Community ecology of the metazoan parasites of snoek *Thyrsites atun* (Euphrasen, 1791) (Perciformes: Gempylidae) off South Africa

MAI Nunkoo1*, CC Reed1 and SE Kerwath1,2

1 Department of Biological Sciences, University of Cape Town, Cape Town, South Africa  
2 Branch: Fisheries Management, Department of Agriculture, Forestry and Fisheries, Cape Town, South Africa  
* Corresponding author, e-mail: irfan.aquares@gmail.com

The parasite assemblage of snoek *Thyrsites atun*, a commercially important fish in the Benguela system, was examined over a one-year period. In all, 16 parasite taxa including eight new host records (*Bolbosoma vasculosum*, *Caligus coryphaenae*, *Caligus dakari*, *Corynosoma australae*, *Hatschekia conifera*, *Nothobomolochus fradei*, *Rhadinorhynchus cadenati*, *Tentacularia coryphaenae*) and four new locality records (*B. vasculosum*, *C. dakari*, *Molicola uncinatus*, *Pseudoterarana* sp.) were recovered from 210 specimens. The dominance of larval helminths in the component community suggests that *T. atun* occupies an intermediate position in the food web. The ‘nestedness metric based on overlap and decreasing fill’ (NODF) indicated that the parasite assemblage exhibited no nestedness (NODF = 73.3, p = 0.103). Generalised additive mixed modelling results indicated that host length is the main determinant of parasite species richness in *T. atun*. PERMANOVA and ANOSIM suggested that infracommunity structure varied little with respect to the sex, length, seasonality and capture region of the host. The stability and randomness in parasite acquisition, as indicated by the lack of nestedness of the parasite assemblage, can be ascribed to the opportunistic feeding behaviour and nomadic movement of *T. atun* in the southern Benguela. The homogeneity of the community structure of long-lived endoparasites suggests that a single *T. atun* stock occurs off South Africa.

Keywords: host traits, multivariate analysis, parasite infracomunity, population structure

Online supplementary material: Distribution maps of each parasite taxon recovered from *Thyrsites atun* off South Africa can be found online at http://dx.doi.org/10.2989/1814232X.2016.1216892.

Introduction

*Thyrsites atun* (Euphrasen, 1791) is a medium-sized, nomadic, predatory gempylid native to the cold coastal waters of the Southern Hemisphere (Nakamura and Parin 1993). It is targeted by fisheries in South Africa, Chile, Argentina and New Zealand (Nakamura and Parin 1993). Off south-west Africa, where *T. atun* is known as snoek, its distribution ranges from Angola to Algoa Bay on South Africa’s east coast, but it occurs mainly in the Benguela ecosystem (Figure 1) (Griffiths 2002) where it is an ecologically significant species (Verheye and Richardson 1998). *Thyrsites atun* is an opportunistic predator that feeds on a wide variety of organisms including annelids, crustaceans, pelagic and demersal teleosts and cephalopods (Griffiths 2002). Off South Africa, mature *T. atun* (>730 mm fork length) undertake an offshore spawning migration between June and October and juveniles recruit in inshore nursery areas off the West and South coasts (Griffiths 2002).

*Thyrsites atun* of the south-eastern Atlantic have been considered historically to consist of a single stock (Crawford et al. 1990), but recent evidence suggests the presence of two subpopulations, separated by the Lüderitz upwelling cell (Griffiths 2003). Previous studies that have used catch data (Crawford et al. 1990), analyses of spatial and temporal distribution, diet, distribution of eggs and larvae (Dudley 1987) and life-history traits (Griffiths 2002, 2003) as possible indicators of stock structure of *T. atun* in the Benguela met with little success. Parasites have been used increasingly as biological tags for the study of movement and stock structure in marine fish (e.g. Lester et al. 2001; Weston et al. 2015). Using a multimethod approach, information about the parasite community of *T. atun* could help elucidate stock structure and movement in the Benguela ecosystem.

Parasite infections can result in negative consequences to *T. atun* fisheries. In New Zealand, the fishery for *T. atun* is impacted by nematode and cestode infections that decrease the aesthetic appeal of the product (Mehl 1970). Furthermore, *T. atun* in Australia and South Africa is infected by the myxozoan parasite *Kudoa thyrsites*, at considerable cost to the respective fisheries (Gilchrist 1923). For example, in South Africa *Koda*-induced myxoliquefaction may render up to 5% of a *T. atun* catch unmarketable (Gilchrist 1923; Crawford 1989; Henning et al. 2013). High levels of helminth parasitism have in the past motivated the implementation of a closed fishing season for *T. atun* in South Africa (Botha 1986). Two parasite genera previously recorded from *T. atun*, namely *Anisakis* and *Molicola*, are potentially pathogenic...
to humans. Anisakids are causative agents of anisakiasis and can trigger severe allergic reactions in humans with repeated and prolonged exposure (Nawat et al. 2005; Nieuwenhuizen et al. 2006). Pteroceroids of Molicola horridus, which parasitise the muscles of several fish species worldwide (Williams and Bunkley-Williams 1996; Knoff et al. 2004a), produce proteins that could elicit an allergic response in fish consumers (Gomez et al. 2008). Despite the high levels of parasitism and its potential consequences for human health, T. atun remains the most important target species of the traditional linefishery in South Africa and an important bycatch species of the offshore trawl fishery (Griffiths 2002; DAF 2012).

A small number of publications, mostly taxonomic in nature, document parasitism of T. atun off New Zealand and South America (e.g. Robinson 1959; Wierzbicka and Gajda 1984; Pena-Rehbein and De Los Rios-Escalante 2012). Off South Africa, T. atun is host to the myxosporean K. thyrsites, the nematodes Anisakis pegreffii and A. simplex C., and unspecified helminths (Gilchrist 1923; Payne 1986; Mattucci and Nascetti 2007). Barnard (1955) also recorded the copepods Caligus pelamydis and C. zei from T. atun, but doubted his identification of the latter. To date, no studies have quantitatively assessed the whole metazoan parasite community of T. atun. Knowledge of the composition and community structure of T. atun parasites would improve understanding of the ecological role of the host and the relationship between different host populations. This information would also help the management of T. atun fisheries by contributing to a holistic stock delineation and allow an assessment of health hazards associated with T. atun parasites. The aim of this study was to document the diversity of the component community and assess the determinants of parasite species richness and the dynamics of the infracomunity of T. atun off South Africa with respect to area, seasonality and life-history stage of individual hosts.

Table 1: The number of Thyrsites atun specimens examined from each region and season, April 2013–March 2014

| Season   | West Coast (n = 91) | South Coast (n = 119) |
|----------|---------------------|-----------------------|
| Autumn   | 0                   | 31                    |
| Winter   | 23                  | 52                    |
| Spring   | 68                  | 10                    |
| Summer   | 0                   | 26                    |

Material and methods

In all, 210 specimens of T. atun collected off South Africa were examined. They were collected over a one-year period (April 2013–March 2014, Table 1) from commercial handline catches landed at various slipways and harbours along the South African coast and from the bycatch of trawlers operating farther offshore (Figure 1). Thyrsites atun were sampled from two regions with distinct oceanographic features: the West Coast, which is influenced by the cold Benguela Current; and the South Coast, which experiences warmer temperatures under the influence of the Agulhas Current (Figure 1). Although the use of fresh hosts is strongly recommended for parasitological investigations (Justine et al. 2012), the T. atun under study were kept frozen at −20 °C until examination. Freezing the samples immediately after capture was essential to prevent the onset of Kudoa-induced myoliquefaction prior to examination.

Prior to processing, each fish was thawed to room temperature, measured to the nearest millimeter (fork length) and weighed to the nearest gram. The skin, fins, mouth, nares and opercula were first examined for the presence of parasites. The gills and eyes were then removed and examined under a dissecting stereomicroscope (Nikon SMZ800). The body cavity was opened, the fish was sexed and all internal organs were carefully removed. The interior of the body cavity was inspected for any macroparasites. Each organ’s external surface was then examined under a dissecting microscope. The gastro-intestinal tract was opened and examined for parasites, both macrocopically and under a dissecting microscope. Finally, the fish was filleted and the number of macroscopic parasites found within the muscle tissue recorded. All detected macroparasites were collected, sorted and identified to the lowest taxon possible based on their morphology and their abundance recorded. Squash samples of tissue from the dorsal muscle, liver, heart, kidneys, spleen, gonads, brain and gall bladder were examined under a compound microscope (Leica ICS50) at magnifications varying from 40× to 1 000× and the presence of any microparasites was noted.

The identification of acanthocephalans followed Costa et al. (2000), Braianovich et al. (2005) and Amin et al. (2011); that of copepods followed Scott and Scott (1912, 1913), Kessler and Grindley (1973), Jones (1985), Boxxhall and El-Rashidy (2009) and El-Rashidy and Boxxhall (2010). Myxozoan identification was based on Gilchrist (1923), Eiras (2006) and Gunter and Adlard (2010). Cestodes and nematodes were identified using Robinson (1959), Anderson (2000) and Knoff et al. (2004b). Molecular
identification techniques, recommended by Mattiucci and Nascetti (2007), were not used for anisakids, because the very large number of worms recovered made it logistically impossible. Prevalence, mean abundance and the abundance range were calculated for each parasite taxon. Prevalence is the proportion of examined hosts infected by a particular parasite taxon and abundance is the number of individuals of a particular taxon infecting a host (Bush et al. 1997). Parasites infecting <1% of hosts examined were considered accidental infections.

Fulton’s condition factor (K) was calculated for each individual fish according to Equation 1, where W is the weight of the fish (g) and FL is the fork length (mm) (Anderson and Neumann 1996):

\[ K = \frac{W}{FL^3} \times 100 \, 000 \]  

A Chi-square test was employed to test whether the sex ratio of the sample differed from unity. Differences in host FL by sex, as well as spatial differences in host FL by sex, were assessed using the Mann–Whitney test. The Kruskal–Wallis test with post hoc pairwise comparisons was used to test for seasonal differences in host FL by sex.

Generalised additive mixed models (GAMMs) (Wood 2006) with Poisson error distribution were employed to assess the influence of host traits (size, sex and condition), seasonality and region of host capture on the parasite species richness (S) of all T. atun examined (n = 210), excluding only accidental infections. The full GAMM comprised smoothing functions for the variables FL and Condition, the categorical variables Sex, Season and Region, whereas Batch examined was modelled as a random effect, such that:

\[ \log(S) = \beta_0 + s(FL) + s(Condition) + Sex + Season + Region + (Sex \times Season) + \alpha_i \]  

where log is the Poisson link function, S denotes the parasite species richness, \( \beta_0 \) is the intercept term for fixed effects, \( s(\cdot) \) are the smoothing functions and \( \alpha_i \) denotes the random effect for Batch \( i \). A batch consists of all T. atun caught at a given location on a particular date. The pseudo-replication induced by the sampling design, where a batch of T. atun most likely originated from the same group of host individuals by being caught either in the same trawl or by the same handline boat, violates the assumption of independence in the data and can lead to parameter overestimation (Thorson and Minto 2015). Hence it was important to include Batch as a random effect to account for the fixed-station, unbalanced and nested sampling design (Zuur et al. 2009). An interaction between Sex and Season was also included in the full model, because male and female T. atun exhibit differences in their movement and feeding patterns during the spawning season (Griffiths 2002).

Backward stepwise selection in conjunction with Akaike’s information criterion (AIC) was used to select the most adequate model (Dobson 2002). Sequential F-tests were used to determine which covariates contributed significantly (\( p < 0.05 \)) to the explained deviance. A Poisson error structure was assumed because S has a discrete distribution and the response variable was not overdispersed. GAMMs were fitted using the mgcv package in R (R Core Team 2014).

Nestedness of the component community was assessed using the ‘nestedness metric based on overlap and decreasing fill’ (NODF) (Almeida-Neto et al. 2008), because it is less susceptible to matrix size and shape compared to other commonly employed nestedness metrics. The significance of nestedness was evaluated by means of null model analysis based on 999 random matrices generated by the ‘quasiswap’ algorithm (Miklós and Podani 2004). This method was chosen because it decreases the probability of biased subsets by converging towards a uniform distribution (Miklós and Podani 2004). This analysis was conducted on presence-absence transformed data of all T. atun examined (n = 210), excluding rare parasite taxa (prevalence <10%), because they can potentially affect detection of nestedness (Ulrich et al. 2009).

We assessed the influence of host size classes (FL <700 mm, 700–899 mm and >899 mm), sex, capture region and seasonality on the parasite community structure using permutational analysis of variance (PERMANOVA; Anderson et al. 2008). PERMANOVA, implemented via the ‘adonis’ function, is well suited to the analysis of ecological data, because it does not depend on any statistical distribution, but rather on permutation of the data to test hypotheses. Sequential (Type I) sum of squares was used because the number of specimens examined for each factor level differed. Because PERMANOVA can be affected by differences in multivariate dispersion, homogeneity of multivariate variance between levels of a factor was tested using the ‘betadisper’ function in the ‘vegan’ package (Oksanen et al. 2015). The influence of host sex, host size class, capture region and seasonality on the similarity of the infracomunity of T. atun was assessed by means of one-way analysis of similarity (ANOSIM) using 999 permutations. ANOSIM yields a global R-value that ranges between −1 and +1. The global R-value indicates whether community structure across factor levels is distinct (\( R > 0.75 \)) or exhibits high similarity (\( R < 0.25 \)) (Clarke and Gorley 2006).

The PERMANOVA and ANOSIM routines described above were first applied to presence-absence transformed data of the whole parasite community of all T. atun examined (n = 210), excluding only accidental infections (C. coryphaenae – see Results) using Jaccard dissimilarities and 9999 permutations. Secondly, the structure of the long-lived, macroscopic endoparasite community (Anisakis spp., C. australis, M. uncinatus, Pseudoterranova sp., T. coryphaenae) with respect to host sex, season and capture region was examined because they are the most commonly used as biological tags by reason of their long residence time within paratenic fish hosts (MacKenzie and Hemmingsen 2015). An unidentified digenean species, encysted within the gill arches, was excluded from this particular analysis, because its abundance could not be determined. In order to mitigate against the effects of ontogenetic accumulation of selected endoparasites on community structure, only the most abundant host size class (700–899 mm, n = 155) was considered in the analysis of long-lived endoparasites. The analysis was based on Bray–Curtis dissimilarities.
of fourth-root transformed abundance data and 9 999 permutations. All multivariate analyses were conducted within the R statistical programming environment.

Results

Sixteen metazoan parasite taxa, of which 12 were identified to species level, were recovered (Table 2). The endoparasite assemblage included two larval nematodes, two myxozoans, plerocercoids of three cestodes, cystacanths of two acanthocephalans (B. vasculosum and C. australis), one adult acanthocephalan (R. cadenati) and one digenean metacercarium, whereas the ectoparasite community comprised five adult copepod species (Table 2). The combined parasite assemblage included eight new host records (B. vasculosum, C. coryphaenae, C. dakari, C. australis, H. conifera, N. fradei, R. cadenati and T. coryphaenae) and four new geographic records (B. vasculosum, C. dakari, M. uncinatus, Pseudoterranova sp.). On average, one T. atun harboured seven parasite taxa (SD 1.9, range 3–13). A single Caligus coryphaenae was recorded from a trawl-caught T. atun and was excluded from all analyses, because it might have been acquired from a donor host while in the net or on deck. It is also possible, however, that handling and freezing of the host specimens affected the detection rates of C. coryphaenae; hence, the species has been included as a new host record. All parasite taxa, except B. vasculosum and R. cadenati, occurred in both regions.

Bolbosoma vasculosum was only recorded from T. atun caught south of Cape Town and R. cadenati only parasitised fish off the West Coast (see supplementary material, available online).

The sex ratio of the sample was biased in favour of females (1.33:1), but did not differ statistically from unity ($\chi^2 = 1.876$, df = 1, $p = 0.171$). The FL of T. atun examined ranged from 411 mm to 1 040 mm. Female T. atun FL (mean 833.3 mm, SD 77.78) was significantly larger than that of males (mean 779.2 mm, SD 108.11; $U = 6 987$, $p = 0.00027$). Females caught off the South Coast (865.9 mm, SD 66.27) were significantly larger than those caught off the West Coast (813.7 mm, SD 78.0; $U = 2 315$, $p = 0.00068$). Male FL also differed between regions ($U = 1 628.5$, $p < 0.00001$). Off the West Coast, males averaged 722.8 mm (SD 116.3), and off the South Coast 833.1 mm (SD 64.1). Seasonally, fork length varied significantly for both females ($\chi^2 = 28.912$, df = 3, $p < 0.00001$) and males ($\chi^2 = 33.067$, df = 3, $p < 0.00001$). Post hoc pairwise tests showed that females caught in summer (749.4 mm, SD 91.5) were significantly smaller than those caught in winter (825.5 mm, SD 69.7) and spring (874.4 mm, SD 63.8, $p < 0.05$), but did not differ from those caught in autumn (817.2 mm, SD 39.2). Significantly smaller male hosts were sampled in summer (670.0 mm, SD 64.9) and autumn (689.3 mm, SD 148.6) than in winter (609.1 mm, SD 79.1) and spring (831.9 mm, SD 59.8; all $p < 0.05$).

Akaike’s information criterion indicated that including Batch as a random effect improved the GAMMs. Random

| Parasite taxon | Site of infection | South Coast | West Coast |
|----------------|------------------|-------------|------------|
|                | Prevalence (%)   | Mean abundance (SD) | Prevalence (%) | Mean abundance (SD) |
| Nematoda       |                  |              |            |
| Anisakis spp.  | BC 100.0         | 163.9 (161.07) | 100.0       | 119.9 (175.1)       |
| 1Pseudoterranova sp. | BC 27.5 | 1.3 (2.77) | 9.2 | 0.3 (0.93) |
| Myxozoa        |                  |              |            |
| Ceratomyxa sp. | GB 7.7           | –            | 5.9        | –                    |
| Kudoa thyrsites (Gilchrist, 1924) | M 98.9 | – | 95.8 | – |
| Cestoda        |                  |              |            |
| Hepatoxyton trichiuri (Holten, 1802) | BC 57.1 | 1.7 (2.15) | 39.5 | 1.4 (3.04) |
| 1Mollicola uncinatus (Linton, 1924) | M 90.0 | 29.4 (31.12) | 90.0 | 27.5 (32.18) |
| 1Tentacularia coryphaenae Bosc, 1802 | BC 49.5 | 1.7 (3.55) | 9.2 | 0.2 (0.64) |
| Copepoda       |                  |              |            |
| 2Caligus coryphaenae Steenstrup and Lutken, 1861 | O 1.1 | 0.01 (0.11) | 0.0 | 0.0 (0.00) |
| 12Caligus dakari van Beneden, 1892 | G, O 78.0 | 4.1 (5.35) | 37.9 | 1.7 (3.37) |
| Caligus zei Normann and Scott T., 1901 | G, O 34.1 | 0.7 (1.58) | 10.9 | 0.3 (1.02) |
| 2Hatschekia conifera Yamaguti, 1939 | G 46.2 | 1.7 (3.94) | 54.6 | 1.7 (2.69) |
| 2Nothobomolochus fradei Marques, 1965 | N, G 95.6 | 15.9 (16.90) | 96.6 | 15.2 (16.59) |
| Acanthocephala  |                  |              |            |
| 12Bolbosoma vasculosum Rudolphi, 1819 | BC 15.4 | 0.2 (0.62) | 0.8 | 0.01 (0.09) |
| 1Corynosoma australe Johnston, 1937 | BC 56.0 | 12.7 (31.62) | 30.3 | 6.0 (16.85) |
| 1Rhadinorhynchus cadenati (Golvan and Houin, 1964) | I 2.2 | 0.03 (0.23) | 10.1 | 0.2 (0.51) |
| Digenea         |                  |              |            |
| Unidentified species | GA 26.4 | – | 47.1 | – |

1 New locality record
2 New host record
effects were consequently included in the final model. Selection procedures favoured a model that included only two significant predictors, host FL and Season (Table 3). The final model accounted for 38.4% of the variation in the data. A reference set of conditions where Season was set to spring and FL was fixed at its mean value was used for predicting the influence of the two significant variables on S (parasite species richness). Host FL ranged from 411 mm to 1 040 mm with a mean of 810.1 mm (SD 95.61). The GAMM predicted a positive relationship between parasite species richness and host length (Figure 2a). Parasite species richness was predicted to exhibit slight seasonal variability (Figure 2b). *Thyrsites atun* caught in spring were expected to harbour more parasite taxa than those caught in any other season, the difference with respect to autumn, winter and summer being 1.3, 1.2 and 0.7 parasite taxa, respectively.

The component community of *T. atun* exhibited no significant nestedness (NODF = 73.3, p = 0.103). PERMANOVA indicated that host size, season and capture region significantly influenced the parasite community structure of *T. atun* (Table 4). ANOSIM showed that these effects were very small and could have been affected by the significant differences in multivariate dispersion (Table 5). The community structure of the long-lived endoparasite assemblage of *T. atun* exhibited both spatial and seasonal variation (Table 4). Nonetheless, a proportion of the seasonal and spatial variation detected in the endoparasitic community structure may be attributed to the significant differences in multivariate dispersion between seasons and across regions (Table 5). ANOSIM failed to detect large differences (global R < 0.25) in the community structure of long-lived parasites between host sexes, seasons and capture regions (Table 5).

**Table 3**: Summary statistics for variables included in the final GAMM fitted to the parasite species richness of *Thyrsites atun*. FL = fork length.

| Covariate | F     | p      |
|-----------|-------|--------|
| FL        | 50.330| <0.00001|
| Season    | 6.353 | 0.00039|

Figure 2: (a) Relationship between host size and predicted species richness (±95% CI) and (b) the predicted seasonal variability in mean (±95% CI) parasite species richness of *Thyrsites atun* caught off South Africa.

**Discussion**

This study is the first to document comprehensively the composition of the parasite component community of *T. atun* off South Africa. The community in South Africa was less speciose than in New Zealand, where 18 parasite taxa have been recorded from *T. atun* (Mehl 1970; Hewitt and Hine 1972; Hurst 1984; Wierzbicka and Gajda 1984; Sobecka 2012). The use of molecular techniques might have revealed higher species richness in the component community of *T. atun* because no less than six genetically distinct anisakids have been recorded off South Africa (Mattiucci and Nascetti 2006). A species previously recorded from *T. atun* off South Africa, *Caligus pelamydis*, was not found in the current study. The explanation may lie in the affinity of *C. pelamydis* to scombrids (Cressey et al. 1983), raising the possibility that Barnard’s record (Barnard 1955) was an accidental infection acquired from a donor fish with which the *T. atun* specimen might have been in contact soon after capture or during handling and storage. The current study also provides the first record of acanthocephalans from *T. atun* and it has confirmed it as host of *Caligus zer*, consequently clearing the doubts expressed by both Barnard (1955) and Dippenaar (2004). The distribution of *B. vasculosum* and *R. cadenati* recorded here is probably an artefact of sampling. It is highly improbable that fish as vagile as *T. atun* (Griffiths 2002) remain in one of the two sampled regions for long periods of time and hence they would presumably harbour the infection in both regions. No monogeneans were found, although they have routinely been recorded elsewhere from active pelagic fish species, including *T. atun* (e.g. Hewitt and Hine 1972; Hutson et al. 2007). The absence of monogeneans may be an artefact of becoming dislodged through (i) hosts coming into contact with fishing gear (e.g. trawl nets) and other fish in the net or hold, (ii) handling of hosts or (iii) freezing. The examination of fresh samples, processed following Justine et al. (2012), is recommended for future studies of *T. atun* parasitology. The fact that half of the parasites recorded from *T. atun* were new host records highlights the low research effort expended on the parasitology of economically important fish species in South Africa.
Table 4: Results of PERMANOVA conducted on the infracommunity data and on the long-lived endoparasite assemblage of *Thyrsites atun* caught off South Africa

| Parasite guild (dissimilarity measure) | Source     | df | SS  | MS   | Pseudo F | R²   | p(perm) |
|--------------------------------------|------------|----|-----|------|----------|------|---------|
| Infracommunity (Jaccard, *n* = 210)  | Fork length| 1  | 1.685 | 0.842 | 9.662    | 0.073 | 0.0001  |
|                                       | Sex        | 1  | 0.129 | 0.129 | 1.482    | 0.006 | 0.2001  |
|                                       | Season     | 3  | 1.979 | 0.659 | 7.563    | 0.086 | 0.0001  |
|                                       | Region     | 1  | 1.666 | 1.666 | 19.104   | 0.072 | 0.0001  |
| Long-lived endoparasites (Bray–Curtis, *n* = 155) | Sex       | 1  | 0.002 | 0.002 | 0.036    | 0    | 0.9349  |
|                                       | Season     | 3  | 0.891 | 0.297 | 6.679    | 0.105 | 0.0001  |
|                                       | Region     | 1  | 0.987 | 0.987 | 22.195   | 0.116 | 0.0001  |

Table 5: Results of test for differences in multivariate dispersion and ANOSIM for the infracommunity data and the long-lived endoparasite assemblage of *Thyrsites atun* caught off South Africa

| Parasite guild (dissimilarity measure) | Factor      | Multivariate dispersion | ANOSIM        |
|--------------------------------------|-------------|-------------------------|---------------|
|                                       |             | *F* | *p* | Global *R* | *p*   |
| Infracommunity (Jaccard, *n* = 210)  | Size class  | 3.099 | 0.047 | 0.105 | 0.002   |
|                                       | Sex         | 0.007 | 0.933 | 0.010 | 0.167   |
|                                       | Season      | 10.629 | 0.000 | 0.151 | 0.001   |
|                                       | Region      | 0.001 | 0.982 | 0.184 | 0.001   |
| Long-lived endoparasites (Bray–Curtis, *n* = 155) | Sex         | 0.063 | 0.802 | 0.021 | 0.056   |
|                                       | Season      | 10.766 | 0.000 | 0.145 | 0.001   |
|                                       | Region      | 15.696 | 0.000 | 0.109 | 0.001   |

Whereas in New Zealand waters anisakids infect the muscle tissue of *T. atun* (Mehl 1970), off South Africa *Anisakis* spp. parasitising *T. atun* are restricted to the body cavity of the host; they consequently do not represent a health hazard for consumers. Nonetheless, workers in the seafood industry are at risk because repeated exposure during the cleaning process may elicit an allergic reaction (Nieuwenhuizen et al. 2006). The presence of *Mollicola uncinitus*, a cestode, in the muscles also does not affect the market demand for *T. atun*, likely on account of the longstanding and still-perpetuated myth that the cestode is part of the fish tissue and consequently has no pathogenic potential (CD van der Lingen, Department of Agriculture, Forestry and Fisheries, pers. comm.). Further work is required to determine the potential health implications of *M. uncinitus* consumption. The high prevalence and long residence time of *Anisakis* spp. and *M. uncinitus* in *T. atun* would render a closed season ineffective as a potential measure to mitigate against exposure.

Given that nematodes, cestodes and acanthocephalans rely on predator–prey interactions for transmission, their presence can be used as evidence that the host preyed on the intermediate hosts in their respective life cycles (Marcogliese 2002). Because these parasites integrate trophic interactions over long time-scales, they are also good indicators of trophic level (Marcogliese 2004). The dominance of larval endoparasitic taxa in the parasite community suggests that *T. atun* occupies an intermediate position in the food web, where it acts as intermediate host for a number of parasite species that mature in elasmobranchs (*H. trichiuri, M. uncinitus, T. coryphaenae*) and marine mammals (*Anisakis* spp., *C. australae, Pseudoterranova* sp.) (Palm 1999; Anderson 2000; Palm et al. 2009; Raga et al. 2009). Euphausiids (Anderson 2000; Gregori et al. 2012; González-Solís et al. 2013), cephalopods (Abollo et al. 1998) and planktivorous fish, such as clupeoids (Reed et al. 2012) and mackerels (Le Roux 2013), all of which are common in the diet of *T. atun* (Griffiths 2002), are known hosts of immature nematodes, digeneans and trypanorhynch cestodes and might be vectors of the endoparasites recorded in *T. atun*.

Species richness is an important property of biological communities. A number of studies have sought to identify the determinants of parasite community composition and structure (Timi and Poulin 2003; Luque et al. 2004; Luque and Poulin 2008), but the identification of general laws in parasite community ecology have, to date, eluded parasitologists (Poulin 2007). The ontogenetic increase in parasite richness detected in this study is a common finding in investigations of fish-parasite relationships (e.g. Sasai et al. 1997; Timi and Poulin 2003; Luque et al. 2004). Large hosts offer more space for parasite settlement and they have generally had a longer period of exposure to parasites than have small hosts (Soares et al. 2014). Large hosts may also have a broader diet (e.g. Griffiths 2002) and typically ingest larger volumes of prey than small hosts, thereby making them more susceptible to trophically transmitted parasite taxa. The low seasonal variation in parasite species richness for hosts of a given length further supports the notion that host size is the key determinant of the richness of *T. atun* infracomunities.

An ecological community is said to exhibit a nested pattern when the species composition of depauperate assemblages is a proper subset of richer assemblages (Ulrich et al. 2009). A structured assemblage would imply that the susceptibility of host individuals to colonisation
by parasites co-varies with abiotic conditions or host traits within a population (Poulin 1997; Sasal et al. 1999; Miguez-Lozano et al. 2012). However, Rohde et al. (1998) noted that nested patterns are not common in fish parasite assemblages and are more likely to be detected when a wide range of host sizes is considered. Because species richness of \textit{T. atun} infracomunities increases with host fork length, a nested pattern of community assembly would be expected. The lack of nestness indicates that the increase in species richness did not follow a predictable pattern, likely as a result of the random movements of \textit{T. atun} and to their opportunistic feeding behaviour.

Parasite infracomunities are the result of acquisition and loss of parasite species throughout a host individual’s lifetime. In \textit{T. atun}, infracomunity structure was not affected by the sex of the host. This is unsurprising because \textit{T. atun} occur as mixed-sex schools in the southern Benguela, and it suggests that the inshore feeding forays of females during the spawning season (Griffiths 2002) are not sufficient to affect the structure of their infracomunities. The lack of a marked difference in parasite community structure for hosts of increasing body size was unexpected, however, as both the diet and distribution of juvenile and adult \textit{T. atun} differ (Griffiths 2002). This result, in conjunction with the seasonal and spatial stability of the community structure, suggests that the endemic area (the region within which infection can occur [Mackenzie and Abaunza 1998]) of \textit{T. atun} parasites in the southern Benguela straddles the range of both juvenile and adult \textit{T. atun}, and that the successful transmission of parasites is unaffected by seasonality. Variation in fish parasite communities, or the lack thereof, has been used to track fish migrations and delineate discrete populations (Timi et al. 2005; Carballo et al. 2012). In the case of \textit{T. atun}, which can travel over large distances, the stability of the endoparasite assemblage suggests that \textit{T. atun} off South Africa comprise a single stock.

We demonstrated that although parasite acquisition in \textit{T. atun} exhibited no pattern, infracomunity structure was repeatable between host sexes, across size classes and between seasons over a one-year period. The study also provides a baseline for spatial comparative studies. The results suggest that the South African \textit{T. atun} population can be considered as a discrete management unit. A comparison of the parasite communities of \textit{T. atun} between the northern and southern Benguela may provide further insight into the stock structure of the species in the South-East Atlantic.

Acknowledgements — We thank C Wilke (Department of Agriculture, Forestry and Fisheries) for his help with sample collection. We are also grateful to Ken Mackenzie (University of Aberdeen) for assistance with species identification. This study was funded by the South African National Research Foundation via a Thuthuka Women in Science grant awarded to CCR.

References

Abollo E, Gestal C, López A, González AF, Guerra A, Pascual S. 1998. Squid as trophic bridges for parasite flow within marine ecosystems: the case of \textit{Anisakis simplex} (Nematoda: Anisakidae), or when the wrong way can be right. In: Payne AL, Lipiński MR, Clarke MR, Roeleveld MAC (eds), Cephalopod biodiversity, ecology and evolution. South African Journal of Marine Science 20: 223–232.

Almeida-Neto M, Guimarães P, Guimarães PR, Loyola RD, Ulrich W. 2008. A consistent metric for nestness analysis in ecological systems: reconciling concept and measurement. Oikos 117: 1227–1239.

Amin OM, Heckmann RA, Ha N. 2011. Description of two new species of \textit{Rhadinorhynchus} (Acanthocephala, Rhadinorhynchidae) from marine fish in Halong Bay, Vietnam, with a key to species. Acta Parasitologica 56: 67–77.

Anderson RC. 2000. Nematode parasites of vertebrates: their development and transmission. Wallingford: CABI Publishing.

Anderson MJ, Gorley RN, Clarke KR. 2008. PERMANOVA+ for PRIMER: guide to software and statistical methods. Plymouth: PRIMER-E.

Anderson RO, Neumann RM. 1996. Length, weight, and associated structural indices. In: Murphy BR, Willis DW (eds), Fisheries techniques. Bethesda: American Fishers Society. pp 447–482.

Barnard KH. 1955. Additions to the fauna-list of South African Crustacea and Pycnogonida. Annals of the South African Museum 63: 1–107.

Botha L. 1986. Major endoparasites of the Cape hakes \textit{Merluccius capensis} and \textit{M. paradoxus}, with brief notes on some conspicuous ectoparasites. South African Journal of Marine Science 4: 45–49.

Boxshall GA, El-Rashidy HH. 2009. A review of the \textit{Caligus productus} species group, with the description of a new species, new synonyms and supplementary descriptions. Zootaxa 2271: 1–26.

Braicovich PE, González RA, T anzola RD. 2005. First record of \textit{Corynosoma australiae} (Acanthocephala, Polymorphidae) parasitizing seahorse, \textit{Hippocampus sp.} (Pisces, Syngnathidae) in Patagonia (Argentina). Acta Parasitologica 50: 145–149.

Bush AO, Lafferty KD, Lotz JM, Shostak AW. 1997. Parasitology meets ecology on its own terms: Margolis et al. revisited. The Journal of Parasitology 83: 575–583.

Carballo MC, Cremon te F, Navone GT, Timi JT. 2012. Similarity in parasite community structure may be used to trace latitudinal migrations of \textit{Odontesthes smitti} along Argentinean coasts. Journal of Fish Biology 80: 15–28.

Clarke KR, Gorley RN. 2006. PRIMER v6: user manual/tutorial. Plymouth: PRIMER-E.

Costa G, Chubb JC, Veltkamp CJ. 2000. Cystacanths of \textit{Bolbooma vasculosum} (Crustacea, Brachyura) from Madeira, Portugal. Crustaceana 77: 1281–1328.

Crawford RJM, Underhill LG, Venter JD. 1990. Handline catches of \textit{Delphinus delphis} (Cetacea, Delphinidae) in the South African waters of the southern Benguela with notes on associated parasites. South African Journal of Marine Science 80: 15–28.

Cressey RF, Collette BB, Russo JL. 1983. Copepods and scadimbroid fishes: a study in host-parasite relationships. Fishery Bulletin 81: 227–265.

DAFF (Department of Agriculture, Forestry and Fisheries). 2012. Status of the South African marine fishery resources 2012. DAFF, Cape Town. Available at www.nda.agric.za/doaDev/sideMenu/fisheries/03_areasofwork/Resources%20Research/STATUS%20REPORT%202012%20FINALB.pdf [accessed 24 August 2016].

Dippenaar SM. 2004. Reported siphonostomatoid copepods parasitic on marine fishes of southern Africa. Crustaceana 77: 1281–1328.

Dobson AJ. 2002. An introduction to generalized linear models. Boca Raton: Chapman & Hall/CRC Press.
Dudley SFJ. 1987. Snoek Thyrsites atun in South African waters: aspects of its biology, distribution and fishery. MSc thesis, University of Cape Town, South Africa.

Eiras JC. 2006. Synopsis of the species of Ceratomyxa Thelohan, 1892 (Myxozoa: Myxosporea: Ceratomyxidae). Systematic Parasitology 65: 49–71.

El-Rashidy HH, Boxshall GA. 2010. Parasitic copepods on immigrant and native clupeid fishes caught in Egyptian coastal waters off Alexandria. Systematic Parasitology 76: 19–38.

Gilchrist JDF. 1923. A protozoal parasite (Chlororomyxum thyrsites, sp. n.) of the Cape sea-fish, the “snoek” (Thyrsites atun, Euphr.). Transactions of the Royal Society of South Africa 11: 263–273.

Gómez-Morales MA, Ludovisi A, Giuffra E, Manfredi MT, Piccolo G, Henning SS, Hoffman LC, Manley M. 2013. A review of Thyrsites atun Griffiths MH. 2003. Stock structure of snoek in the Leptotheca Gunter N, Adlard R. 2010. The demise of Hutson KS, Ernst I, Mooney AJ, Whittington ID. 2007. Metazoan Hewitt GC, Hine PM. 1972. Checklist of parasites of New Zealand Kingdoms 99: 37–47.

Kensley B, Grindley JR. 1973. South African parasitic Copepoda. Annals of the South African Museum 62: 69–130.

Knoff M, Sai Clemente SC, Pinto RM, Lanfredi RM, Gomes DC. 2004a. Taxonomic reports of Otobothrioidae (Eucestoda, Trypanorhyncha) from elasmobranch fishes of the southern Benguela. MSc thesis, University of Cape Town, South Africa.

Lester RJG, Thompson C, Moss H, Barker SC. 2001. Movement and stock structure of narrow-barred Spanish mackerel as indicated by parasites. Journal of Fish Biology 59: 833–842.

Luque JL, Mouliot D, Poulin R. 2004. Parasite biodiversity and its determinants in coastal marine teleost fishes of Brazil. Parasitology 128: 671–682.

Luque JL, Poulin R. 2008. Linking ecology with parasite diversity in Neotropical fishes. Journal of Fish Biology 72: 189–204.

MacKenzie K, Aboanza P. 1998. Parasites as biological tags for stock discrimination of marine fish: a guide to procedures and methods. Fisheries Research 38: 45–56.

MacKenzie K, Hemmingsen W. 2015. Parasites as biological tags in marine fisheries research: European Atlantic waters. Journal of Fish Biology 142: 54–67.

Marcogliese DJ. 2002. Food webs and the transmission of parasites to marine fish. Parasitology 124: S83–S99.

Marcogliese DJ. 2004. Parasites: small players with crucial roles in the ecological theater. EcoHealth 1: 151–164.

Mattucci S, Nascetti G. 2006. Molecular systematics, phylogeny and ecology of anisakid nematodes of the genus Anisakis Dujardin, 1845: an update. Parasite 13: 99–113.

Mattucci S, Nascetti G. 2007. Genetic diversity and infection levels of anisakid nematodes parasitic in fish and marine mammals from Boreal and Austral hemispheres. Veterinary Parasitology 148: 43–57.

Mehl JAP. 1970. Two fleece parasites of barracouta (Teleostei: Gempylidae) from eastern Cook Strait. New Zealand Journal of Marine and Freshwater Research 4: 241–247.

Miklós I, Podani J. 2004. Randomization of presence–absence matrices: comments and new algorithms. Ecology 85: 86–92.

Miguez-Lozano R, Pardo-Carranza TV, Blasco-Costa I, Balbuena JA. 2012. Spatial structure of helminth communities in the golden grey mullet, Liza aurata (Actinopterygii: Mugilidae), from the Western Mediterranean. The Journal of Parasitology 98: 904–12.

Nakamura I, Parin NV. 1993. FAO species catalogue, Vol. 15. Snake mackerels and cutlassfishes of the world (families Gempylidae and Trichiuridae). An annotated and illustrated catalogue of the snake mackerels, snoeks, escolars, gemfishes, sackfishes, domine, oifish, cutlassfishes, scabbardfishes, hairtails, and frostfishes known to date. FAO Fisheries Synopsis, No. 125, Vol. 15. Rome: Food and Agriculture Organization.

Nawo Y, Hatz C, Blum J. 2005. Sushi delights and parasites: the risk of fishborne and foodborne parasitic zoonoses in Asia. Travel Medicine 41: 1297–1303.

Nieuwenhuizen N, Lopata AL, Jeelbhy MF, Herbert DR, Robins TG, Brombacher F. 2006. Exposure to the fish parasite Anisakis causes allergic airway hyperreactivity and dermatitis. The Journal of Allergy and Clinical Immunology 117: 1098–1105.

Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'Hara R al. 2015. Vegan: community ecology package. R package version 2.0-10. Available at http://CRAN.R-project.org/package=vegan [accessed 5 December 2015].

Palm HW. 2019. Ecology of Pseudoterranova decipiens (Krabbe, 1878) (Nematoda: Anisakidae) from Antarctic waters. Parasitology Research 85: 638–646.

Palm HW, Waeschenbach A, Olson PD, Littlewood DTJ. 2009. Molecular phylogeny and evolution of the Trypanorhyncha Diesing, 1863 (Platyhelminthes: Cestoda). Molecular Phylogenetics and Evolution 52: 351–367.
Payne AIL. 1986. Observations on some conspicuous parasites of the southern African kingklip Genypterus capensis. South African Journal of Marine Science 4: 163–168.

Pena-Rebain P, De Los Rios-Escalante P. 2012. Use of negative binomial distribution to describe the presence of Anisakis in Thyrsites atun. Brazilian Journal of Veterinary Parasitology 21: 78–80.

Poulin R. 1997. Species richness of parasite assemblages: evolution and patterns. Annual Review of Ecology and Systematics 28: 341–358.

Poulin R. 2007. Are there general laws in parasite ecology? Parasitology 134: 763–776.

Robinson ES. 1959. Some new cestodes from New Zealand marine fishes. Transactions of the Royal Society of New Zealand 86: 381–392.

Rohde K, Almeida-Neto M, Gotelli NJ. 2009. A consumer’s guide to nestedness analysis. Oikos 118: 3–17.

Verheye HM, Richardson AJ. 1998. Long-term increase in crustacean zooplankton abundance in the southern Benguela upwelling region (1951–1996): bottom-up or top-down control? ICES Journal of Marine Science 55: 803–807.

Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM. 2009. Mixed effects models and extensions in ecology with R. Berlin: Springer.