

Halfway up the trophic chain: development of parasite communities in the sparid fish *Boops boops*

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SUMMARY

We examined the patterns of composition and structure of parasite communities in the Mediterranean sparid fish *Boops boops* along a gradient of fish sizes, using a large sample from a single population. We tested the hypothesis that species forming the core of the bogue parasite fauna (i.e. species which have a wide geographical range and are responsible for recognizable community structure) appear early in the fish ontogeny. The sequential community development observed supported the prediction that core species appear in the fish population earlier than rare and stochastic species. There was also a strong correlation between the order of 'arrival' of the species and their overall prevalence. Six key species were responsible for recognizable community structure across size/age cohorts; the addition to this baseline community of key parasite species resulted in a nested structure that is linked to differential species abundance rather than fish size. Information on the life-cycles, distribution and host range of the parasites is used to explain the observed patterns of parasite community structure. We conclude that the small mouth size of *B. boops* coupled with suction feeding may provide a setting for passive sampling as a mechanism leading to non-random parasite community structure.

Key words: *Boops boops*, Sparidae, Mediterranean, parasites, community development, nested structure.

INTRODUCTION

Although the idea that infection by metazoan parasites increases with age in fish hosts is not new (see Dogiel *et al.* 1958), recent empirical evidence suggests that a wide range of host traits, such as body size and/or age (e.g. Guégan and Huguény, 1994; Lo *et al.* 1998; Vidal-Martinez *et al.* 1998; Poulin, 2000; Johnson *et al.* 2004), habitat and diet (e.g. trophic status, feeding rates; Sasal *et al.* 1999; Muñoz *et al.* 2006), degree of vagility (Kennedy, 1990), social behaviour and schooling (Bartoli *et al.* 2000; Luque *et al.* 2004) act jointly to provide structure to fish parasite communities. However, studies at the host population level are necessary to pinpoint the role of host age *per se*, and these are still few.

Nested subset analyses have proved a useful analytical tool to detect size/age-associated compositional heterogeneity across fish parasite assemblages (Guégan and Huguény, 1994; Poulin and Valtonen, 2001; Timi and Poulin, 2003). An ontogenetic shift in host diet and/or habitat utilization

is a straightforward mechanism that can produce nested patterns of infracommunity structure (e.g. Rohde *et al.* 1998; Poulin and Valtonen, 2001). However, the addition of size-dependent parasites (i.e. with prevalence increasing with size due to higher feeding rates of the host and/or accumulation of parasites) to a baseline community of size-independent parasite species can also result in a nested structure in the absence of a strict diet shift (Zelmer and Arai, 2004). Therefore, other approaches must be combined to nested subsets analyses to determine exactly how the acquisition of parasites in relation to host age serves to structure parasite communities.

Here, we address these questions using a model species. The bogue, *Boops boops* (L.), is an omnivorous (trophic level 2.5–2.97), demersal to semi-pelagic non-migratory species of fish. It is gregarious, found on the shelf of the coastal pelagic zone at a depth range 0–350 m (Froese and Pauly, 2007). Although the bogue is perhaps one of the most abundant species in both the Mediterranean and the North-East Atlantic (Valle *et al.* 2003; Boyra *et al.* 2004), data on its feeding habits are scarce and somewhat ambiguous. Thus, Bell and Harmelin-Vivien (1983), who considered *B. boops* to be microphagic carnivores, found that juveniles normally feed high in the water column but, on occasions, descend

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to browse on algae within the seagrass canopy. They recorded fairly large quantities of algae eaten by juveniles, whereas Bauchot and Hureau (1986) considered that juveniles are mostly carnivorous and adults mostly herbivorous. Linde *et al.* (2004) classified *B. boops* as suction-feeding secondary planktivores, Karpouzi and Stergiou (2003) as omnivores, and Stergiou and Karpouzi (2002) as omnivorous with a preference for plant material but also feeding on a wide range of invertebrates. Finally, Fernández *et al.* (2001) suggested that *B. boops* is mainly herbivorous whereas Ruitton *et al.* (2005) have shown that grazing of algae by bogue only occurs in the post-spawning period.

B. boops hosts a large number of metazoan parasites (67 species) among which we identified a group of 9 species with a wide geographical distribution, forming the core of the bogue parasite fauna and consistently present in both Mediterranean and N.E. Atlantic fish (Pérez-del Olmo *et al.* 2007a). A pilot study on bogue revealed positive or negative (depending on the parasite species) correlations of abundance with fish size (unpublished observations). This size-associated variability in some bogue parasites (see also Renaud *et al.* 1980; Saad-Fares and Combes, 1992) raises the question as to whether the observed community parameters are inherent to parasite communities in *B. boops* or merely artefacts of sampling heterogeneity with respect to fish size. Knowledge of size-related variation in parasite community composition and abundance among hosts in a fish population is essential for the adequate application of multivariate statistical analyses of entire parasite communities as biological tags of fish populations (Williams and MacKenzie, 2003, and references therein). Therefore, a study on the demography of parasite community structure as a function of size of individual hosts in bogue has important implications for investigations seeking to establish the harvest localities of fish or surveying post-oil spill recovery using bogue parasites (e.g. Power *et al.* 2005; Pérez-del Olmo *et al.* 2007b).

Here, using a single population sample from a single habitat, we examine the patterns of composition and structure of parasite communities in *B. boops* along a gradient of fish sizes in order to test the prediction that species forming the core of the parasite fauna and being responsible for recognizable community structure should appear in the fish population earlier than rare and stochastic species (e.g. Vidal-Martinez *et al.* 1998). We provide novel data on the sequential development of an unusual sparid-metazoan system characterized by high transmission rates and low levels of host specificity, focusing on (i) variation in community parameters, (ii) distributions of 'key' parasite species, and (iii) predictability of community composition with size. We further explore data on the life-cycles, distribution and host range of the parasites in the

Mediterranean, and on host biology, to explain the observed patterns of parasite community structure.

MATERIALS AND METHODS

A total of 130 *B. boops* was collected by local fishermen in 2 days in June 2005 off Santa Pola (Spanish Mediterranean coast). Fish, transferred on ice to the laboratory, were measured [total length (TL, cm), standard length (SL, cm), weight (W, g)], labelled, and packed individually before being frozen. A subsample of fresh fish was examined to obtain live parasite material for a precise identification. Ecto- and endo-parasites were recovered according to a standardized protocol. All metazoan parasites were identified and counted. Worms were fixed and stored in 70% ethanol. Trematodes, monogeneans and acanthocephalans were stained with iron acetocarmine and examined as permanent mounts in Canada balsam. Nematode larvae were identified on temporary mounts in saline solution or glycerine. Voucher specimens have been deposited in the Parasite Collection of Cavanilles, Institute of Biodiversity and Evolutionary Biology, University of Valencia, Spain.

Ecological terms follow Bush *et al.* (1997). Species with a prevalence of >30% will be referred to henceforth as common, those with a prevalence of ≤30% as rare and those with prevalence <10% as accidental. Component population size refers to the total number of individuals of a given species in the total sample. Observed species density distributions within total communities in each size-class were tested for fit to the null model of no interspecific interaction (Janovy *et al.* 1995). Due to the non-normal distribution of the data, Spearman rank correlations (r_s) and non-parametric tests (Mann-Whitney (M-W) and Kruskal-Wallis (K-W)) were applied for statistical comparisons with a Bonferroni correction in *post-hoc* tests. Prevalences were compared with Fisher's exact test. Analyses were carried out using the statistics program SPSS[®] 12.0.

The data set (SL 10.2–25.0 cm) was stratified into 5 size-classes with 3.0 cm intervals (ranges and means in Table 2). All parasite taxa were divided into 2 groups (labelled 'D' and 'F' in Table 1; parasite assemblages referred to as DA and FA in the text) with respect to the mode of infection: (i) D, transmitted to fish directly or *via* cercarial penetration; and (ii) F, food-transmitted parasites. Parasites were classified into 3 categories with regard to their host specificity: (i) bogue specialists (BS); (ii) sparid generalists (SG); and (iii) generalists (G). Parasite life-cycle and host specificity data were compiled from an exhaustive search of literature sources and both the Host-Parasite Database (<http://www.nhm.ac.uk/research-curation/projects/host-parasites/database/>) and the Host-Parasite Catalogue compiled by the Natural History Museum, London. Data for

the regional distribution of parasites were taken from a complete checklist of parasites of *B. boops* (see Pérez-del Olmo *et al.* 2007a).

Nested subset analyses were carried out for the total parasite communities and separately for the separate matrices containing either directly transmitted or food-transmitted parasites using the Nestedness Temperature Calculator Program of Atmar and Patterson (1995). The latter matrices were further stratified by size-class and subjected to analysis. Matrices were packed maximally and the nestedness metric 'temperature' (T) was calculated. For each matrix, the value of T was compared with those of 1000 random matrices generated by Monte-Carlo simulations, with no row or column constraints, to assess the probability of randomly obtaining a matrix with the same or higher degree of order.

RESULTS

Parasites of B. boops off Santa Pola

Species composition, prevalence and abundance of each parasite in each size-class sample are summarized in Table 1. A total of 26 parasite species was found in the 130 fish examined from Santa Pola. These include 3 additional new host records (*Camallanus* sp., *Cucullanellus* sp. and *Tormopsolus* sp.). With respect to the mode of infection, 16 species were parasites with complex life-cycles transmitted to the final host by ingestion of the second intermediate/paratenic host. This group accounted for 84.6% of all parasites in the overall sample (range for size-class samples: 77.4–93.8%) and included 9 species of trematode with a high representation of the superfamily Hemiuroidea (6 species, 53.5% of individuals transmitted *via* food ingestion), 6 nematodes and a larval cestode. The remaining 10 species were parasites transmitted to fish directly (3 monogenean and 3 crustacean species) or *via* cerarial penetration (4 larval trematodes).

Generalist parasites comprised a considerable part of the component community in *B. boops* (16 species, 53.5% of all individuals) compared with bogue specialists (3 species, 35.4%) and sparid generalists (4 species, 11.1%). This excludes 3 taxa not identified to the species level but only being represented by 1 specimen each in the total sample (see Table 1).

Fig. 1 shows the distribution of parasites in relation to their first appearance and prevalence in the size-class samples. Thirteen species colonized the fish of size-class 1. Seven species appeared for the first time in the second size-class and 3, 2 and 1 species were added to the species lists of the subsequent samples, respectively.

Five groups of species can be distinguished with respect to their prevalence and persistence in the 5 samples stratified by size. Six species (*B. israelensis*,

A. stossichii, *H. communis*, *Hysterothylacium aduncum*, *Microcotyle erythrini* and *Lecithocladium excisum*) were found in all 5 samples with high prevalence (>30%, common species; except for *L. excisum* with a prevalence of 15.0% in size-class 1). Of these, the first 3 species were the most frequent in all 5 size-class samples (prevalence: >60%, overall range: 83–100%) and represented the vast majority (78–95%) of the parasites found. Three species (*Cardiocephaloides longicollis*, *Proisorhynchus crucibulum* and *Scolex pleuronectis*) were recovered in all samples but at low prevalences (<30%, rare species). Four species occurred at low prevalences in 4 samples, and 6 species were found with low prevalences in 2 or 3 samples. Finally, a group of 7 species occurred in only one size-class and, with the exception of *Peniculus fistula*, in a single fish (accidental species). There was a highly significant negative correlation between the order of the 'arrival' of the species (coded 1–5, according to the size-class) and the prevalence at which they infected fish ($r_s = -0.643$, $P = 0.0004$; $n = 26$).

Host size and parasite community descriptors

All specimens of *B. boops* examined were infected with 2–13 parasite taxa and harboured 7–245 individual parasites. Species density distributions in all 5 samples were found to fit the null model of no interspecific interaction based on frequency of co-occurrences (Janovy *et al.* 1995). Data on the mean parasite infracommunity richness and abundance in each size-class are given in Table 2. Assemblages formed by the two parasite groups with different transmission strategies (direct *vs* food transmitted) are presented as separate subsets.

Infracommunities tended to increase in richness and abundance with host size ($r_s = 0.399$, $P < 0.0001$ and $r_s = 0.251$, $P = 0.004$, respectively). This positive association was stronger in DA ($r_s = 0.389$, $P < 0.0001$ and $r_s = 0.593$, $P < 0.0001$, respectively) and significant for the number of species only in FA ($r_s = 0.210$, $P = 0.017$). Furthermore, there were significant differences in the distributions of species and individual parasites among the 5 size-classes (see Table 2). These differences were largely due to the higher parasite load in the largest size-classes (4 and 5) compared to size-classes 1 and 2. With respect to the distributions of individual parasites the lowest abundance of food-transmitted parasites in size-class 2 and the substantially higher load of directly-transmitted parasites in large fish (class 4–5) contributed to the overall significant differences for total communities by size (see Table 2).

Despite the narrow range of lengths within size classes, some within-class variability was observed. Thus, there were correlations between richness or abundance and host length in some size classes (see Table 2 for details).

Table 1. Prevalence (P%) and abundance (mean, MA \pm s.d. (median shown if >0 only)) of parasites in the sample of *Boops boops* stratified by size(na, not applicable; BS, bogue specialist; SG, sparid generalist; G, generalist; D, transmitted *via* direct infection; F, transmitted *via* food ingestion. Hemiuroideans marked with a star.)

Parasite species	Mode of infection & Specificity	Size-class 1		Size-class 2		Size-class 3		Size-class 4		Size-class 5	
		P%	MA \pm s.d. (M)	P%	MA \pm s.d. (M)	P%	MA \pm s.d. (M)	P%	MA \pm s.d. (M)	P%	MA \pm s.d. (M)
Monogenea											
<i>Cyclocotyla bellones</i>	D, G	—	—	—	—	2.9	0.03 \pm 0.2	17.2	0.17 \pm 0.4	4.8	0.05 \pm 0.2
<i>Microcotyle erythrini</i>	D, SG	35.0	1.55 \pm 3.2	57.7	1.31 \pm 1.5 (1)	73.5	2.12 \pm 2.1 (1)	100.0	8.83 \pm 7.7 (7)	95.2	10.19 \pm 8.0 (10)
<i>Pseudaxine trachuri</i>	D, G	15.0	0.25 \pm 0.7	7.7	0.15 \pm 0.6	11.8	0.21 \pm 0.6	20.7	0.28 \pm 0.6	—	—
Digenea											
<i>Aphanurus stossichii</i> *	F, G	85.0	3.05 \pm 2.1 (3)	96.2	7.69 \pm 11.8 (4.5)	91.2	6.38 \pm 5.6 (5)	96.6	9.28 \pm 15.1 (5)	90.5	6.29 \pm 7.7 (4)
<i>Arnola microcirrus</i> *	F, SG	5.0	0.10 \pm 0.5	—	—	—	—	—	—	—	—
<i>Bacciger israelensis</i>	F, BS	95.0	15.25 \pm 18.1 (9)	88.5	6.58 \pm 9.2 (4.5)	94.1	10.29 \pm 9.0 (9)	82.8	16.21 \pm 19.6 (10.5)	85.7	36.19 \pm 53.9 (12)
<i>Cardiocephaloides longicollis</i> met.	D, G	10.0	0.20 \pm 0.7	19.2	0.31 \pm 0.7	17.7	0.18 \pm 0.4	20.7	0.28 \pm 0.6	28.57	0.43 \pm 0.8
<i>Hemiurus communis</i> *	F, G	100.0	21.00 \pm 17.4 (18)	96.2	9.12 \pm 7.2 (6)	94.1	13.79 \pm 22.4 (8.5)	93.1	13.93 \pm 27.3 (5)	95.2	6.76 \pm 5.9 (1)
<i>Lecithocladium excisum</i> *	F, G	15.0	0.20 \pm 0.5	34.6	0.42 \pm 0.6	41.2	0.65 \pm 1.0	55.2	1.21 \pm 1.8 (1)	33.3	0.43 \pm 0.7
<i>Magnibursatus bartolii</i> *	F, BS	—	—	—	—	—	—	3.4	0.03 \pm 0.2	4.8	0.05 \pm 0.2
Opecoelidae gen. sp.	F, na	—	—	—	—	2.9	0.03 \pm 0.2	—	—	—	—
<i>Proisorhynchus crucibulum</i> met.	D, G	10.0	0.20 \pm 0.7	3.9	0.15 \pm 0.8	20.6	2.29 \pm 7.4	13.8	2.34 \pm 9.67	9.5	0.14 \pm 0.5
<i>Robphildollfusium martinezgomezi</i>	F, BS	—	—	11.5	0.27 \pm 1.0	—	—	—	—	4.8	0.05 \pm 0.2
<i>Stephanostomum euzeti</i> met.	D, G	—	—	11.5	0.31 \pm 0.9	23.5	0.29 \pm 0.6	24.1	0.28 \pm 0.5	4.8	0.05 \pm 0.2
<i>Tetrochetus corypahenae</i> *	F, G	—	—	3.9	0.04 \pm 0.2	—	—	—	—	—	—
<i>Tormopsolus</i> sp. met.	D, G	5.0	0.05 \pm 0.2	—	—	5.9	0.06 \pm 0.2	3.4	0.03 \pm 0.2	—	—
Cestoda											
<i>Scolex pleuronectis</i>	F, G	10.0	0.15 \pm 0.5	15.4	0.15 \pm 0.4	14.7	0.21 \pm 0.5	20.7	0.72 \pm 2.1	19.0	1.67 \pm 6.8
Nematoda											
<i>Anisakis simplex sensu lato</i> larva	F, G	—	—	3.9	0.04 \pm 0.2	5.9	0.06 \pm 0.2	24.1	0.24 \pm 0.4	14.3	0.33 \pm 1.1
<i>Canallamus</i> sp.	F, na	—	—	—	—	—	—	3.4	0.03 \pm 0.2	—	—
<i>Pseudocapillaria adriatica</i>	F, G	—	—	3.9	0.04 \pm 0.2	—	—	—	—	4.8	0.05 \pm 0.2
<i>Contracaecum</i> sp. larva	F, G	—	—	—	—	2.9	0.06 \pm 0.3	—	—	—	—
<i>Cucullanellus</i> sp.	F, na	—	—	3.9	0.04 \pm 0.2	—	—	—	—	—	—
<i>Hysterothylacium aduncum</i> larva	F, G	35.0	0.50 \pm 0.8	61.5	0.96 \pm 1.1	44.1	0.79 \pm 1.0	69.0	1.17 \pm 1.2 (1)	81.0	1.86 \pm 1.6
Isopoda											
<i>Ceratothoa oestroides</i>	D, SG	5.0	0.40 \pm 1.8	—	—	2.9	0.03 \pm 0.2	—	—	4.8	0.05 \pm 0.2
Copepoda											
<i>Naobranchia cygniformis</i>	D, SG	—	—	19.2	0.19 \pm 0.4	20.6	0.21 \pm 0.4	24.1	0.31 \pm 0.6	19.1	0.19 \pm 0.4
<i>Peniculus fistula</i>	D, G	—	—	—	—	—	—	—	—	9.5	0.10 \pm 0.3
Component community richness			13		17		18		17		18
Proportion of individuals transmitted via food chain			0.94		0.91		0.86		0.77		0.83
Proportion of generalist individuals			0.60		0.70		0.66		0.54		0.28

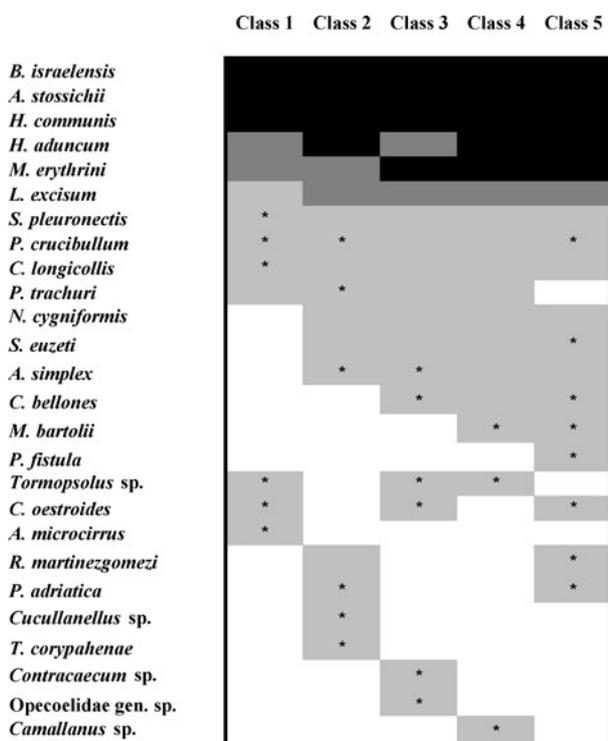


Fig. 1. Schematic illustration of colonization and persistence (order of appearance and prevalence status) of bogue parasites in the component communities of the five size-class samples. ■, prevalence >60%; ■, prevalence 30–60%; ■, prevalence 10–30%; ■, prevalence <10%.

Key parasite species

Six species (1 bogue specialist, 1 sparid generalist and 4 generalists) were present in all size samples (most with prevalences of >60% in at least 3 samples, see Fig. 1), and represented the majority of the parasites recovered in each size-class (96.8, 93.9, 90.3, 91.5 and 95.2% of all individuals, respectively). Of these, *B. israelensis*, *H. aduncum* and *M. erythrini* showed a positive correlation between abundance and fish size ($r_s = 0.179$, $P = 0.041$; $r_s = 0.281$, $P = 0.001$; and $r_s = 0.646$; $P < 0.0001$, respectively) in contrast to *H. communis* that exhibited a negative association ($r_s = -0.379$; $P < 0.0001$). No significant relationship was found for *A. stossichii* and *L. excisum*.

A tendency for an increase in prevalence with size was detected for *H. aduncum* ($\chi^2 = 8.284$; $P = 0.004$) and *M. erythrini* ($\chi^2 = 30.954$; $P < 0.0001$). However, with the exception of the monogenean *M. erythrini*, which had distinctly higher prevalences in the largest fish (classes 4–5 as compared to 1–2), the prevalence of infection by the dominant species did not differ significantly among the 5 size-classes of fish (see Fig. 2A). The abundance of *M. erythrini* also exhibited the most significant differences between size-classes (all $P < 0.00001$), following the prevalence divergence pattern (Fig. 2B). The abundance of the other key species exhibited a few significant

differences among size samples (Fig. 2B). A comparison of the within-class abundance distributions of the 3 most abundant trematode species showed significant differences exclusively in size-class 1 and 5. The smallest fish had more individuals of *H. communis* than *A. stossichii* and *B. israelensis* ($P < 0.0001$; $P = 0.023$), whereas in the largest fish, there were more individuals of *B. israelensis* ($P = 0.014$; $P = 0.006$).

There was a strong positive correlation ($r_s = 0.813$, $P = 0.008$) between the regional distribution (measured by the number of records in Pérez del Olmo *et al.* 2007a) and local prevalence in our total sample of 9 taxa (*B. israelensis*, *A. stossichii*, *H. communis*, *L. excisum*, *H. aduncum*, *Anisakis simplex*, *M. erythrini* and *Ceratothoa oestroides*, forming the core of bogue fauna, plus unidentified tetraphyllidean larva *Scolex pleuronectis*) known from both the Mediterranean and Atlantic.

Host size and non-random community structure

The pooled infracommunities in *B. boops* produced a significantly nested matrix, as did the assemblages, resulting from food ingestion (FA) and direct infection (DA) (Table 3). There were significant correlations between the standard length of individual fish and their rank order in the packed matrix in the total community and FA datasets (the latter being rather weak, with low values for both r_s and P) but not in the DA dataset. Significant nested subset patterns were observed among FA of the 5 size-classes, as well as among DA of the larger fish (size-classes 3–5). With the exception of class 4 DA, no significant association between the rank order and size of fish was detected (Table 3).

In contrast, there was a strong association between the rank position in the matrix and component population size of parasites (total communities, $r_s = -0.961$, $P < 0.0001$; FA, $r_s = -0.949$, $P < 0.0001$; DA, $r_s = -0.854$, $P = 0.0016$). Furthermore, the order of species in the packed matrix of total communities was not related to either the mode of transmission (direct infection *vs via* food ingestion, $P > 0.05$) or host specificity (generalists *vs* specialists, $P > 0.05$). The 6 'key' species exhibited consistently the highest ranks in all subsets.

With the exception of *M. erythrini*, these key species also exhibited the most idiosyncratic distributions, which resulted in a characteristic gradual increase to a peak, of idiosyncratic temperatures of the infracommunities with the lowest richness in DA subsets (pooled and size-class 2–5 sets). Generally, the 'kinds' of species contributing to 'erosion' of the uniform distributions of temperatures across hosts differed between FA and DA. Three main groups were distinguished: (i) species 'unexpectedly' present in most species-poor assemblages, (ii) species with erratic occurrence showing both

Table 2. Community parameters of parasite assemblages, significance of differences and length correlations of infracommunity richness and abundance in the 5 size subsamples of *Boops boops*(Abbreviations as in the Material and Methods section; ns, $P > 0.05$.)

	Size-class 1 ($n=20$)	Size-class 2 ($n=26$)	Size-class 3 ($n=34$)	Size-class 4 ($n=29$)	Size-class 5 ($n=21$)	Significance of differences
Fish total length [TL, range (mean) in cm]	12.8–15.1 (13.9)	15.5–18.5 (17.0)	18.3–22.0 (20.4)	21.7–27.0 (23.6)	25.5–29.6 (26.9)	—
Fish standard length [SL, range (mean) in cm]	10.2–12.9 (11.9)	13.2–15.7 (14.7)	16.0–18.9 (17.4)	19.0–21.9 (20.5)	22.0–25.0 (23.2)	—
Total communities						
Mean no. of species \pm s.d.	4.25 \pm 1.2	5.38 \pm 1.5	5.74 \pm 1.6	6.72 \pm 1.9	6.10 \pm 1.5	K-W H = 27.11 $P < 0.00001$
Mean no. of individuals \pm s.d.	42.90 \pm 22.1	27.77 \pm 15.1	37.68 \pm 25.8	55.34 \pm 44.5	64.86 \pm 52.2	K-W H = 20.50 $P = 0.0004$
No. of species <i>vs</i> Fish length (r_s , P)	ns	$r_s = 0.398$ $P = 0.044$	ns	$r_s = -0.443$ $P = 0.016$	ns	—
No. of individuals <i>vs</i> Fish length (r_s , P)	ns	ns	ns	$r_s = -0.380$ $P = 0.042$	$r_s = 0.511$ $P = 0.018$	—
Assemblages resulting from food ingestion (FA)						
Total no. of species	7	11	9	9	10	—
Mean no. of species \pm s.d.	3.45 \pm 0.8	4.19 \pm 1.0	3.94 \pm 1.0	4.48 \pm 1.3	4.33 \pm 1.1	K-W H = 11.24 $P = 0.0239$
Mean no. of individuals \pm s.d.	40.25 \pm 21.6	25.35 \pm 14.7	32.26 \pm 25.5	42.83 \pm 42.2	53.67 \pm 51.9	K-W H = 11.75 $P = 0.0193$
No. of species <i>vs</i> Fish length (r_s , P)	ns	$r_s = 0.405$ $P = 0.040$	ns	ns	ns	—
No. of individuals <i>vs</i> Fish length (r_s , P)	ns	ns	ns	ns	$r_s = 0.493$ $P = 0.023$	—
Assemblages resulting from direct infection (DA)						
Total no. of species	6	6	9	8	8	—
Mean no. of species \pm s.d.	0.80 \pm 0.7	1.19 \pm 0.8	1.79 \pm 1.1	2.24 \pm 1.18	1.76 \pm 0.8	K-W H = 27.15 $P < 0.00001$
Mean no. of individuals \pm s.d.	2.65 \pm 3.9	2.42 \pm 1.9	5.41 \pm 7.7	12.52 \pm 11.9	11.19 \pm 7.7	K-W H = 51.51 $P < 0.00001$
No. of species <i>vs</i> Fish length (r_s , P)	ns	ns	ns	$r_s = -0.434$ $P = 0.019$	ns	—
No. of individuals <i>vs</i> Fish length (r_s , P)	ns	ns	ns	ns	ns	—

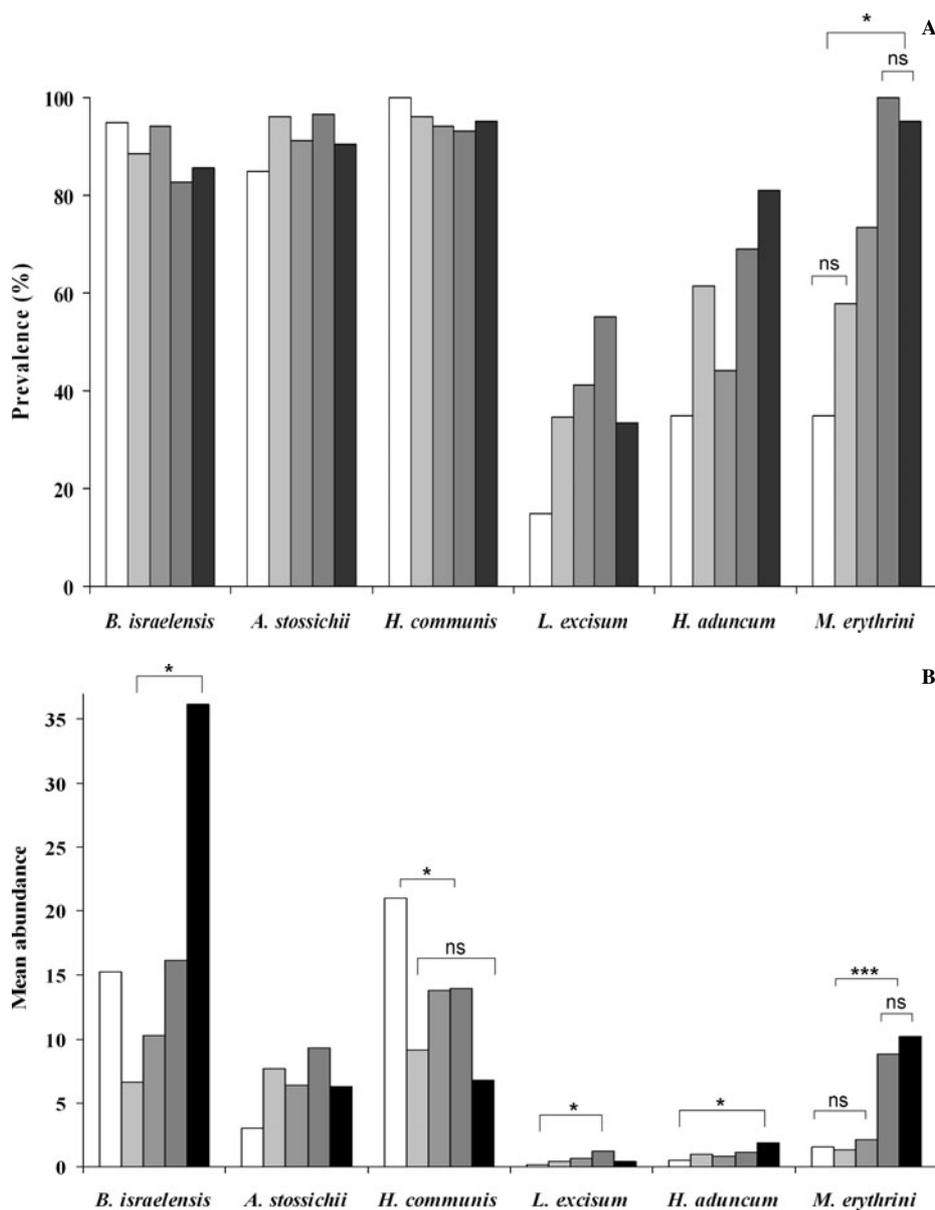


Fig. 2. Prevalence (A) and mean abundance (B) of the key species in parasite communities of *Boops boops* off Santa Pola. Error bars omitted for clarity. Differences between host size classes (the 5 columns, in order) indicated by asterisks (*, $P < 0.05$; ***, $P < 0.001$; ns, not significant).

unexpected absences and presences, and (iii) species with low occurrence showing a few accidental unexpected presences. The first group was only detected in FA and consisted of the 3 most prevalent species (*B. israelensis*, *H. communis*, and *A. stossichii*), whereas the species of the third group were mostly represented in the DA (see Table 3). Species of the second group were detected in both DA (*P. crucibulum*, *C. longicollis* and *N. cygniformis*) and FA (*H. aduncum*, *L. excisum* and *S. pleuronectis*).

DISCUSSION

The 26 species found in this study comprised $\sim 40\%$ of the parasites of *B. boops* throughout its distributional range (67 species; see Pérez-del Olmo

et al. 2007a). A characteristic feature of the parasite community in *B. boops* off Santa Pola was the high representation of parasites with complex life-cycles that are transmitted to fish *via* food ingestion (16 species comprising $>80\%$ of all parasite individuals) and the dominance of trematodes (mostly hemiuroids, comprising more than half of the individuals transmitted *via* the food chain in the total sample). The present data only partially support the suggestion for a strong phylogenetic element of the trematode fauna of sparids (Bartoli *et al.* 2005), since generalist parasites transmitted to *B. boops* from other sympatric species comprised a large percentage of the community (62% of all species and $>50\%$ of all individuals). Of the 3 bogue specialists, only *B. israelensis* exhibited substantial abundance.

Table 3. Nested subset analyses results for the metazoan infra-assemblages in *Boops boops* from off Santa Pola (1000 Monte-Carlo simulation runs)

(ns, not significant; AMIC, *A. microcirrus*; ASTO, *A. stossichii*; BISR, *B. israelensis*; CBEL, *C. bellones*; CLON, *C. longicollis*; COES, *C. oestroides*; HADU, *H. aduncum*; HCOM, *H. communis*; LEXC, *L. excisum*; MERY, *M. erythrini*; NCYG, *N. cygniformis*; PCRU, *P. crucibulum*; PFIS, *P. fistula*; PTR A, *P. trachuri*; SEUZ, *S. euzeti*; SPLE, *S. pleuronectis*; TORM, *Tormopsolus sp.*)

Data set	Matrix temperature	Matrix fill (%)	Random temperature \pm s.d.	<i>P</i> value	Correlation between host rank in packed matrix and SL	Top colonisers	Idiosyncratic species (top colonisers marked with a *)
Total metazoan communities	13.7	21.9	62.3 \pm 2.5	3.75 \cdot 10 ⁻⁶²	$r_s = -0.349$; $P < 0.0001$	HCOM; ASTO; BISR; MERY; HADU	BISR*; HADU*; MERY*; ASTO*; LEXC; CLON; SPLE; NCYG
Assemblages resulting from food ingestion (FA)	13.1	25.6	60.6 \pm 3	4.59 \cdot 10 ⁻⁴⁷	$r_s = -0.191$; $P = 0.03$	ASTO; HCOM; BISR; HADU; LEXC	BISR*; HCOM*; HADU*; LEXC*
Size-class 1	11.8	49.2	49.2 \pm 7.9	9.69 \cdot 10 ⁻⁷	ns	HCOM; BISR; ASTO; HADU; LEXC	LEXC*; BISR*; HADU*; AMIC
Size-class 2	16.7	38.1	54.6 \pm 6.5	2.69 \cdot 10 ⁻⁹	ns	HCOM; ASTO; BISR; HADU; LEXC	ASTO*; SPLE; BISR*; LEXC*
Size-class 3	14.8	43.7	54.8 \pm 5.8	3.83 \cdot 10 ⁻¹²	ns	BISR; HCOM; ASTO; LEXC; HADU	ASTO*; HCOM*; SPLE; LEXC*
Size-class 4	11.2	49.8	54.7 \pm 6.1	5.05 \cdot 10 ⁻¹³	ns	ASTO; HCOM; BISR; HADU; LEXC	BISR*; LEXC*; HADU*; HCOM*
Size-class 5	20.2	43.3	52.9 \pm 7.0	1.46 \cdot 10 ⁻⁶	ns	ASTO; HCOM; BISR; HADU; LEXC	BISR*; HADU*; HCOM*; LEXC*
Assemblages resulting from direct infection (DA)	12.1	18.4	44.6 \pm 4.0	1.86 \cdot 10 ⁻¹⁶	ns	MERY; CLON; NCYG; SEUZ; PTR A	PFIS; PCRU; TORM
Size-class 1	59.3	20.5	29.2 \pm 11.9	ns	ns	MERY; PTR A; TORM	PCRU; CLON
Size-class 2	23.3	23.4	35.9 \pm 9.7	ns	ns	MERY; CLON; NCYG	PCRU; CLON*
Size-class 3	13.7	23.3	41.0 \pm 7.4	1.17 \cdot 10 ⁻⁴	ns	MERY; SEUZ; CLON	NCYG; PCRU
Size-class 4	15.9	28.0	45.3 \pm 7.9	9 \cdot 10 ⁻⁵	$r_s = 0.407$; $P = 0.03$	MERY; SEUZ; NCYG	PCRU; TORM; CLON
Size-class 5	13.0	22.0	34.9 \pm 8.7	0.005	ns	MERY; CLON; NCYG	COES; CBEL

The observed sequence of infection with parasites of bogue size-classes clearly supports the hypothesis that species with wide geographical distributions should appear in the fish population earlier than rare and stochastic species since all helminths (7 species) and the isopod *Ceratothoa oestroides* identified as the 'core' of the bogue parasite fauna were already present in size-class 1 comprised of juvenile 1-year-old fish. Furthermore, 6 of these key parasites in developing communities persisted as common (prevalence typically of >60%) in all subsequent size samples and represented the vast majority (>90%) of the individuals. Finally, all species added to communities in larger fish were either rare or accidental; only 5 persisted in subsequent size-class samples, but showing low intensities of infection.

The present observations are supported by the data on another large Mediterranean sample of *B. boops* from the Gulf of Lion, which includes fish sizes below the range of Santa Pola sample (Renaud *et al.* 1980). These authors found that 6 of the 'core' bogue parasites infect fish of smaller size (juveniles as small as 11 cm (TL); 9 cm for *B. israelensis*) and are consistently present in larger fish (up to 20 cm). These include the 4 key species of our study (i.e. *B. israelensis*, *A. stossichii*, *H. communis* and *H. aduncum*) plus the isopods *Ceratothoa paralella* and *C. oestroides*. Saad-Fares and Combes (1992) also found that *B. israelensis* and *A. stossichii* infect bogue off Lebanon at an early age (young-of-the-year juvenile fish; forklength: <10 cm).

In spite of the uncertainties regarding the diet of bogue, the most detailed surveys clearly demonstrate that copepods represent the prevailing portion of its food (55.7% and 98.0%, respectively; see Jukic, 1972 for data from Eastern Mediterranean and Bell and Harmelin-Vivien, 1983 for data from Western Mediterranean). Information on parasite life-cycles supports this notion, since harpacticoids (*Acartia* spp.) act as intermediate hosts for 4 common species (*H. communis*, *A. stossichii*, *L. excisum* and *H. aduncum*) and indicate 3 additional alternative routes of transmission for the key parasites of bogue: (i) ctenophores (*H. communis*, *L. excisum*, *B. israelensis* and *H. aduncum*), (ii) chaetognaths (*H. communis* and *A. stossichii*), and (iii) amphipods (*B. israelensis* and *H. aduncum*). Furthermore, the presence of 7 accidental species can be also attributed to transmission *via* either the main food resource (e.g. harpacticoid and calanoid copepods (*Contracaecum* sp., *A. simplex*, *M. bartolii* and *A. microcirrus*) or chaetognaths (*T. coryphaenae* and *A. simplex*) and plants (*R. martinizgomezi*).

The only species that exhibited a notable positive correlation with size and an increase in both prevalence and abundance in the larger size-classes (SL > 19 cm, over 4 years old) was the directly transmitted monogenean *M. erythrini*. This species appeared on the gills of the smallest fish (SL = 10.2 cm)

and persisted thereafter, but at much lower prevalence and abundance in younger fish (1–3 years old). Host body size is perhaps the main determinant of monogenean species richness and abundance due to increased gill habitat heterogeneity and surface in larger fish (Rohde, 1989); this may explain the observed increase of infection levels of *M. erythrini* in older fish.

Overall, the correlation with size of the abundance of the other key parasites (all diet-transmitted) was either not significant (*A. stossichii* and *L. excisum*), weakly positive (*B. bacciger* and *H. aduncum*) or moderately negative (*H. communis*). Whereas the association of the abundance of *H. aduncum* and size is due to a slight larval accumulation as a function of fish age (Poulin, 2000), the differences in abundance distributions of *H. communis* between juvenile (SL 10.2–12.9 cm; 1 year old) and larger fish (SL > 13.0 cm, 2–8 years old) may indicate differential microhabitat use. For most demersal fish species, there is a trend for fish size to increase with depth, with juveniles occurring in shallower waters and older fish at greater depths (Cushing, 1976; MacPherson and Duarte, 1991). Studies of fish landings from different types of fishing gear in the Mediterranean support this tendency for *B. boops*, since purse seine landings off Lebanon were exclusively comprised of juvenile young-of-the-year individuals (TL 5.40–14.30 cm; Bariche *et al.* 2006) and a discard study in North West Mediterranean indicates that bogue collected by bottom trawl between 14 and 35 m were all small-sized juveniles (Sánchez *et al.* 2004). Visual fish counts in the area close to Santa Pola have shown that *B. boops* were represented predominantly by fish in the larger size categories (TL 20–29 cm), with no juvenile fish being recorded at depths between 35 and 40 m where adults were found at highest abundances. On the other hand, the juvenile fish cohort (TL < 15 cm) was much less abundant in the overall counts and only observed at somewhat lower depths (30 m) where no adults were recorded (Dempster *et al.* 2002). These data support the hypothesis of a bathymetric juvenile-mature segregation effect on the distribution of *H. communis* within the bogue population off Santa Pola.

Parasite infracommunities were rich and abundant from an early age. The observed complexity of FA, in particular, meets the prediction of Kennedy *et al.* (1986) for diverse helminth communities in hosts with selective feeding on prey that serve as intermediate hosts for a wide variety of helminths. Although infracommunities tended to increase in richness and abundance with host size, the differences in richness/abundance distributions were mostly due to the higher infection levels in older fish (SL > 19 cm, 4–8 years old), perhaps related to an increase in feeding rates. Since trematodes encysting on vegetation and transmitted to fish *via* grazing

are few (Bartoli, 1987; Jousson and Bartoli, 1999), we expected that a notable decrease of both richness and abundance in older fish would support the statement made by Bauchot and Hureau (1986) that juveniles are predominantly carnivorous and adults mostly herbivorous. However, we did not observe an abrupt change in parameters to indicate an ontogenetic diet shift; rather, our data suggest that plant grazing by bogue is only occasional and does not affect the assemblages of food-transmitted parasites (see also Ruitton *et al.* 2005). The observed variability and lower abundance of infracommunities in size-class 2 might relate to increased vagility as an effect of a transition in bathymetric distribution of fish reaching maturity or to the presence of 1-year-old fish in this sample.

Although bogue parasite communities and those of gastrointestinal parasites, in particular, were rich and abundant, we found no supportive evidence for interspecific competition. The present results indicate a neutral structure in all 5 size-class subsamples, since no departures from the null model of independent acquisition were observed in the species density distributions (Janovy *et al.* 1995). Species co-existence in our system appears to be favoured by the different microhabitats utilized by the parasites. Indeed, the most abundant and prevalent species in our study did not exhibit substantial microhabitat overlap. *M. erythrini* is a gill parasite, *A. stossichii* inhabited the oesophagus and anterior stomach, whereas *H. communis* and *L. excisum* were found predominantly in the posterior stomach, and *B. israelensis* in the caeca.

A key result was the recognition of repeatable community structure across size/age cohorts of *B. boops* which translated into a nested subset pattern at the lowest scale, i.e. infracommunities within the individual cohorts. This was not unexpected, considering previous studies on developing communities (Poulin and Valtonen, 2001; Timi and Poulin, 2003; Vidal-Martinez and Poulin, 2003) and the high richness and abundance of infracommunities in bogue resulting from lowered specificity and the presence of several species utilizing more than a single route of transmission. However, the higher-level order that delineates predictability of parasite community structure in Santa Pola's bogue could not be completely attributed to either accumulation over time or segregation of species among different size-class hosts. Thus, although the total communities exhibited significant moderate correlation between host rank positions in the packed matrix and size, the 2 assemblages (FA and DA) differed. FA exhibited a weak correlation with size, whereas no significant correlation was detected in DA. Furthermore, nested patterns were repeated in virtually all size-class subsets within a fairly narrow size range and in the absence of significant correlations between host rank positions and fish size.

Finally, key parasites both contributed to, and reduced nestedness, and there was a strong association between the rank position in the matrix and component population size of parasite species.

Poulin and Guégan (2000) suggested a possible link between non-random community compositional patterns and a positive relationship between spatial distribution and local abundance of faunas. The present study system seems to provide an illustration of this prediction. Thus, the strong positive correlation between the regional distribution and local abundance of the core species of bogue fauna observed at both component and infracommunity levels, and the fact that these largely contributed to the homogeneity in parasite community structure and composition in Santa Pola's bogue population, both support the prediction.

In addition to being an unusual sparid, with respect to the specificity of its parasites, bogue appears to be the best candidate (at least among the Mediterranean omnivorous fishes) to provide a setting for the action of passive sampling as a mechanism leading to non-random parasite community structure. Mouth size is one of the most important factors determining foraging ability and consequently fish diet (Breck, 1993; Magnhagen and Heibo, 2001). Karpouzi and Stergiou (2003) have shown that bogue possesses the smallest mouth dimensions among 18 Mediterranean species (including a group of 12 omnivorous species). Ontogenetic changes in diet often are related to alterations in mouth structures (Castro and Hernández-García, 1995). However, Stergiou and Karpouzi (2002) have not reported significant alterations in mouth structures of *B. boops* with increasing body size. This information, together with the exceptionally slow increase in mouth area with length (Karpouzi and Stergiou, 2003) which does not allow consumption of large prey by *B. boops* during its life span, suggests that individual fish are homogeneous and equally accessible to food-transmitted parasites. This proposal is supported by the fact that bogue attains its maximum trophic level early in its life span (at 20 cm (size-class 3 in our study), see Stergiou and Karpouzi, 2002). On the other hand, suction feeding does not allow for active prey selection.

The small mouth size/area in *B. boops* coupled with suction feeding, while restricting prey size to small invertebrates suspended in the water column, thus facilitates passive ingestion of substantial quantities of potential second intermediate hosts of the key food-transmitted parasite species (copepods, chaetognaths, ctenophores and occasionally small amphipods), which explains their co-occurrence in all size groups and few differences in abundance. However, this non-selective feeding pattern also leads to ingestion of a large additional suite of parasites utilizing the same intermediate host groups. This addition to a baseline community of key parasite species results

in a nested structure which is linked to the differential species abundance rather than fish size.

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