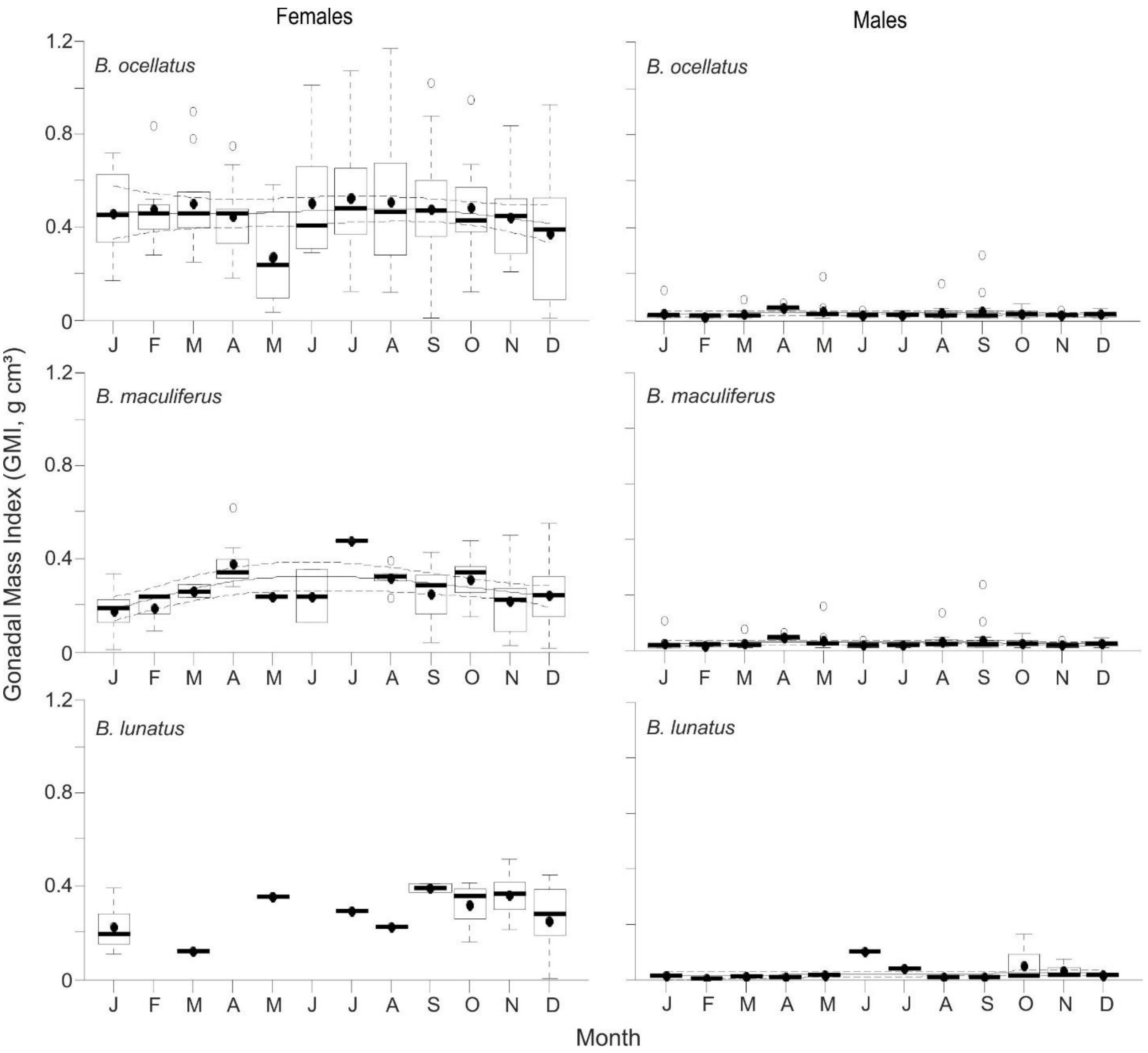

Figure 8. Seasonal pattern in gonadal mass index (GMI; g cm^3) for *B. ocellatus*, *B. maculiferus* and *B. lunatus*, for both years combined. Note that GMI values in plots are not sqrt-transformed. Curves are GAM model predictions and dotted lines represent the 95% confidence intervals. Boxplots: full dots and horizontal bars indicate mean and median values; boxes represent the range within which the central 50% of the values fall; bars represent the data range excluding outliers; outliers are observations more 1.5 times the box range and are represented by open circles. Due to the low number of observations for female B. *lunatus*, no GAM curve could be predicted.

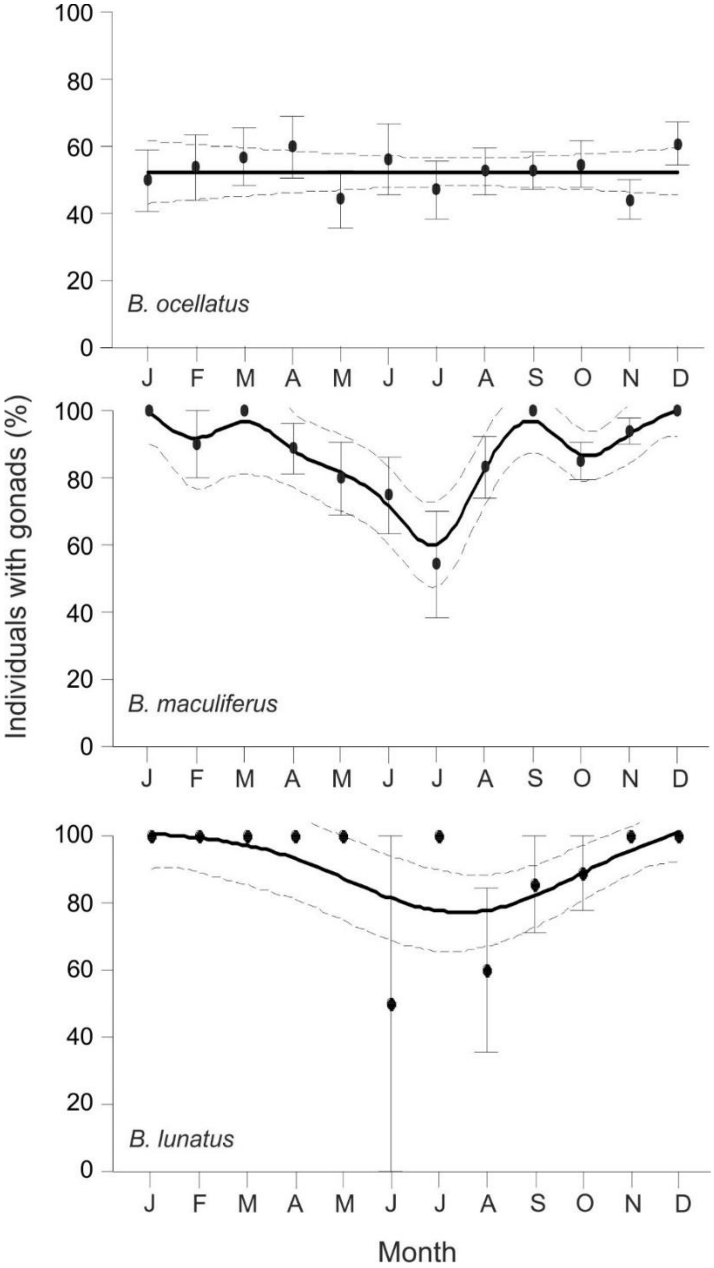

Figure 9. Proportion of flatfishes with gonads present (> 0.01 g) along the year in *B. ocellatus*, *B. maculiferus* and *B. lunatus*, for both sexes and years combined. Curves are GAM model predictions and dotted lines represent the 95% confidence intervals. Full dots indicate mean values and bars represent the data range.