



ORIGINAL ARTICLE

Growth, reproduction and recruitment patterns of the wide-eyed flounder, *Bothus podas* Delaroche (Pisces: Bothidae), from the Azores

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Abstract

The wide-eyed flounder, *Bothus podas*, occurs in many East Atlantic sub-tropical and temperate inshore areas and is the dominant flatfish in shallow-water areas around the Azores. The aim of this study was to examine the growth, reproductive biology and recruitment patterns of the wide-eyed flounder in the Azores. Adult fish samples were obtained by spear fishing and SCUBA hand netting at Faial Island. Juveniles were obtained from a complementary monthly beach-seining programme undertaken at Porto Pim Bay, Faial. Sex and development stage were determined by macroscopic examination of gonads, whereas age estimates were obtained by counting the number of opaque bands in the otoliths. In the Azores, *B. podas* reaches 6 years old, which is more than reported for the central Mediterranean, the only other population of this species that has been studied. The studied population has a sex ratio biased to males, which contrasts to a previous observational study, which noted a female-biased sex ratio. Spawning time, as determined from the gonadosomatic ratio and the macroscopic examination of gonads, was between July and September. This time period agrees with behavioural observations in the same area. Sexual maturity was estimated at a total length (TL₅₀) of 14.1 cm and at an age (A₅₀) of 1.7 years. Small juveniles occur on sandy inshore nursery areas for most of the year, but mainly between July and August each year. The presence of small fish throughout most of the year could suggest a protracted settlement period or slow growth on occasions on the shallow-water nursery grounds.

Key words: *Bothus podas*, growth, insular populations, maturity, sex ratio, spawning

Introduction

Most studies on the life history patterns of flatfish (Pleuronectiformes) focus on commercially important species, such as plaice, *Pleuronectes platessa* (e.g. Modin & Pihl 1994; Nash et al. 1994a), sole, *Solea solea* (e.g. Deniel et al. 1989; Child et al. 1991; Rogers 1994), flounder, *Platichthys flesus* (e.g. Fonds et al. 1992; Andersen et al. 2007) and dab, *Limanda limanda* (e.g. Bolle et al. 1994) in the North Atlantic. Comparable information for left-eyed flounders (Bothidae) is lacking. The wide-eyed flounder, *Bothus podas* Delaroche 1809, has a wide distribution from the Azores in the west to the Adriatic in the east and from the Bay of Biscay along the coast of Africa to Angola (Nielsen 1986). Most of the publications on the wide-eyed flounder are occurrence records

and faunistic lists for the Atlantic and Mediterranean (e.g. Maigret & Ly 1986; Falcon et al. 1993; Santos et al. 1997; Afonso et al. 1999; Demestre et al. 2000). Other studies have focused on early life history (Kalinina 1988; Fukui 1997), the growth and diet of adults (Schintu et al. 1994), the diet of juveniles (Darnaude et al. 2001), chromosome analysis (Vitturi et al. 1993), and habitat preferences (García-Charton & Pérez-Ruzafa 2001).

Bothus podas is by far the most abundant flatfish inhabiting the coastal waters around the Azores Archipelago (Nash et al. 1991, 1994b; Santos et al. 1994; Afonso 2002). *Bothus podas* has no commercial value, but appears to be of ecological importance in these relatively rare shallow-water, sandy-bottom areas. Except for a brief note on the spawning season and growth made by Nash et al. (1991) and the

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description of reproductive behaviour and social organization (Carvalho et al. 2003), there have not been any studies specifically focusing on the reproductive biology of this species.

The social organization of *B. podas* populations is based on a harem mating system, where males are dominant over females (Carvalho et al. 2003). Males defend territories, which include several smaller territories occupied by females and both sexes actively defend their territories against conspecifics throughout the year. Resident females probably mate exclusively with their dominant male. This reproductive strategy appears to be common for the genus, as it has also been reported in the three tropical *Bothus* species: *B. ocellatus* Agassiz, 1831, *B. lunatus* Linnaeus, 1758 and *B. ellipticus* Poey, 1860 at Bonaire, Antilles (Konstantinou & Shen 1995).

The aim of the present study was to examine the growth, reproductive biology and recruitment patterns of the wide-eyed flounder, *Bothus podas*.

Material and methods

In total, 512 individuals of *B. podas* were sampled between September 1997 and August 1999 in the Azores. They were caught by spear fishing and SCUBA hand netting at Faial Island (see Figure 1 for location). Juveniles were obtained from a complementary monthly beach-seining programme undertaken at Porto Pim Bay, Faial [see Santos & Nash (1995) for a detailed description of the area]. Porto Pim Bay, located on the southeast corner of the

island, is a small (approximately 280 m wide) beach facing southwest. The north and south coasts of the beach area are rocky. The southern border is the edge of the Monte da Guia protected area. The maximum tidal range is 1.4 m, with a maximum horizontal area of the beach at low water of approximately 30 m (i.e. 8400 m²). The seine used was 20 m long (32 mm stretch mesh in the wings reducing through 15 mm to 8 mm in the centre). The effective fishing area (291 m² per haul) was estimated by using the method of Kubecka & Bohm (1991). Beach-seine hauls were undertaken at low tide at night with a new moon to reduce the variability in catches due to tidal, daily and lunar patterns in the community structure (Nash & Santos 1998) and the catchability of this species.

Each specimen was measured to the nearest millimetre for total length (TL), and weighed to the nearest 0.01 g for total weight (TW), gonad weight and, after all organs were removed, eviscerated weight. Sex was established by macroscopic examination of the gonads. The sexual state, based on the macroscopic appearance of the gonad, was staged according to a slightly modified version of a maturation scale used for the turbot (Jones 1974): immature (stage 0); developing (stage 1); pre-spawning (stage 2); spawning (stage 3), spent (stage 4) or resting (stage 5).

The sex ratio (expressed as male: female) was analysed by 1 cm TL classes. Deviations from the 1:1 null hypothesis were statistically tested with the

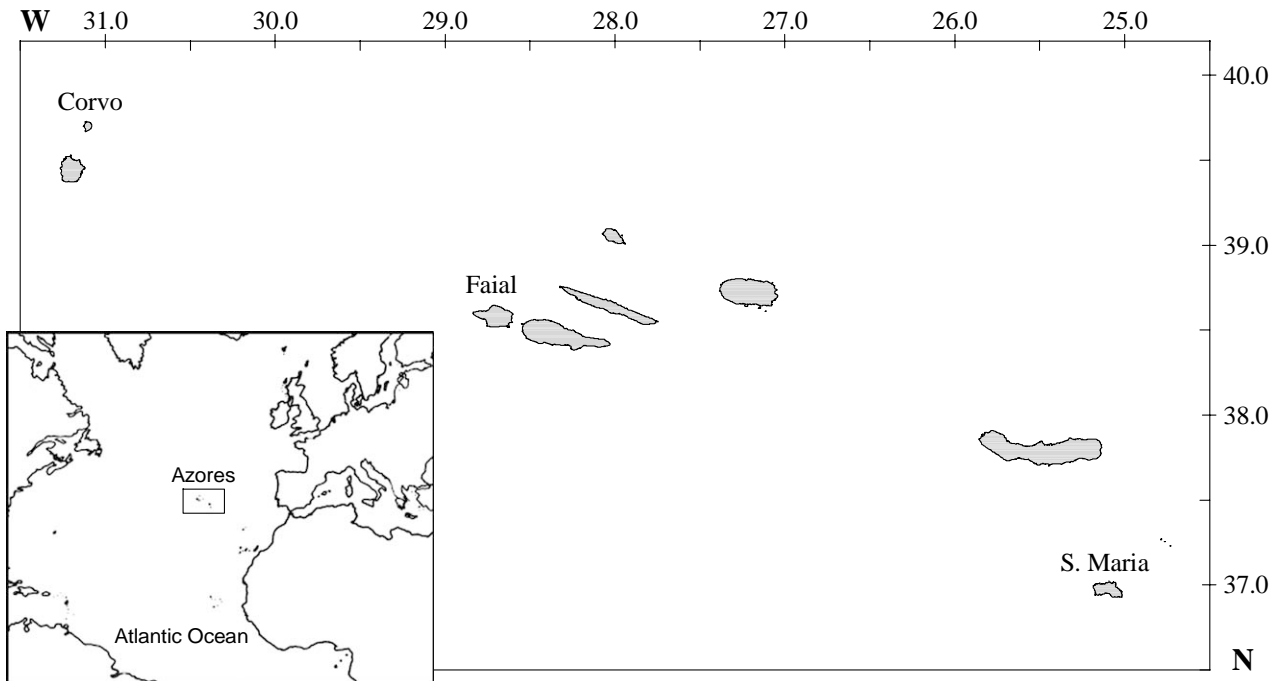


Figure 1. Location of the Azores archipelago, Portugal, showing Faial Island, where the sampling took place.

chi-squared test (χ^2) using 0.05 as the significance level.

Estimates of length (TL₅₀) and age (A₅₀) at maturity were obtained by fitting the relative proportion of mature individuals (stages 1, 2 and 3) over 1 cm TL classes and by age to logistic curves, using the Levenberg–Marquardt algorithm (Marquardt 1963) to solve non-linear least squares regression: $P_X = (1 + e^{-a(X-b)})^{-1}$, where P_X is the proportion of mature fish at length or age X ; a and b are estimated parameters, a is the slope of the curve and b corresponds to a proportion of 0.5 mature fish.

Determination of the spawning season was achieved by analysing the monthly gonadal maturity stages and mean gonadosomatic index (GSI) using eviscerated weight. To avoid possible size-dependent biases, only individuals greater than TL₅₀ were considered.

Sagittal otoliths were collected from 239 specimens and read whole, under a reflecting light, while immersed in a solution of 70% ethanol. Both otoliths from each pair were read and age estimates were obtained by counting the number of opaque bands from the nucleus to the margin under a dissecting microscope. Ages were assigned to each fish assuming the birth date of 1 January. Growth parameters were estimated by fitting the Von Bertalanffy growth model to the observed length at age data by using the Levenberg–Marquardt algorithm (Marquardt 1963).

The reproductive cycle, including the time of spawning, is known to be influenced by environmental cues such as water temperature (Bye 1984; van der Kraak & Pankhurst 1996; Morato et al. 2003). In order to examine this influence, water temperature was continuously measured at 30 min intervals at 25 m depth using underwater datalog-

gers (StowAway® TidbiT®) between August 1997 and the end of the study and during the beach-seine sampling at Porto Pim Bay, Faial, using a mercury bulb thermometer.

Results

Water temperatures in the sheltered shallow bay and in the coastal area at 25 m depth followed similar annual patterns. Minimum values of mean monthly water temperature were observed from February to April (15.7–15.9°C at 25 m depth and 14.3–16.0°C in the shallow bay), whereas maximum values were observed from July to October (18.9–21.5°C at 25 m depth and 20.6–22.0°C in the shallow bay). The maximum recorded daily temperatures were observed from July to September (23.1–24.5°C). Sheltered bay temperatures were, in general, higher and the peak occurred earlier.

In total, 512 individuals were examined, of which 136 were males, 65 were females and 300 were immature. The sex of the remaining 11 individuals was unidentified. The overall sex ratio of male to female was 1: 0.48, which was significantly different from a 1: 1 sex ratio ($\chi^2 = 25.08$; $P < 0.001$).

TL of the fish collected during the sampling period ranged from 2.7 to 23.4 cm, and TW from 0.1 to 157.9 g. The length–frequency distribution was similar for both sexes: males ranged in length from 10.6 to 23.4 cm TL and females from 10.2 to 22.1 cm TL (Figure 2).

Of the 239 otoliths analysed, 232 (97%) had recognizable banding patterns and seven (3%) were discarded, as they were either broken or difficult to interpret. Opaque edges were observed in 12.0% of the read otoliths during July and in 6.25% during August, and may indicate the formation of annual ring structures in the otoliths. Age estimates ranged

Table I. Monthly proportion of maturity stages per sex in *Bothus podas* and the mean water temperature (°C) at 25 m depth for Faial Island during the period studied.

Month	Females						Males						Temperature (°C)	
	1	2	3	4	5	n	1	2	3	4	5	n	Mean	Range
January													16.5	14.3–17.4
February	0.60				0.40	5	1.00					14	15.7	14.0–16.9
March	0.33				0.67	6	0.92				0.08	13	15.7	14.0–16.7
April	1.00					2	1.00					4	15.9	13.9–16.9
May													16.7	14.0–19.3
June	1.00					6	1.00					22	17.7	14.0–20.1
July		0.08	0.92			12	0.08		0.83		0.08	12	18.9	14.8–23.1
August		0.14	0.86			7	0.25		0.75			12	21.1	14.6–24.5
September	0.29	0.57		0.14		7	0.64	0.09			0.27	11	21.5	15.1–24.2
October	0.69				0.31	13	0.40				0.60	20	20.7	15.1–23.3
November				1.00		1							19.1	15.3–22.3
December					1.00	1	1.00					1	17.7	15.0–20.4

1, developing; 2, pre-spawning; 3, spawning; 4, spent; 5, resting.

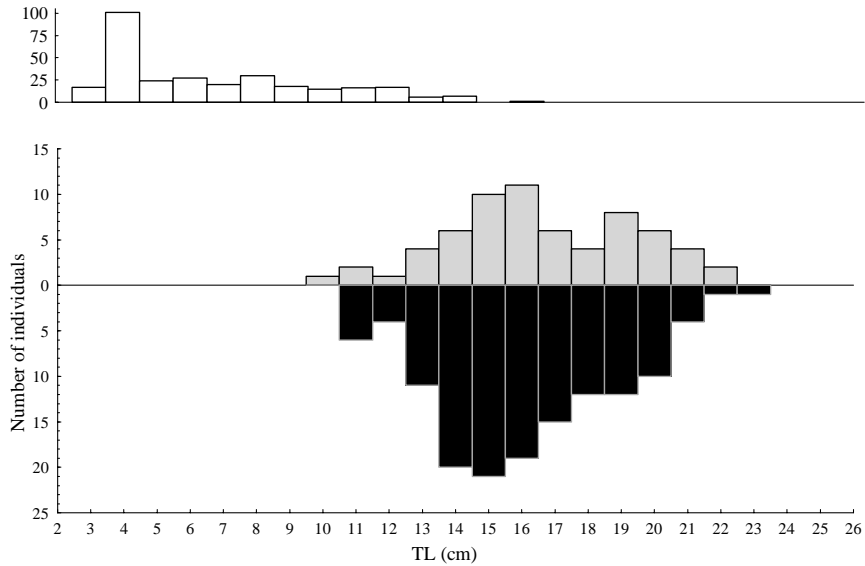


Figure 2. Length–frequency distribution of female (■; n=65), male (■; n=136) and unsexed (□; n=300) wide-eyed flounder, *Bothus podas*, from the Azores.

from 0+ to 5+ years (Figure 3). All fish caught with a beach seine in Porto Pim less than 9 cm TL (n=190) were assumed to be O-group and the otoliths were not read. The mean TL at age indicated a fast early growth and were estimated as 11.3 cm at age 1 year, 14.8 cm at age 2 years, 17.9 cm at age 3 years, 19.6 cm at age 4 years, and 20.6 cm at age 5 years. The von Bertalanffy growth parameters for the combined sexes were estimated as $TL_{\infty}=21.777$ (standard error=0.770); $k=0.583$ (standard error=0.048); $t_0=0.041$ (standard error=0.031) where $r=0.910$; $P<0.01$ and $n=422$.

The length at first maturity (TL_{50}) for the combined sexes was 14.10 cm (standard error =

0.090; Figure 4a), whereas the age at first maturity (A_{50}) was 1.67 years (standard error=0.070; Figure 4b). The proportion of mature *B. podas* at each macroscopic maturity stage varied seasonally (Table I). The proportion of fish in the developing stage was greatest from February to June (>0.70), peaking between April and June, although developing males were observed throughout the year. Pre-spawning and spawning individuals were first observed in July, and then throughout August. In September, five fish in the pre-spawning stage occurred; post-spawning fish were observed from September to November, whereas resting individuals were apparent from September to March.

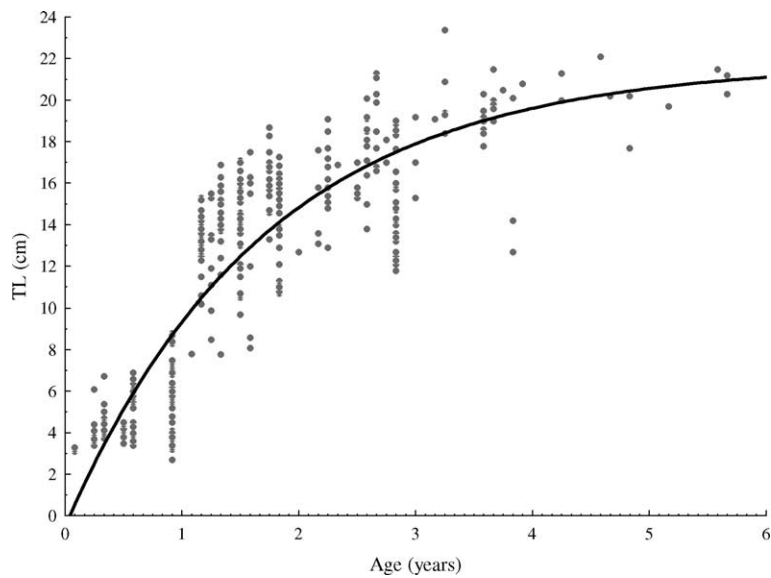


Figure 3. Age–length relationship for wide-eyed flounder, *Bothus podas*, from the Azores.

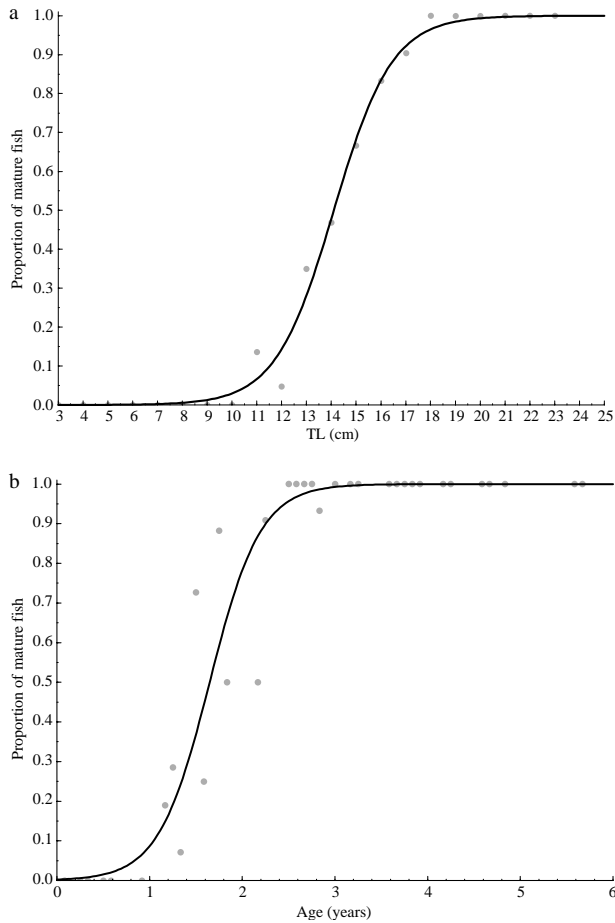


Figure 4. Length (a) and age (b) at first maturity of wide-eyed flounder, *Bothus podas*, from the Azores. $TL_{50} = 14.10$ (standard error = 0.09, $R = 0.997$) cm; $A_{50} = 1.67$ (standard error = 0.07, $R = 0.939$) years.

The GSI for both sexes appeared to vary seasonally (Figure 5a, b). The average GSI was much lower for males than for females. The testes never exceeded 0.24% of the fish eviscerated body weight, whereas female gonads represented up to 5.7% of fish eviscerated weight. The monthly mean values of GSI increased rapidly from June to July in both sexes, corresponding to the first observation of pre-spawning fish. The maximum GSI in females occurred between July and September, corresponding to the occurrence of fish in pre-spawning and spawning maturity stages, before a rapid decline from September to October, corresponding to the appearance of post-spawners. In males, the mean GSI steadily decreased from July to October. In both sexes, the highest values of GSI occurred in July, when the proportion of spawning individuals reached its maximum, whereas the lowest values occurred from October to April, corresponding to the post-spawning, resting and early development stages. Comparing the monthly mean values of GSI and the mean water temperatures during this period, it is

suggested that spawning is initiated by an increase in water temperature, with optimal spawning temperatures ranging between approximately 19 and 21°C.

In general, *B. podas* were present in small numbers all year round at Porto Pim Bay, with occasional peaks in abundance that did not occur consistently among the months of the survey period (Table II). Maximum abundance (for years combined) occurred in July, followed by a sharp decrease to October. Mean densities displayed a large interannual variation (Figure 6). During 1997, the densities were very low and wide-eyed flounders (all greater than 6.0 cm TL) were only observed during October and December. During 1998, the density estimates varied largely between the months sampled. From January to April, flounders were absent or the densities were low. Peaks in abundance were observed during late July (96.2 individuals 1000 m^{-2}) and late November (113.4 individuals 1000 m^{-2}). During 1999, *B. podas* densities were relatively high from late March (36.7 individuals 1000 m^{-2}) to July (18.3 individuals 1000 m^{-2}), whereas the peak was observed during late September (60.7 individuals 1000 m^{-2}).

The seasonal length–frequency distribution indicates the presence of small individuals (3–4 cm TL) throughout the year (Figure 6). The continual presence of small individuals makes it difficult to infer a settlement period. Only one individual smaller than 3 cm TL was caught during the survey (November). The mean TL for the theoretical 0-group individuals ranged between 3.8 and 4.8 cm from January to June, and between 6.1 and 9.3 cm from July to December, with the exception of September, when the mean length observed was 4.7 cm TL. The occurrence of individuals larger than 12 cm TL was occasional.

Discussion

The wide-eyed flounder, *B. podas*, is quite wide ranging, but is generally found in areas where there is a suite of other flatfish species and where it presumably has to compete for a ‘niche’. Although it would be interesting to compare the life history traits and dynamics of this species in an assemblage with and without potentially competing flatfishes, this study can only present the life history characteristics for where there is little or no potential niche overlap (Nash et al. 1991).

The maximum age of *B. podas* in the Azores appears to be 5+ years. This is a longer life span than in the central Mediterranean, where this species only appears to reach approximately 3+ years (Schintu et al. 1994). The L_{∞} in standard length (17.5 cm central Mediterranean) is similar to that

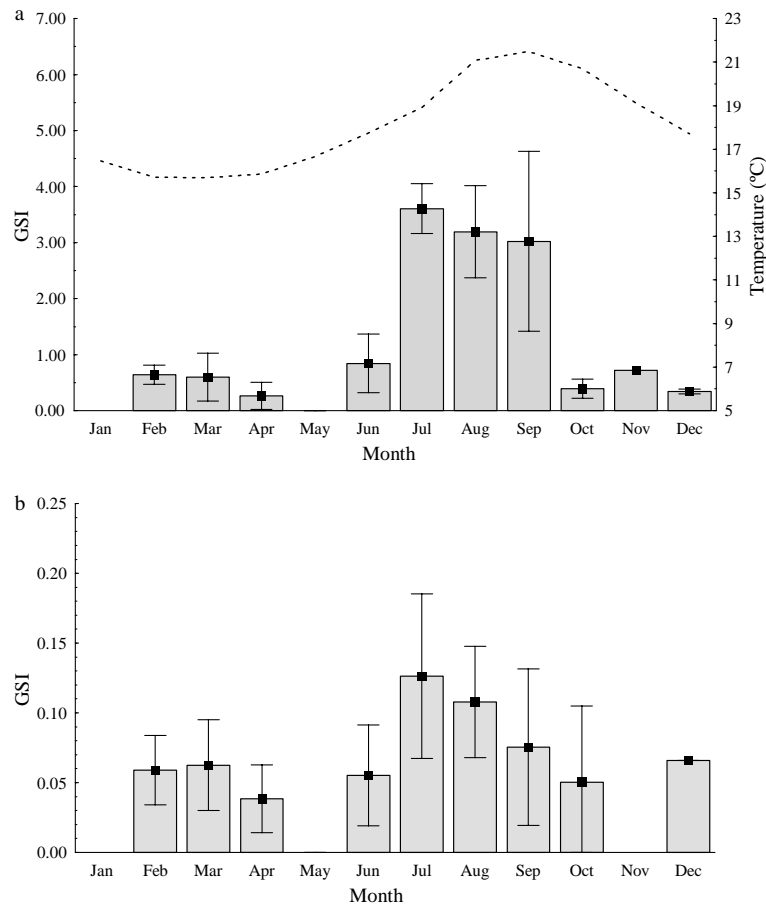


Figure 5. Monthly mean value of gonadosomatic index (GSI) (± 1 standard deviation) for mature female (a) and male (b) wide-eyed flounder, *Bothus podas*, from the Azores. The monthly variation in water temperature ($^{\circ}\text{C}$) at 25 m depth is also presented (dotted line).

found for the Azores [17.17 cm, converted from TL using the equation in Morato et al. (2001)]. Generally, growth rates increase with increasing temperature, whereas size and age at maturity decrease with increasing temperature.

Life history traits also appear to reflect latitudinal variations. *Bothus podas* is a sub-tropical species and

has a characteristically high growth rate (sexes combined). Miller et al. (1991) used the relationship between $\text{TL}_{50}/\text{TL}_{\text{max}}$ and k (from the von Bertalanffy growth curve) to look at life history traits. In their analysis they used the female growth curve only. A female plus immatures only growth curve was calculated solely for comparative purposes

Table II. Average monthly number of *Bothus podas* caught by beach-seining in Porto Pim Bay, Faial Island, Azores, during the period August 1997 to September 1999. Each haul had an effective fishing area of 291 m².

Month (cm)	Average number (seine ⁻¹)	Average number (1000 m ⁻²)	Average of total length (cm)	Range of total length
January	2.0	6.9	4.0	3.1–7.8
February	0	0		
March	5.3	18.3	4.2	3.4–12.6
April	6.6	22.7	4.8	3.7–11.8
May	7.3	25.2	3.8	3.5–4.4
June	5.7	19.5	4.1	3.5–4.5
July	16.7	57.3	6.2	3.3–13.5
August	0	0		
September	8.8	30.4	4.7	3.1–8.7
October	1.4	4.9	9.3	7.1–12.2
November	14.1	48.6	7.1	2.7–11.2
December	0.3	1.2	6.1	6.1–6.1
Total	6.9	23.7	5.7	2.7–13.5

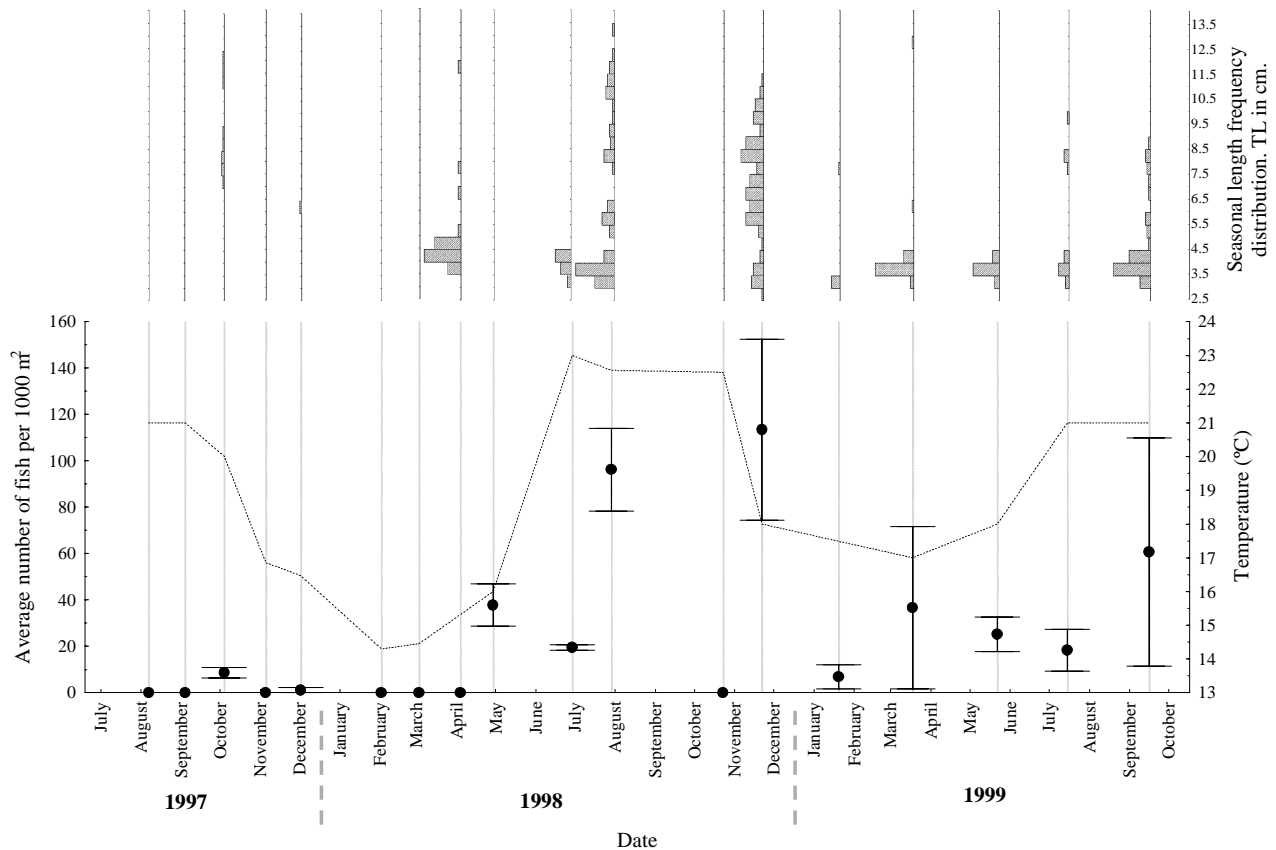


Figure 6. Average number (\pm standard error) of the wide-eyed flounder, *Bothus podas*, caught on each beach-seining in Porto Pim Bay, Faial Island, Azores. The corresponding length–frequency distribution of the catches (histogram) and the mean water temperature (dotted line) at Porto Pim Bay are also presented.

($TL_{\infty} = 24.93$; $k = 0.37$; $t_0 = -0.072$). Using the equations given in Miller et al. (1991), a maximum female length of 22.1 cm and $TL_{50}/TL_{max} = 0.64$ the predicted k is 0.37. This is in exceptionally good agreement with the observed value. This therefore suggests that *B. podas* shows r-traits (i.e. opportunistic), but, as with yellowtail flounder, could be relatively invariable (with respect to the size at maturity, mortality and longevity) over a geographical range. In other species, the variation in life history characteristics can be quite dramatic. For instance, in North Atlantic populations of the long rough dab, two patterns in life histories emerged: southern populations are characterized by faster growth, earlier maturation, and winter–spring spawning, whereas northern populations are characterized by slower growth, later maturation and a spring–summer spawning (Walsh 1994).

The present results indicate that the population has a sex ratio biased to males. This is in contrast to a previous observational study, which noted a female-biased sex ratio of one male to two females, consistent with the harem system of the species (Carvalho et al. 2003). However, that study most probably underestimated the total number of males

in the population because smaller males under 14 cm do not show apparent external dimorphism (larger sizes, greater inter-orbital distances, pronounced ocular and supra-orbital spines and a blunt head – Nash et al. 1991; Carvalho et al. 2003) and can be mistaken for females. Additionally, it remains possible that the catch data from the present study biased the sex ratio towards males because of a catchability difference among sexes, that is, males are most likely to be caught because of their aggressive and inquisitive territorial behaviour (pers. observ.).

These considerations suggest that the population most probably has a sex ratio close to 1:1, implying that a portion of the mature males are excluded from regular breeding given their harem system. This would explain the occurrence of smaller roving males observed in the vicinity of harem territories that are vigorously chased away by dominant harem males (Carvalho et al. 2003). Therefore, both the population structure (this study) and the social dynamics support the existence of strong intraspecific competition in the wide-eyed flounder. This would also explain the existence of smaller maturing males throughout the year, as larger (older) males

possess larger territories with larger harems (Carvalho et al. 2003), thus potentially excluding smaller males through competition.

Wide-eyed flounders in maturity stage 3 (ready to spawn) occurred between July and August, with spent fish in September and November. This suggests spawning between July and September and supports the interpretation of the GSI data, which suggested spawning over the same months. The spawning period of July to September is also consistent with the behavioural studies of Carvalho et al. (2003), where the courtship behaviour and spawning activity occurred during the first 2 h of sunlight, on a daily basis, between July and September, with a peak in August. Thus, spawning is at or around the highest water temperature.

The reproductive cycle, including the time of spawning, is highly influenced by environmental cues, such as water temperature and photoperiod (Bye 1984; van der Kraak & Pankhurst 1996; Morato et al. 2003). Miller et al. (1991) commented that bothids (among others) in tropical and temperate regions have extended spawning periods, coupled with batch egg production and serial spawning. They further noted that spawning in bothids appears to be cued to warming or cooling trends. In the Azores, the spawning activity of *B. podas* appears to be promoted by the increase in water temperature, during late spring and early summer, with optimal temperatures ranging between 19 and 21°C. However, a wider time series would be useful in clarifying this assumption, one which would permit the assessment of the monthly evolution of mature individual and GSI values between warmer and colder years. The coupling of peak spawning times with temperature and plankton peak production times (May–July) suggests further investigation.

The maturity cycle should, however, be validated through the histological examination of gonads. The presence of developing individuals throughout the year, mainly 2-group males, needs further study.

The largest numbers of juveniles (30–40 mm TL) occurred in August/September, during 1997–1999 and in 1989–1990 (Nash et al. 1991). The presence of small fish throughout most of the year could suggest a protracted settlement period or slow growth on occasions on the shallow-water nursery grounds. It appears that most of the spawning is between July and September, which means that the eggs and larvae are in the water column prior to metamorphosis and settlement for some considerable time (9–10 months). Alternatively, they could appear in the nursery areas earlier in the year, e.g. December onwards, but were too small to be captured with the gear used in this study and be

growing relatively slowly due to the relatively low water temperature. Sobrinho-Gonçalves & Isidro (2001) found *B. podas* larvae only in February. This study covered February to June 1998 and thus does not shed light on the earlier time period. However, these data overlap with the current data set. The abundances were very low, which could suggest that either, in general, abundance was low and the probability of gaining any meaningful inferences from abundance data is low or that the majority of larvae were already on the nursery ground (or at least in the vicinity of the nursery) by February. The period of time between spawning and appearance on the nursery grounds in shallow water is still in need of further study.

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