Journal of Helminthology (2001) **75**, 209–214 DOI: 10.1079/JOH200051

Anisakid infection in the European shag *Phalacrocorax aristotelis aristotelis*

E. Abollo, C. Gestal and S. Pascual*

Área de Parasitología, Grupo PB2, Facultad de Ciencias, Universidad de Vigo, Aptdo 874-36200 Vigo, Spain

Abstract

A total of 100 specimens of the European shag *Phalacrocorax aristotelis aristotelis* were examined for anisakid infections in the south-east North Atlantic. The taxonomic status of the anisakid nematodes was studied by structural analysis using light and scanning electron microscopy. Two species, *Contracaecum septentrionale* and *C. rudolphii* A (Nematoda: Ascaridoidea), occurred in the European shag with high values of prevalence and mean intensities of infection. These constitute new host records for both parasites, widening their known geographical distribution. Although the histopathology associated with the infections indicated that the anisakids did not have the potential to cause bird death, the parasites are capable of contributing to and hastening avian mortality in the case of heavily-parasitized cormorants and when stressed by xenobiotics and/or through a synergetic effect by other bioagressors.

Introduction

The world population of the Atlantic subspecies, *Phalacrocorax aristotelis aristotelis* (Linnaeus, 1758) is between 70,000 and 90,000 pairs. This subspecies is the most meridian in its distribution, with an estimated population of about 2200–2300 pairs in the Iberian Peninsula waters (Velando *et al.*, 1995). On the Galician coast, Velando *et al.* (1995) recorded 86% of the European shag to be from the Atlanto-Iberian Peninsula waters. As wild seabird populations decline and interest in their conservation increases, the importance of studies on the impact of diseases on wildlife at a population level has been recognized (Dobson & May, 1986; May, 1988). In fact, large bird populations, in man-protected bird sanctuaries, may turn these habitats into real epidemiotopes (Kinne, 1985). The incomplete understanding of wildlife disease epidemiology also arises from a traditional approach to investigating disease in wildlife and the difficulties involved in collecting such information (Plowright, 1988). A review by Grenfell & Gulland (1995) on the impact of parasitic infectious diseases on survival and reproduction of wild seabird populations emphasized that most of these studies are made without qualitative (e.g. via pathological examination of carcasses that are found accidentally) and/or quantitative assessments.

*Author for correspondence
Fax: (9) 86 812556
E-mail: spascual@correo.uvigo.es

Piscivorous seabirds are known to occupy an important position in marine food webs, equivalent to that of larger fish and mammals. Observations and estimations of the order of magnitude of seabird predation on marine fish (Sanger, 1972; Idyll, 1973; Wiens & Scott, 1975; Prévost, 1976; Laws, 1977; Furness, 1978a,b, 1982; Furness & Cooper, 1982) suggest the immense impact of seabirds on marine ecosystems and resources. Parasites may also play an important role in marine ecosystems by regulating or destabilizing the dynamics of wildlife seabird populations (May, 1988; Dobson & Hudson, 1992; McCurdy *et al.*, 1998). Despite this, and as a consequence of this lack of interest in seabird biology (Ainley, 1980), their diseases and aetiological-related bioaggressors have also received little attention (Lauckner, 1985a).

Members of the genus *Contracaecum* are adult nematodes in the stomachs of seals and piscivorous seabirds. The nematodes are acquired by feeding on infected fish, which in turn acquire them by feeding on other fish and crustaceans (Anderson, 1992). While the epizootiology of species of *Contracaecum* in marine mammals has received considerable attention (Dailey, 1985; Lauckner, 1985b), those species in piscivorous seabirds have largely been neglected (Lauckner, 1985a) especially studies on the taxonomy, epidemiology, pathology and life cycles. A total of 63 species within the genus *Contracaecum* have been recorded from birds worldwide (Yamaguti, 1961). Barus *et al.* (1978) also noted that more than 50 species of *Contracaecum* occur in fish-eating birds in the Palaearctic Region. Nevertheless, early reports on *Contracaecum* species are usually difficult to evaluate because of inadequate taxonomic descriptions (Fagerholm, 1988; Fagerholm *et al.*, 1996).

The purpose of the present study is to present some diagnostic, demographic and pathological aspects of the anisakid infections in the European shag, based upon taxonomic and histological examinations.

Material and methods

A total of 100 cormorants, *P. a. aristotelis*, beached on the coast of Galicia, Ría de Vigo during June 1996 to December 1997, were examined for anisakid nematodes. For taxonomic identification, parasites were removed with forceps from semidigested food items in the alimentary tract of the shag following the recommendations of Doster & Goater (1997).

For diagnostic morphological studies, the anisakids were preserved in 70% ethanol, cleared in lactophenol, and examined by light microscopy (LM), following standard protocols (Berland, 1982; Gibson, 1984; Fagerholm & Lovdahl, 1984). General descriptions of *C. rudolphii* sensu lato and *C. septentrionale* were taken from LM observations of Hartwich (1964) and Kreis (1955), respectively. For microtopographical diagnosis under the scanning electron microscopy (SEM), the head and tail portions of each adult nematode were processed by passing the material through a series of increasing concentrations of ethanol prior to critical point drying and then coating with gold. The number and distribution patterns of the caudal papillae and papillae-like structures in adult males of ascaridoid nematodes were analysed according to Fagerholm (1991). These microtopographic structures are recognized as valid taxonomic characters for species identification in ascaridoid nematodes. Other microscopical valid taxonomic characters were taken according to Hartwich (1974) and Gibson (1983).

Portions of heavily-parasitized stomachs were fixed in formaldehyde 10% for 24 h, the tissues processed by routine methods for histopathological evaluation (Culling *et al.*, 1985) and then stained with haematoxylin-eosin (H-E).

Demographic parasitic values were expressed in terms of prevalence and mean intensity of infection following Bush *et al.* (1997).

Results

Parasite identification

The nematode material was assigned to two species, *C. septentrionale* Kreis, 1955 and *C. rudolphii* A Hartwich, 1964. By LM, both species showed a triangular mouth opening into the oesophagus, with a short rounded ventricle, which bears a posterior appendix and an anterior intestinal caecum. The caecum and ventricular appendix are approximately of equal length.

Structural characterization of C. septentrionale

In both sexes, adult nematodes of *C. septentrionale* show strong cuticular striations in the anterior third of the body. Posterior to the cephalic region, the cuticle is raised into a series of concentric grooves and folds, forming an annulated collar. Adult worms have three lips, without cuticular dentigerous ridges, and the interlabiae are well developed (fig. 1A). The interlabiae,

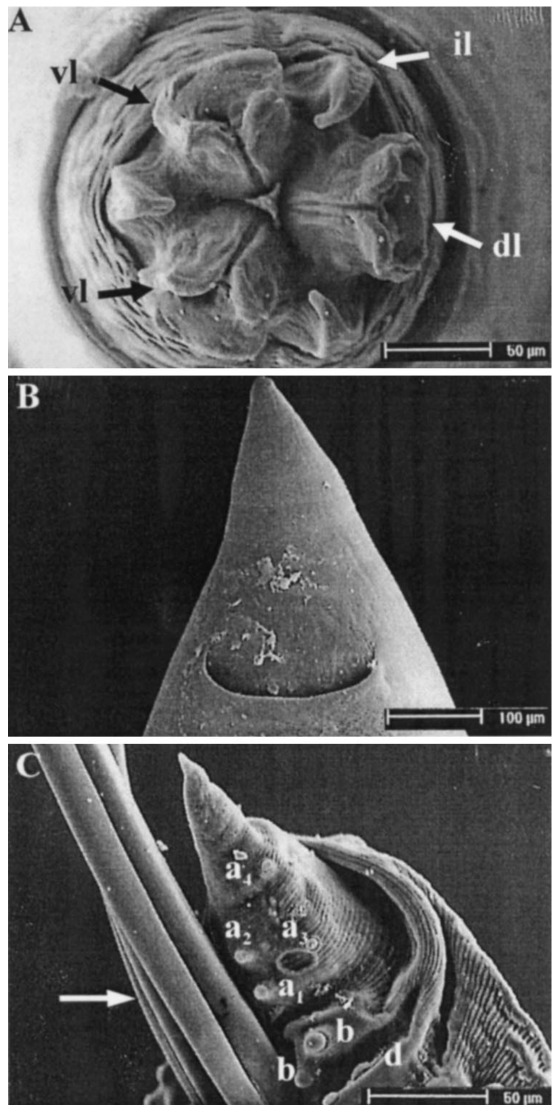

Fig. 1. Scanning electron micrographs of adult *Contracaecum septentrionale*. (A) Apical view of the cephalic region with triradiate opening of the oesophagus, two ventrolateral lips (vl), one dorsolateral lip (dl) and the interlabiae (il). (B) Female, ventral view of the posterior end. (C) Male, ventrolateral view of the posterior end with caudal papillae: distal papillae (a_1–a_4), paracloacal papillae (b), proximal papillae (d) and spicules (arrow).

https://doi.org/10.1079/JOH200051 Published online by Cambridge University Press

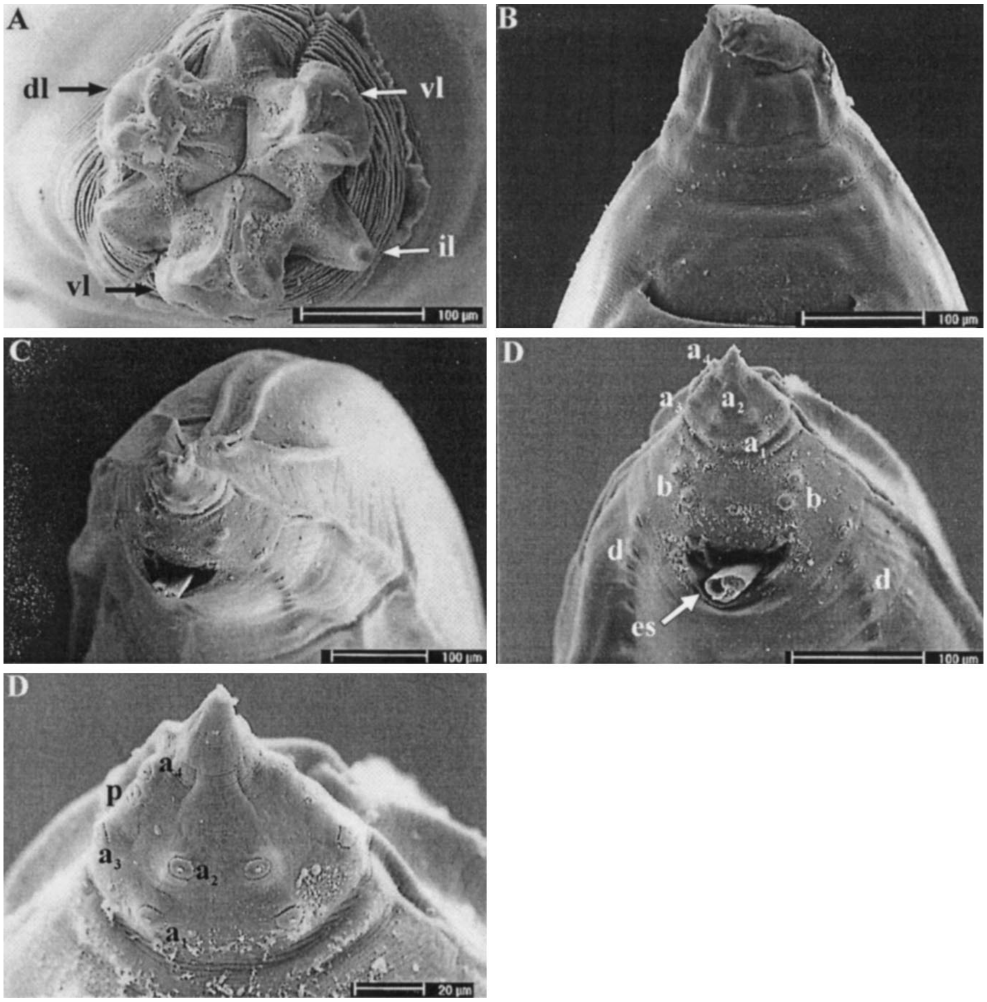

Fig. 2. Scanning electron micrographs of adult *Contracaecum rudolphii* A. (A) Apical view of the cephalic region with triradiate opening of the oesophagus, two ventrolateral lips (vl), one dorsolateral lip (dl) and the interlabiae (il). (B) Female, ventral view of the posterior end. (C) Male, dorsoventral view of the posterior end of a male, showing the dorsal cuticular striation. (D) Male, ventral view of the posterior end with caudal papillae: distal papillae (a_1–a_4), paracloacal papillae (b), proximal papillae (d) and espicules (es). (E) Distal papillae (a_1–a_4), including a papillated phasmid (p).

without bifurcate tips, reach four-fifths of the length of the lips. The excretory pore is situated immediately posterior to the ventral interlabiae. In females, the tail is conical and pointed (fig. 1B), whereas in males, the tail is short with a pronounced fold and sharp tip (fig. 1C). The spicules of the male have a rounded tip. Thirty to thirty five pairs of proximal caudal papillae arranged in two longitudinal, single rows, two pairs of separated paracloacal papillae and four pairs of distal papillae are present on the posterior end of the male (fig. 1C).

Structural characterization of C. rudolphii *A*

By SEM, adults of *C. rudolphii* A characteristically showed three lips without cuticular dentigerous ridges, and well developed interlabiae (fig. 2A). The interlabiae have a trapezoidal shape. Immediately behind the lips, transverse cuticular striae form a collar of deep folds, except for a lateral V-shaped region devoid of striation in the neck region. The cephalic region is slightly larger in diameter than the collar. Rounded, papillate deirids are present. The postanal tail is short and conical, with a sharp tip (fig. 2B). Dorsally, on the posterior end of the males the cuticle is striated (fig. 2C), and ventrally the males possess numerous proximal caudal papillae arranged in two longitudinal, single rows, two pair of separated paracloacal papillae, four pairs of distal papillae, and a pair of phasmids between and level with sublateral distal papillae (fig. 2D,E).

Delimiting species

In *C. rudolphii* A, the distal papillae are distributed so that they form a quadrant with the phasmid in the middle of the two lateral distal papillae. However, in *C. septentrionale*, the phasmid lies just dorsal to the

Table 1. Demographic parameters of infection by the anisakid nematodes *Contracaecum septentrionale* and *C. rudolphii* A.

Parasite species	P	I	A
C. septentrionale	15 (3–30)	5.80±1.92 (3–8)	0.97±2.31
C. rudolphii A	100	19.05±16.16 (1–68)	19.05±16.16

P, prevalence (%, 95% C.I.); I, mean intensity (mean ± S.E.; range); A, abundance (mean ± S.E.).

posterior-most lateral distal papillae. Moreover, the papillae of *C. rudolphii* A have a larger diameter than those of *C. septentrionale*. Under LM, the blunt distal end of the spicule indicates that the length of the tip is at least 1.5× the total of the diameter of the spicule in the region near the distal end for *C. rudolphii* A whereas for *C. septentrionale* the tip of the spicule is rather short (0.4× spicule width).

Demographic parameters

Table 1 shows the demographic parameters of infection by anisakid nematodes in the digestive tract of the European shag. The male:female:L_4 proportion was 10:6.6:5.0 and 10:8.3:7.5 for *C. rudolphii* A and *C. septentrionale*, respectively. Anisakid infections were observed in all developmental stages of the host birds, i.e. in adult, immature and chick cormorants.

Histopathology

Larvae (L_4) and adults of *C. septentrionale* and *C. rudolphii* A were found in the oesophagus and proventriculus of *P. a. aristotelis*. The heads of the worms often penetrated into the wall of the proventriculus, forming tiny ulcers (1–1.5 mm) resulting in some destruction of the proventricular lining. The anterior portions of anisakids invaded the mucous epithelium, glandular tissue, lamina propia and submucosa of the proventriculus. At the point of worm attachment, connective tissue was observed to encapsulate the heads of anisakids with a variable cellular infiltration. Around the area of penetration, necrotized tissues and ulcerated-adjacent glandular tissues were present. The space around the nematodes frequently showed haemorrhages, lymphocytes and eosinophilic granulocytes, host necrotic tissues and cell debris.

In a single host with symptoms of having ingested oil, we observed the penetration of the anisakids into the lamina muscularis, although the parasites did not cross the stomach wall. This individual host showed generalized haemorrhaging and an extensive necrosis of the surrounding tissues.

When the nematodes detached, they left minute scars on the stomach wall. These lesions in regression were located in the mucous epithelium and the glandular tissue. Histologically, the scars consisted of an amorphous substance surrounded by fibrin and host necrotic tissues. In some cases, massive inflammatory responses with heavy cellular infiltrates were also observed.

Discussion

The taxonomic validity of several species within the genera *Contracaecum* has been questioned by Fagerholm & Gibson (1987). This is not only due to the morphological similarity of cryptic or sibling species but also to inadequate descriptions. The application of SEM (Fagerholm & Gibson, 1987; Fagerholm, 1991; Klöser & Plötz, 1992; Hugot *et al.*, 1991) and allozyme electrophoresis (Nascetti *et al.*, 1990, 1993; Orecchia *et al.*, 1994; D'Amelio *et al.*, 1990, 1991; Cianchi *et al.*, 1992), has made possible more accurate identification of species within the genus.

Fagerholm (1991) and Fagerholm *et al.* (1996) demonstrated that SEM provides a means of defining more precisely the surface topographical features of species, although these features should also be used in combination with traditional methods. The basic arrangement and number of caudal papillae and papillae-like structures in adult males examined in this work were found to be rather stable and conform well with the descriptions of *C. rudolphii* sensu lato and *C. septentrionale* given by Kreis (1955) and Fagerholm (1988, 1991). The above described structures are also similar to the pattern described for other species within this genus from piscivorous seabirds (Fagerholm, 1988, 1991).

Otherwise, genetic studies based on allozymes have shown that many of the genera of ascaridoid nematodes infecting seabirds comprise several morphologically similar but genetically distinct species (D'Amelio *et al.*, 1990, 1991; Cianchi *et al.*, 1992). As formal morphological descriptions of the various species within each genus have yet to be completed, specific names have not been assigned and the species have provisionally been designated as types A, B, etc. D'Amelio *et al.* (1990, 1991) and Cianchi *et al.* (1992) found that *C. rudolphii* sensu lato, parasitic in the cormorant *Phalacrocorax carbo* in central and southern Europe, is composed of two sibling species, A and B. Preliminary genetic analyses of our specimens from the European shag examined in the southeastern Atlantic coast have revealed that *P. a. aristotelis* harbour the sibling species *C. rudolphii* A (E. Abollo, unpublished data). The present study is the first to report *C. rudolphii* A and *C. septentrionale* parasitizing *P. a. aristotelis* in temperate Atlanto-Iberian waters.

Moreover, as high prevalences and intensities of infection of *P. a. aristotelis* with *C. rudolphii* A were recorded, it seems that this host species plays an important role in the life cycle of the parasite. In addition, as the demographic values of other parasitic species within the genera *Contracaecum* parasitizing other seabirds species (e.g. *Larus cachinnans*, *Alca torda*, *Uria aalge* and *Fratercula arctica*) in the sampling area are low (E. Abollo, unpublished data), we can establish that *C. rudolphii* A represents a major component of the *Contracaecum* fauna in the area. Additionally, we may consider the Cíes archipelago (a LIC or special area of conservation in the Ría de Vigo) as an endemiotope in the parasite life-cycle.

Our observations suggest that the natural site of infection of anisakids seems to be the proventriculus. The presence of this parasite in the oesophagus may be due to post-mortem migration of the nematode. This phenomenon is common for other members of anisakids parasitizing vertebrate hosts (Abollo *et al.*, 1998). Otherwise, the biased sex ratio of L_4 and adult nematodes in the European shags found an excess of males of *C. rudolphii* A and *C. septentrionale*. Our data is in agreement with published data, which indicate the absence of a consistent pattern in the sex ratios among species of ascaridoid nematodes (Myers, 1957; Young & Lowe, 1969; Young, 1972; Brattey & Ni, 1992).

Similar pathology to the one observed herein has previously been described in seabirds, primarily in association with nematodes of the genus *Contracaecum* (Fagerholm *et al.*, 1996). However, we did not find clusters of anisakids forming distinct ulcerated nodular lesions as observed in the study of Fagerholm *et al.* (1996).

Apparently, *C. septentrionale* and *C. rudolphii* A, although they infect their host in high numbers, may not be the prime cause of death. Owre (1962), Huizinga (1971) and Fagerholm *et al.* (1996) suggested that *Contracaecum* spp. fed on gut contents rather than on host tissue and the present observations are consistent with this interpretation. However, destruction of the proventricular lining has a detrimental effect on the host (Fagerholm *et al.*, 1996). Perhaps such cases, especially those stressed by secondary bacterial infections and/or xenobiotics (e.g. oil), might result in lethal peritonitis or predilection to a variety of stresses (Fagerholm *et al.*, 1996). Our conclusion is that *C. septentrionale* and *C. rudolphii* A have the potential to contribute to host mortality. This supports the view initially postulated by Oglesby (1960) and Fagerholm *et al.* (1996) for *C. micropapillatum* and *C. magnipapillatum*, respectively, that these nematodes are capable of contributing to and hastening avian mortality.

Acknowledgements

Thanks are due to Dr Fagerholm (Institute of Parasitology, Abo Akademi, Finland) and Professor Paggi and Dr Mattiucci (Istituto di Parassitologia, Universitá degli Studi di Roma, La Sapienza, Roma, Italia) for their help during identification of the nematode material. We wish to thank Dr A. Velando (University of Vigo) for his help during sample collection. We also thank CACTI-Universidad de Vigo for their help advice on SEM. Financial assistance was provided by the Consellería de Educación e Ordenación Universitaria, Xunta de Galicia under the Project XUGA 30110A97.

References

Abollo, E., López, A., Gestal, C., Benavente, P. & Pascual, S. (1998) Macroparasites in cetaceans stranded on the northwestern Spanish Atlantic coast. *Diseases of Aquatic Organisms* **32**, 227–231.

Ainley D.G. (1980) Birds as marine organism: a review. *Report of the Californian Cooperative Oceanic Fish Investigation* no. 21, 48–53.

Anderson, R.M. (1992) *Nematode parasites of vertebrates. Their development and transmission*, 578 pp. Cambridge, CAB International and Cambridge University Press.

Barus, V., Sergeeva, T.P., Sonin, M.D. & Ryzhikov, K.M. (1978) *Helminths of fish-eating birds of the Palaeartic Region. I. Nematoda.* Prague, Academia.

Berland, B. (1982) Basic techniques involved in helminth preservation. ICOPA V. Workshop: 'Technology as applied to museum parasite collections'. Toronto.

Brattey, J. & Ni, I.-H. (1992) Ascaridoid nematodes from the stomach of harp seals, *Phoca groelandica*, from Newfoundland and Labrador. *Canadian Journal of Fish Aquatic Science* **49**, 956–966.

Bush, A.O., Lafferty, K.D., Lotz, J.M. & Shostak, A.W. (1997) Parasitology meets ecology on its own terms: Margolis *et al.* revisited. *Journal of Parasitology* **83**, 575–583.

Cianchi, R., Orecchia, P., Berland, B., Paggi, L., D'Amelio, S., Mattiucci, S., Nascetti, G. & Bullini, L. (1992) Genetic studies on some *Contracaecum* species, parasites of fish-eating birds. *Abstract of 6th European Multicolloquium of Parasitology*, The Hague, The Netherlands, 127.

Culling, C.F.A., Allison, R.T. & Barr, W.T. (1985) *Cellular pathology technique*. Butterworth & Co. Ltd.

D'Amelio, S., Nascetti, G., Mattiucci, S., Cianchi, R., Orecchia, P., Paggi, L., Berland, B. & Bullini, L. (1990) Ricerche electroforetiche su alcune specie del genere *Contracaecum*, parassiti di uccelli ittiofagi (Ascaridida: Anisakidae). *Parassitologia* **32**, (Suppl. 1), 77.

D'Amelio, S., Mattiucci, S., Nascetti, G., Orecchia, P., Paggi, L. & Bullini, L. (1991) *Contracaecum rudolphii* s.l. in pesci de uccelli ittiofagi dei laghi del Parco Nazionale del Circeo. *Oebalia* (Suppl. 17), 569–570.

Dailey, M.D. (1985) Diseases of Mammalia: Cetacea. pp. 805–847 *in* Kinne, O. (*Ed.*) *Diseases of marine animals*, Vol. IV, Part 2. Hamburg, Biologische Anstalt Helgoland.

Dobson, A.P. & Hudson, P.J. (1992) Regulation and stability of a free-living host-parasite system: *Trichostrongylus tenuis* in red grouse. II. Population models. *Journal of Animal Ecology* **61**, 487–500.

Dobson, A.P. & May, R.M. (1986) Disease and conservation. pp. 345–365 *in* Soule, M. (*Ed.*) *Conservation biology, the science of scarcity and diversity.* Sunderland, Massachusetts, Sinauer Associates.

Doster, G.L. & Goater, C.P. (1997) Collection and quantification of avian helminths and protozoa. pp. 396–418 *in* Clayton, D.H. & Moore, J. (*Eds*) *Host–parasite evolution. General principles and avian models.* New York, Oxford University Press.

Fagerholm, H.-P. (1988) Patterns of caudal papillae in *Contracaecum osculatum* (Nematoda) and some related species from different regions of the world. *International Journal for Parasitology* **18**, 1039–1051.

Fagerholm, H.-P. (1991) Systematic implications of male caudal morphology in ascaridoid nematode parasites. *Systematic Parasitology* **19**, 215–228.

Fagerholm, H.-P. & Gibson, D.I. (1987) A redescription of the pinniped parasite *Contracaecum ogmorhini* (Nematoda, Ascaridoidea), with an assessment of its antiboreal circumpolar distribution. *Zoologica Scripta* **16**, 19–24.

Fagerholm, H.-P. & Lovdahl, M. (1984) Induced morphometric variation in the preparation of nematode parasites for the LM and SEM. *ICOPA V*, Toronto, 245–247.

Fagerholm, H.-P., Overstreet, R.M. & Humphrey-Smith, I. (1996) *Contracaecum magnipapillatum* (Nematoda, Ascaridoidea): resurrection and pathogenic effect of a common parasite from the proventriculus of *Anous minutus* from the Great Barrier Reef, with a note on *C. variegatum*. *Helminthologia* **33**, 195–207.

Furness, R.W. (1978a) An outbreak of parasitic necrosis in turkeys caused by *Plagiorchis laricola* (Skrjabin). *Journal of Helminthology* **15**, 35–36.

Furness, R.W. (1978b) Shetland seabird communities: the possible impact of new fishing techniques. *Ibis* **120**, 108–109.

Furness, R.W. (1982) Competition between fisheries and seabird communities. *Advances in Marine Biology* **20**, 225–307.

Furness, R.W. & Cooper, J. (1982) Interactions between breeding seabird and pelagic fish populations in the southern Benguela region. *Marine Ecology and Progress Series* **8**, 243–250.

Gibson, D.I. (1983) The systematics of ascaridoid nematodes. A current assessment. pp. 321–338 *in* Stone, A.R., Platt, M.M. & Khalil, L.F. (*Eds*) *Concepts in remote systematics.* London, Academic Press.

Gibson, D.I. (1984) Technology as applied to museum collections. The collection, fixation and conservation of helminths. *Systematic Parasitology* **6**, 241–255.

Grenfell, B.T. & Gulland, F.M.D. (1995) Introduction: ecological impact of parasitism on wildlife host populations. *Parasitology* **111**, (Suppl.), S3–S14.

Hartwich, G. (1964) Revision der vogelparasitischen Nematoden Mitteleuropas-Die Gattung *Contracaecum* Railliet and Henry, 1912 (Ascaridoidea). *Mitteilungen aus dem Zoologischen Mueum in Berlin* **40**, 15–53.

Hartwich, G. (1974) Keys to genera of Ascaridoidea. pp. 15 *in* Anderson, R.C. Chabaud, A.G. & Wilmott, S. (*Eds*) *ClH Keys to the nematodes of vertebrates.* Farnham Royal, Commonwealth Agricultural Bureaux.

Hugot, J.P., Morand, S. & Vassart, M. (1991) Morphological study of *Contracaecum magnicollare* (Nematoda, Anisakidae) from *Anous minutus* (Aves, Laridae). *Systematic Parasitology* **20**, 229–236.

Huizinga, H.W. (1971) Contracaecinasis in pelicaniform birds. *Journal of Wildlife Diseases* **7**, 198–204.

Idyll, C.P. (1973) The anchovy crisis. *Scientific American* **228**, 22–29.

Kinne, O. (1985) *Diseases of marine animals*, Vol. IV, Part 2. Hamburg, Biologische Anstalt Helgoland, pp. 543–552.

Klöser, H. & Plötz, J. (1992) Morphological distinction between adult *Contracaecum radiatum* and *Contracaecum osculatum* (Nematoda, Anisakidae) from the Weddell seal (*Leptonychotes weddelli*). *Zoologica Scripta* **21**, 129–132.

Kreis, H.A. (1955) *Contracaecum septentrionale*, ein neuer parasit aus dem kormoran; sein lebenslauf, sowie angaben über die entwicklung der Anisakinae. *Zoologische für Parasitenkunden* **17**, 106–121.

Lauckner, G. (1985) Diseases of aves (marine birds). pp. 627–643 *in* Kinne, O. (*Ed.*) *Diseases of marine animals*, Vol. IV, Part 2. Hamburg, Biologische Anstalt Helgoland.

Lauckner, G. (1985) Diseases of Mammalia: Pinnipedia. pp. 683–794 *in* Kinne, O. (*Ed.*) *Diseases of marine animals*, Vol. IV, Part 2. Hamburg, Biologische Anstalt Helgoland.

Laws, R.W. (1977) The significance of vertebrates in the Antartic marine ecosystem. pp. 411–438 *in* Llano, G.A. (*Ed.*) *Adaptations within Antarctic ecosystems.* Houston, Gulf Publ. Co.

May, R.M. (1988) Conservation and disease. *Conservation Biology* **2**, 28–30.

McCurdy, D.G., Shtler, D., Mullie, A. & Forbes, M.R. (1998) Sex-biased parasitism of avian hosts: relations to blood parasite taxon and mating system. *Oikos* **82**, 303–312.

Myers, B.J. (1957) Nematode parasites of seals in the eastern Canadian Arctic. *Canadian Journal of Zoology* **35**, 291.

Nascetti, G., Cianchi, R., Mattiucci, S., D'Amelio, S., Orecchia, P., Paggi, L., Berland, B. & Bullini, L. (1990) Struttura genetica di specie antartiche del genere *Contracaecum* (Ascaridida: Anisakidae). *Parassitologia* **32**, (Suppl. 1), 187.

Nascetti, G., Cianchi, R., Mattiucci, S., D'Amelio, S., Orecchia, P., Paggi, L., Brattey, J., Berland, B., Smith, J.W. & Bullini, L. (1993) Three sibling species within *Contracaecum osculatum* (Nematoda, Ascaridida, Ascaridoidea) from the Atlantic Arctic-Boreal region: reproductive isolation and host preferences. *International Journal for Parasitology* **23**, 105–120.

Oglesby, L.C. (1960) Heavy nematode infestation of white pelican. *Auk* **77**, 354.

Orecchia, P., Mattiucci, S., D'Amelio, S., Paggi, L., Plötz, J., Cianchi, R., Nascetti, G., Arduino, P. & Bullini, L. (1994) Two new members in the *Contracaecum osculatum* complex (Nematoda, Ascaridoidea) from the Antarctic. *International Journal for Parasitology* **24**, 367–377.

Owre, O.T. (1962) Nematodes in birds of the Order Pelecaniformes. *Auk* **79**, 114.

Plowright, W. (1988) Research on wildlife diseases, is a reappraisal necessary? *Revue Scientific and Technical de l'Office International d'Epizootologies* **7**, 783–795.

Prévost, J. (1976) Population, biomass, and energy requirements of Antarctic birds; attempted synthesis. SCAR/SCOR Conf. Living Marine Resources of the Southern Oceans (Woods Hole).

Sanger, G.A. (1972) Preliminary standing stock and biomass estimates of seabirds in the subarctic Pacific region. pp. 589–611 *in* Takenouti, A.Y. (*Ed.*) *Biological oceanography of the northern North Pacific Ocean.* Tokyo, Idemitsu Shoten.

Velando, A., Ortega-Ruano, J.E. & Docampo, F. (1995) La población de cormorán moñudo en el Atlàntico ibérico. *Quercus* **116**, 16–22.

Wiens, J.A. & Scott, J.M. (1975) Model estimation of energy flow in Oregon coastal seabird populations. *Condor* **77**, 439–452.

Yamaguti, S. (1961) *Systema Helminthum, I, II.* New York, Interscience Publishers.

Young, P.C. (1972) The relationship between the presence of larval anisakine nematodes in cod and marine mammals in British home waters. *Journal of Applied Ecology* **9**, 459–485.

Young, P.C., Lowe, D. & (1969) Larval nematodes from fish of the subfamily Anisakinae and gastro-intestinal lesions in mammals. *Journal of Comparative Pathology* **79**, 301–313.

(Accepted 16 November 2000)