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ORIGINAL PAPER

Deep-water life cycle of *Anisakis paggiae* (Nematoda: Anisakidae) in the Irminger Sea indicates kogiid whale distribution in north Atlantic waters

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Abstract The study of the beryciform *Anoplogaster cornuta* from the Irminger Sea (north Atlantic) revealed the presence of the anisakid nematode *Anisakis paggiae* inside the body cavity, representing a new host and locality record. This deep-sea fish was infected with *Anisakis* larvae at a prevalence of 57.1% and a mean intensity of 2.2, with no correlation between the fish standard length and the number of accumulated *A. paggiae*. Kogiid whales (*Kogia breviceps*, *K. sima*), the typical final hosts of this parasitic nematode, have not yet been recorded so far in the north. Because *A. cornuta* does not migrate outside the Irminger Sea, and by using the parasite as an indicator for the presence of the final hosts, *A. paggiae* must have been introduced through migratory kogiid final hosts. This would extend their range of distribution into the Irminger Sea. The depth range of the meso- and bathypelagic *A. cornuta* and the frequent occurrence of *Anisakis* inside this deep-sea fish demonstrate an oceanic deep-water life cycle for *A. paggiae* in the north Atlantic.

Keywords Deep-sea fish · *Anisakis paggiae* · Zoogeography · Metazoan parasites · Irminger Sea · Kogiidae · Sibling species

Introduction

Marine mammals are a diverse group of 130 species including cetaceans (whales, dolphins and porpoises), pinnipeds (sea lions, walrus and true seals), sirenians (manatees and dugongs), two otters and the Polar bear (Jefferson et al. 2008). The 86 recent whale species in the order Cetacea belong to the suborders Odontoceti (toothed whales) and Mysticeti (baleen whales) (e.g. Nikaido et al. 2001; Jefferson et al. 2008; Yang 2009). Cetaceans live in distinct regions of the world oceans, although some species can be considered cosmopolitan. Because of different habitat preferences, cetacean species distribute in tropical or polar and marine or estuarine regions, or any variation in between. They inhabit particular depths, temperature ranges or oceanographic regimes (Jefferson et al. 2008).

Baleen whales, sperm whales and some other large toothed whales have extensive, predictable seasonal migrations, allowing a maximum exploitation of food resources as well as mating and breeding purposes (e.g. Jefferson et al. 2008). Sperm whales include the families Physeteridae (modern sperm whale) and Kogiidae (pygmy and dwarf sperm whales). Both families are known from typical deep-water habitats in the tropics and the temperate zones. They feed mostly in deep waters (meso- and bathypelagial), primarily on cephalopods and less frequent

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on deep-sea fishes and crustaceans (e.g. decapods) (e.g. Beatson 2007; West et al. 2009).

Despite frequent whale strandings, parasitological studies on cetaceans are fairly limited compared to fish. They harbour a variety of metazoan parasites including digeneans, cestodes, nematodes and acanthocephalans (e.g. Colón-Llavina et al. 2009). Beside pseudophyllidean cestodes, ascaridoid nematodes of the genus *Anisakis* are the predominant parasites in the digestive tract. The use of molecular markers has revealed that this genus includes at least nine distinct species, *A. simplex* (Rudolphi, 1809; s.s., Nascetti et al., 1986)), *A. pegreffii* (Campana-Rouget & Biocca, 1955) and *A. simplex* C (Rudolphi, 1809; C, Mattiucci et al., 1997) (representing the *A. simplex* complex), *A. typica* (Diesing, 1860; Palm et al., 2008), *A. ziphidarum* (Paggi et al., 1998), *A. nascettii* (Mattiucci et al., 2009), *A. paggiae* (Mattiucci et al., 2005), *A. brevispiculata* (Dollfus, 1966) and *A. physeteris* (Baylis, 1920) (the latter three representing the *A. physeteris* complex). They are morphologically very similar but genetically different with distinct host preferences, life cycles and zoogeographical distribution (Klimpel et al. 2008; Mattiucci and Nascetti 2008; Mattiucci et al. 2009). According to Mattiucci and Nascetti (2006) and Valentini et al. (2006), *A. brevispiculata* and *A. paggiae* are host specific for the whale family Kogiidae, mainly in the mid- and southern Atlantic Ocean.

The Common Fangtooth, *Anoplogaster cornuta* (Valenciennes, 1833) (Beryciformes, Anoplogastridae), is a worldwide distributed deep-sea fish (between 46°N and 46°S in the Atlantic Ocean). In tropical and temperate seas, this species is found within a depth range of 2–4,992 m, where the adult specimens stay in a favoured depth of 500–2,000 m. The predatory *A. cornuta* reaches a maximum standard length of 15.2 cm and feeds mainly on fish and cephalopods, while the planctonic larvae mainly feed on crustaceans (Post 1986; Froese and Pauly 2010). Due to few parasitological studies that have been carried out on bathypelagic fish, the knowledge on the parasite fauna of *A. cornuta* is scarce (Klimpel et al. 2009). Ho (1987) described the parasitic copepod *Tautochondria dolichoura* from a specimen in the western North Atlantic; however, so far, no data on the endoparasite fauna are available.

We herewith genetically identify *Anisakis* larvae from the deep-water teleost *Anoplogaster cornuta* from the Irminger Sea. Identification of the host-specific *A. paggiae* allows comments to be made on the putative life cycle of this species and its final host distribution in northern waters. Implications for the general life cycle patterns of *Anisakis* nematodes in the North Atlantic are discussed.

Methods

Sample collection

Fish were sampled in June 2003 on board of the German research vessel Walther Herwig III during the field phase of the international research cruise WH 252. The cruise was part of a co-ordinated effort of ICES (International Council for the Exploration of the Sea) undertaking an international survey using hydroacoustics and trawl fisheries on oceanic redfish (*Sebastes mentella*) in the eastern Irminger Sea and adjacent waters. Sampling was conducted with a Gloria 1024 pelagic net at a trawling speed between 3.3 and 4.1 knots. A total of 21 specimens of *Anoplogaster cornuta* were caught between 52°14.83′ and 58°44.74′N and 37°01.09′ and 51°06.99′W (trawling depth range 300–950 m, mean depth 718 m). In the laboratory on board, the standard length (SL, to the nearest 0.1 cm) and total weight (TW, to the nearest 0.1 g) were taken. The fishes were kept deep frozen at −40°C until subsequent examination.

Parasitological examination

The presence of anisakid nematodes within the organs was studied by using a stereomicroscope. The body cavity was opened to examine the liver, stomach, pyloric caeca, intestine and gonads for nematodes. The stomach contents were also removed. The nematodes were freed from the host tissue and morphologically identified by using existing keys and descriptions. *Anisakis* third-stage larvae (L3) were stored in absolute (~99.9%) ethanol for molecular identification. The ecological and parasitological terminology follows Bush et al. (1997). We use the following terms and definitions: (a) final host—where a parasite reaches sexual maturity, (b) intermediate host—required by a parasite to complete its life cycle, usually it undergoes considerable morphological or physiological change and (c) paratenic host—not required by a parasite to complete its life cycle, without detectable morphological change.

PCR amplification and sequencing of ITS-1, 5.8S and ITS-2

Genomic DNA was isolated and purified from individual *Anisakis* larvae using a genomic DNA extraction kit (Peqlab Biotechnology GmbH, Erlangen, Germany) according to the instructions of the manufacturer. The rDNA region comprising the ITS-1, 5.8S, ITS-2 and flanking sequences (=ITS+) was amplified by using the previously described primers NC5 (5′-GTA GGT GAA CCT GCG GAA GGA TCA TT-3′) and NC2 (5′-TTA GTT

TCT TTT CCT CCG CT-3′) (Zhu et al. 2000). PCR (50 μl) included 25 μl Master-Mix (Peqlab Biotechnology GmbH, Erlangen, Germany) containing dNTP, $MgCl_{2}$, Buffer and Taq-Polymerase, 3 μl of each primer, 14 μl aqua dest and 5 μl genomic DNA. Each PCR was performed in a thermocycler (Peqlab, Germany) under the following conditions: after initial denaturation at 91°C for 1 min, 40 cycles of 94°C for 45 s (denaturation), 55°C for 45 s (annealing), 72°C for 45 s (extension), followed by a final extension at 72°C for 10 min. Samples without DNA were included in each PCR run. PCR products were examined on 1% agarose gels. A 100-bp ladder marker (peqGOLD, Erlangen, Germany) was used to estimate the size of the PCR products. To identify the anisakid nematodes, the PCR products were purified with E.Z.N.A. Cycle-Pure Kit (Peqlab Biotechnology GmbH, Erlangen, Germany). Afterwards, a total volume of 7 μl, including 2 μl primer (individually) and 5 μl of the PCR product (250 ng/μl), was sequenced by Seqlab (Goettingen GmbH, Germany). The obtained sequences were identified via GenBank and aligned with previously characterized sequences of anisakid nematodes, using CLUSTALW (1.83) Multiple Sequence Alignments (Thompson et al. 1994). Among the observed *Anisakis* species, the nucleotide sequence of all three regions was compared. The accession numbers of *Anisakis paggiae* from *Anoplogaster cornuta* were deposited in the Genbank under the accession numbers GU295973, GU295974, GU295975 and GU295976.

Our sequences of *A. paggiae* were compared with selected sequences from Genbank (Table 1) to create a distance table (Kimura-2-parameter) and to calculate the base differences using Mega4.0.2 (Kimura 1980; Tamura et al. 2007) (Table 2). A sequence of the rDNA ITS-1, 5.8S and ITS-2 of *Pseudoterranova decipiens* from the Atka mackerel (*Pleurogrammus azonus*, GenBank AB277824) was included as out-group to root the phylogenetic tree. The optimal evolution model for our data for the maximum-likelihood and Bayesian inference analyses was estimated using Modeltest 3.7 (Posada and Crandall 1998). The HKY85+*G* substitution model was the best fitting

Table 1 Information and accession numbers of anisakid nematode sequences used for comparative analyses

Parasite	Code	Locality	Host	Accession
Anisakis simplex (s.s.)	*Asimss*	Morocco	*Trachyrincus scabrus*	EU718471.1
Anisakis pegreffii	*Apeg*	Morocco	*Trachyrincus scabrus*	EU718479.1
Anisakis typica	*Atyp*	Thailand	*Rastrelliger kanagurta*	AB432909.1
Anisakis simplex C	*Asim*C	Canada	*Pseudorca crassidens*	AY826722
Anisakis physeteris	*Aphy*	Japan	*Scomber scombrus*	AB277821.1
Anisakis ziphidarum	*Azip*	South Africa	*Ziphius cavirostris*	AY826725.1
Anisakis nascettii (sp.A)	*Anas*	Madeira	*Aphanopus carbo*	AY260555
Anisakis brevispiculata	*Abrev*	Japan	*Theragra chalcogramma*	EU624344
Anisakis paggiae	*Apag*REF	Japan	*Theragra chalcogramma*	EU624345.1
Anisakis paggiae	*Apag*	Greenland	*Anoplogaster cornuta*	GU295973
Pseudoterranova decipiens	*Pdec*	Japan	*Theragra chalcogramma*	AB277824

Table 2 Pairwise nucleotide differences for ITS-1, 5.8S and ITS-2 sequences between *Anisakis* taxa

	Asimss	*Apeg*	*Asim*C	*Atyp*	*Azip*	*Anas*	*Abrev*	*Aphy*	*Apag*	*Apag*REF	*Pdec*
Asimss		2	5	147	43	64	103	101	97	99	130
Apeg	0.00240		5	148	42	63	104	100	96	98	131
*Asim*C	0.00602	0.00602		146	42	67	103	99	97	99	129
Atyp	0.21698	0.21876	0.21531		136	139	141	139	146	150	156
Azip	0.05507	0.05372	0.05375	0.20188		53	102	96	86	88	117
Anas	0.08450	0.08308	0.08879	0.22595	0.07015		129	114	102	104	124
Abrev	0.14806	0.14970	0.14806	0.21878	0.14879	0.17721		35	41	41	94
Aphy	0.14525	0.14362	0.14199	0.21422	0.13945	0.16938	0.04653		48	49	101
Apag	0.13621	0.13463	0.13621	0.22199	0.12229	0.14656	0.05490	0.06490		2	84
*Apag*REF	0.13938	0.13779	0.13938	0.22759	0.12549	0.14985	0.05468	0.06593	0.00250		84
Pdec	0.19329	0.19505	0.19163	0.23798	0.17523	0.18665	0.13645	0.14767	0.11905	0.11837	

Absolute nucleotide differences above the diagonal. Kimura-2-parameter (Kimura 1980, K2P) distances below the diagonal model for the data set. The estimated parameters were distribution shape parameters (α) = 0.2719, kappa = 4.2269 and nucleotide frequencies $A = 0.25380$, $C = 0.19690$, $G = 0.26550$ and $T = 0.28380$. Maximum-likelihood analysis was performed using PAUP* v4.0 (Swofford 2003) including 1,000 bootstrap replicates. Bayesian inference (BI) analyses were performed with MrBayes 3.1 (Huelsenbeck and Ronquist 2001) using four MCM chains and default heating values (1.000.000 generations). Posterior probabilities were estimated (Larget and Simon 1999).

Results

Anisakid nematodes and food items of *Anoplogaster cornuta*

The 21 examined specimens of *Anoplogaster cornuta* had a mean standard length of 12.7 cm (11.3–15.2 cm) and a mean total weight of 84.8 g (51.8–154.1 g). *Anoplogaster cornuta* was parasitized by a total of 26 third-stage larvae (L3) of *Anisakis paggiae* (molecular identification of 4 specimens see below, 12 specimens revealed sequences with a large number of not specified base pairs). They were isolated from the mesenteries around the organs at a prevalence of 57.1% and a mean intensity of 2.2 (range 1–6). No correlation was found between the fish standard length and the number of accumulated *A. paggiae* (Fig. 1). The stomach contents of the examined *A. cornuta* consisted solely of fish remains, while 71.4% of the stomachs were empty.

Genetic identification

The ITS-1, 5.8S and ITS-2 sequences were determined for 4 *Anisakis* nematodes that were isolated from the 12 infected *Anoplogaster cornuta*. Identification via GenBank showed that all samples belonged to *Anisakis paggiae* within the *A. physeteris* sibling species complex. The length of the PCR products including the three regions ITS-1, 5.8S and ITS-2 was 810 bp. The length of the partial ITS-1 and full ITS-2 sequences of *A. paggiae* was 363 and 290 bp, respectively. The 5.8S sequences were all 157 bp long. The $G + C$ contents of all sequences were 49.0% (ITS-1), 52.0% (5.8S) and 48.0% (ITS-2). The obtained sequences were aligned with a sequence of *A. paggiae* (EU624345.1) from *Theragra chalcogramma*, Japan. They all differed in the same 6 positions (transition in ITS-1/2, pos. 208, 601; deletion in ITS-2, pos. 585–588) and showed a sequence identity of 99% compared with the included reference.

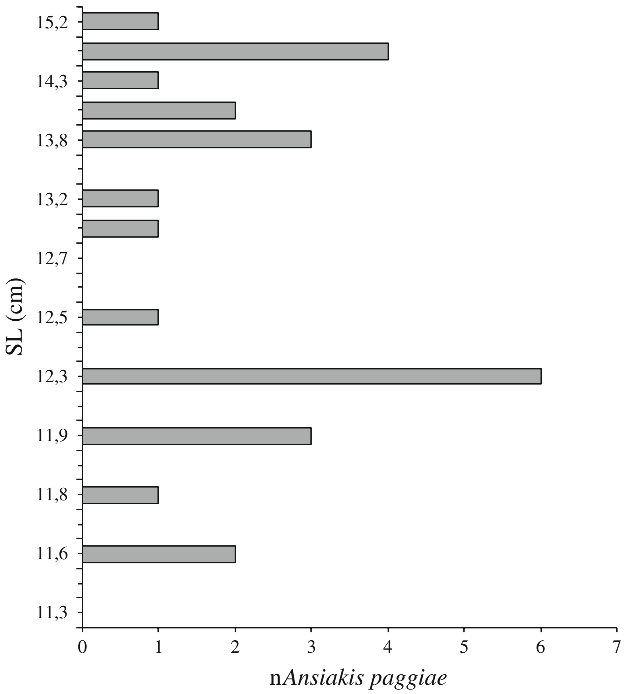

Fig. 1 Random distribution of *Anisakis paggiae* in the investigated fish species *Anoplogaster cornuta* over the size range (standard length = SL, in cm) from the Irminger Sea

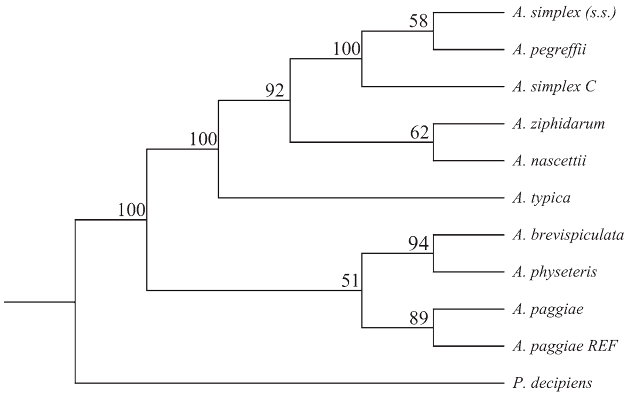

Fig. 2 *Anisakis* spp. consensus phylogenetic tree resulting from maximum-likelihood analysis for ITS-1/5.8S/ITS-2 regions of 11 sequences. Probabilities (%) are given for internal branches. Specimen information is listed in Table 1. Bootstrap values were calculated over 1,000 replicates. Result of Bayesian inference (BI) analyses not given. They revealed similar results

The phylogenetic analyses classified *A. paggiae* as part of the *A. physeteris* complex, supported by a bootstrap value of 52% (Fig. 2).

Discussion

The transmission pathways of parasites with indirect life cycles are fully embedded within the food web of aquatic ecosystems. Consequently, anisakid nematodes follow closely the trophic relationships among their successive hosts, from invertebrates into teleosts and finally into marine mammal final hosts. As such, anisakid nematodes are useful as biological indicators for their final host distribution and abundance (Mattiucci et al. 2007; Klimpel et al. 2010). The present study identifies for the first time *Anisakis paggiae* from the body cavity of the deep-water fish *A. cornuta* at a mean depth of 718 (range: 300–950) m. *Anisakis paggiae* was genetically characterized and morphologically described as an adult parasite of the kogiid species *Kogia breviceps* (pigmy sperm whale) and *K. sima* (dwarf sperm whale) off the Florida and South African Atlantic coast (Mattiucci et al. 2005; Valentini et al. 2006). Scanty data are so far available regarding the identification of the intermediate hosts. Mattiucci et al. (2007) analysed different fish from Atlantic waters and recorded larval *A. paggiae* in predatory *Merluccius merluccius* (depth range: 30–1,075, usually 70–400 m) and *Xiphias gladius* (depth range: 0–800, usually 0–400 m). *Anoplogaster cornuta* is a meso-/bathypelagic fish that had a high prevalence of infestation above 50%. The random distribution of *A. paggiae* in differently sized *Anoplogaster cornuta* indicates its role as a second intermediate host in the life cycle of the parasite (see Palm 1999). Consequently, deep-water teleosts (mesopelagic fish) that transfer the parasites into larger paratenic host species (such as *X. gladius*) might play a crucial role within the life cycle of this anisakid nematode species.

Within the boreal region of the North Atlantic, *A. simplex* (s.s.), *A. brevispiculata*, *A. pegreffii, A. physeteris*, *A. ziphidarum* and herewith *A. paggiae* have been recorded from their final or intermediate hosts. In the northern hemisphere, adult *A. simplex* (s.s.) are mainly parasites of the Delphinidae, Phocoenidae and Balaenopteridae (Mattiucci and Nascetti 2008). The larval stages occur in a variety of epipelagic fish and cephalopods (e.g. Mattiucci et al. 1998; Klimpel et al. 2008; Mattiucci and Nascetti 2008). While *A. physeteris* is host specific for the sperm whale and can be expected to have an extensive range of distribution in the world oceans, *A. paggiae* has been so far reported from kogiid whales only. They have not been recorded that far north in the Irminger Sea. However, the high abundance of *A. paggiae* in a common deep-water fish in these northern waters may indicate that the final hosts migrate further northwards within the North Atlantic Ocean, than known so far from the reported range of distribution for the kogiids *K. breviceps* and *K. sima*.

The pigmy and dwarf sperm whales are widespread in tropical and temperate seas, where they feed on mid- and deep-water cephalopods, fish and occasionally crustaceans (Fig. 3). The bathymetric distribution and the species

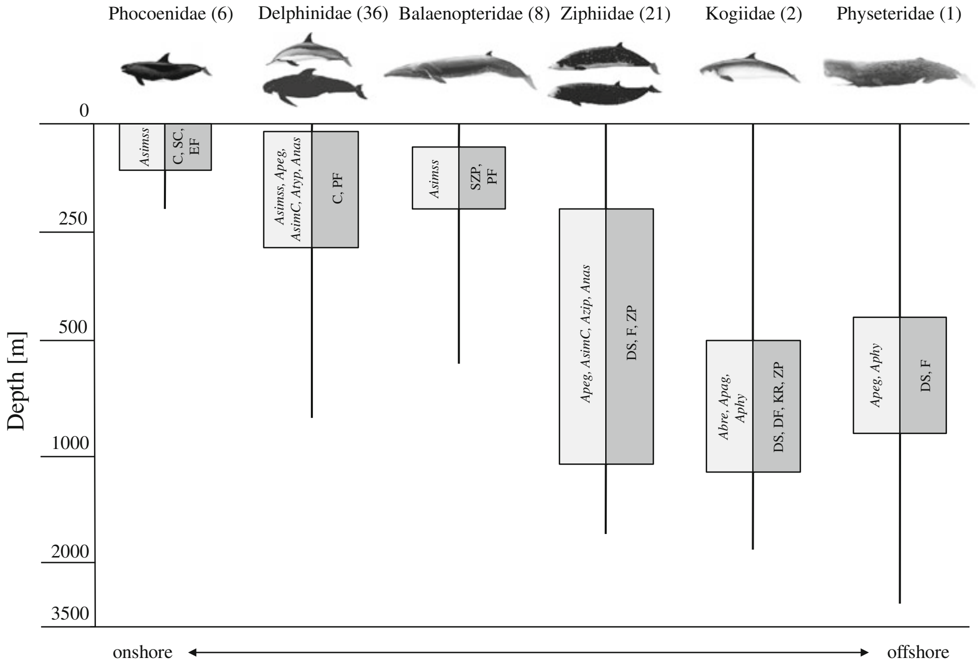

Fig. 3 Shore affinity, maximum depth distribution with main foraging depths, favoured prey (according to Reyes 1991; Perrin and Gilpatrick 1994; Westgate et al. 1995; Willis and Baird 1998; Croll et al. 2001; Heide-Jørgensen et al. 2002; Panigada et al. 2003; Croll et al. 2005; Jefferson et al. 1993, 2008; Perrin et al. 2009) and detected anisakid sibling species (*boxes*) of cetacean families. The numbers in *brackets* indicate the number of species. Abrev: *Anisakis brevispiculata*, Anas: *A. nascettii*, Apag: *A. paggiae*, Apeg: *A. pegreffii*, Aphy: *A. physeteris*, Atyp: *A. typica*, AsimC: *A. simplex* C, Asimss: *A. simplex* (s.s.), Azip: *A. ziphidarum*, C: Cephalopoda, DS: deep-sea squids, DF: deep-sea fishes, EF: epipelagic fish, F: fish, KR: krill, PF: pelagic fish, SC: small Crustacea, SF: small fishes, SZP: small zooplankton and ZP: zooplankton

composition of the prey items in the diet of *K. breviceps* in New Zealand waters indicate its most common water depth. According to Beatson (2007), the majority of the diet species are vertical migrators, suggesting that *K. breviceps* feeds in a water depth between 650 and 1,100 m. In the Gulf of Mexico, *Kogia* species are present year round in water depths of 400–3,500 m, but most frequently occur between 400 and 1,000 m (Mullin et al. 1994; Davis et al. 1998; Baumgartner et al. 2001). These areas include locations of frequent upwelling events that concentrate zooplankton biomass and the cephalopod prey along the continental shelf (Davis et al. 1998). Stomach content analyses support deep-water cephalopods as the primary source of diet, with myctophid fishes and shrimps as secondary prey (e.g. Ross 1978; McAlpine et al. 1997; Pauly et al. 1998; Wang et al. 2002; Beatson 2007; West et al. 2009). West et al. (2009) studied the stomach contents of seven pygmy sperm whales (*K. breviceps*) from the Hawaiian Islands. The two most numerically abundant cephalopod families in the stomachs were the Histioteuthidae and Cranchiidae. Species of these families (e.g. *Stigmatoteuthis hoylei*, *Taonius pavo* and *Liocranchia reinhardti*) were identified in all seven whale stomachs and collectively represented an estimated 58.0% of the total prey biomass. Furthermore, typical meso- and bathypelagic fish species and deep-water decapods (e.g. *Pasiphaea tarda*) were of secondary importance. These data demonstrate that the most common feeding of the Kogiidae takes place in the meso- and bathypelagic zone.

The life cycle of *A. paggiae* is unknown. Our data, however, demonstrate that the life cycle can take place in the deep-water surroundings of the Irminger Sea. Both so far recorded whale species with a common distribution in the Irminger Sea (*Physeter catodon*, Physeteriidae, and *Hyperooden ampullatus*, Ziphiidae) have not been recorded to harbour *A. paggiae*. Consequently, kogiids as the only reported final hosts for *A. paggiae* must have dispersed the eggs and larvae. Accounting for the high prevalence of *Anisakis* in the investigated fish, a possible introduction of eggs or infected invertebrates from southern regions into the Irminger Sea through ocean currents seems to be unlikely. *Anoplogaster cornuta* can be considered as second intermediate host that gets infected through the unknown invertebrate first intermediate hosts (see Palm 1999). Most likely, deep-water cephalopods or other teleosts serve as paratenic hosts that also accidentally transfer the parasite larvae into the upper water layers. Some might even be considered a “dead end” within the parasite’s life cycle. This *A. paggiae* life cycle contrasts the known pathways of *Anisakis simplex* (s.s.) in the east Greenland Sea, which mainly takes place in the epipelagic zone. Onshore cephalopods (e.g. *Sepia officinalis* and *Allotheuthis subulata*) and species from the polar regions of the Atlantic Ocean (e.g. *Illex coindetii* and *Todarodes sagittatus*) have been identified as hosts for the third-stage larvae of *A. simplex* (s.s.) and *A. pegreffii* (Abollo et al. 2001; Mattiucci & Nascetti 2008), however, mainly in coastal and bank areas between 20 and 200 m (Moiseev 1991).

The existence of nine morphologically similar but genetically different species within the *Anisakis* sibling species complexes is based on differences in the life cycle ecology and host preferences, allowing sympatric existence and even co-occurrence in the same intermediate and final hosts. Our sequence analyses show that our examined specimens all differ in the same positions compared with the included reference. This might be explained with the existence of a northern *A. paggiae* population. However, further evidence is needed based on population genetics analyses. Figure 2 presents the consensus phylogenetic tree resulting from the maximum-likelihood analysis, which is in principal congruent to the published tree by Mattiucci et al. (2009), derived from mtDNA sequences. However, most recent studies still demonstrate inconsistencies in the branching order of the clade including the *A. physeteris* complex (e.g. Mattiucci and Nascetti 2008, Valentini et al. 2006), placing either *A. physeteris* or *A. paggiae* monophyletic. This suggests the investigation of additional DNA markers in future studies.

Conclusions

Our results support the hypothesis that *Anisakis* species in the east Greenland Sea utilize different life cycle pathways, linked to the feeding ecology of their final hosts and the structure of the respective food web. *Anisakis paggiae* follows a deep-water or meso-/bathypelagic life cycle that involves meso- and bathypelagic fish as second and possibly deep-sea cephalopods or other teleosts as paratenic hosts. The latter might accidentally transfer the parasite larvae into the upper water layers, where they can be considered as a “dead end” for the parasite. Identification of *A. paggiae* in the Irminger Sea indicates that the kogiid final hosts also distribute so far northwards. The life cycle of *A. paggiae* contrasts that of *A. simplex* (s.s.) in the north Atlantic, which mainly takes place in the epipelagic zone. Existence of nine morphologically similar but genetically different species within the genus *Anisakis* is based on differences in the life cycle ecology and host preferences, allowing sympatric existence and even co-occurrence in the same intermediate and also final hosts (see Fig. 2). We do suggest similar deep-water (‘mesopelagic?’) life cycles for other species within the *A. physeteris* sibling species complex, *A. ziphidarum* and *A. nascettii* (e.g. Klimpel et al. 2008), in accordance with the most common feeding ecology and depth range of their reported final hosts (see Fig. 3).

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References

Abollo E, Gestal C, Pascal S (2001) *Anisakis* infestation in marine fish and cephalopods from Galician waters: an updated perspective. Parasitol Res 87:492–499

Baumgartner MF, Mullin KD, May LN, Leming TD (2001) Cetacean habitats in the northern Gulf of Mexico. Fish Bull 99:219–239

Beatson EL (2007) The diet of pygmy sperm whales, *Kogia breviceps*, stranded in New Zealand: implications for conservation. Rev Fish Biol Fisher 17:295–303

Bush O, Lafferty AD, Lotz JM, Shostak AW (1997) Parasitology meets ecology on his own terms: Margolis et al. revisited. J Parasitol 83:575–583

Colón-Llavina MM, Mignucci-Giannoni AA, Mattiucci S, Paoletti M, Nascetti G, Williams EH Jr (2009) Additional records of metazoan parasites from Caribbean marine mammals, including genetically identified anisakid nematodes. Parasitol Res 105:1239–1252

Croll DA, Acevedo-Gutierrez A, Tershy BR, Urban-Ramirez J (2001) The diving behaviour of blue and fin whales: is diving duration shorter than expected based on oxygen stores? Comp Biochem Physiol 129:797–809

Croll DA, Marinovic B, Benson S, Chavez FP, Black N, Ternullo R, Tershy BR (2005) From wind to whales: trophic links in a coastal upwelling system. Mar Ecol Prog Ser 289:117–130

Davis RW, Fargion GS, May N, Leming TD, Baumgartner M, Evans WE, Hansen LJ, Mullin K (1998) Physical habitats of cetaceans along the continental slope of north-central and western Gulf of Mexico. Mar Mamm Sci 14:490–507

Froese R, Pauly D (2010) Fishbase. World wide web electronic publication. www.fishbase.org, Version (03/2010)

Heide-Jørgensen MP, Bloch D, Stefansson E, Mikkelsen B, Ofstad LH, Dietz R (2002) Diving behaviour of long-finned pilot whales *Globicephala melas* around the Faroe Islands. Wildl Biol 8:307–313

Ho JS (1987) *Tautochondria dolichoura* n.g., n.sp., a copepod parasitic on the bathypelagic fish *Anoplogaster cornuta* (Valenciennes) in the western north Atlantic. Syst Parasitol 9:179–184

Huelsenbeck JP, Ronquist F (2001) MrBayes: bayesian inference of phylogeny. Bioinformatics 17:754–755

Jefferson TA, Leatherwood S, Webber MA (1993) FAO species identification guide. Marine mammals of the world. UNEP/FAO, Rome

Jefferson TA, Webber MA, Pitman RL (2008) Marine mammals of the world, a comprehensive guide to their identification. Elsevier, Amsterdam

Kimura M (1980) A simple method for estimating evolutionary rate of base substitutions through comparative studies of nucleotide sequences. J Mol Evol 16:111–120

Klimpel S, Kellermanns E, Palm HW (2008) The role of pelagic swarm fish (Myctophidae: Teleostei) in the oceanic life cycle of *Anisakis* sibling species at the Mid-Atlantic Ridge. Parasitol Res 104:43–53

Klimpel S, Busch MW, Kellermanns E, Kleinertz S, Palm HW (2009) Metazoan deep-sea fish parasites. Acta Biologica Benrodis, Supplement 11. Verlag Natur & Wissenschaft, Solingen

Klimpel S, Busch MW, Kuhn T, Rohde A, Palm HW (2010) The *Anisakis simplex* complex off the South Shetland Islands (Antarctica): endemic populations versus introduction through migratory hosts. Mar Ecol Prog Ser 403:1–11

Larget B, Simon B (1999) Markov chain Monte Carlo algorithms for the Bayesian analysis of phylogenetic trees. Mol Biol Evol 16:750–759

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

Mattiucci S, Nascetti G (2008) Advances and trends in the molecular systematic of anisakid nematodes, with implications for their evolutionary ecology and host-parasite co-evolutionary processes. Adv Parasit 66:47–148

Mattiucci S, Paggi L, Nascetti G, Ishikura H, Kikuchi K, Sato N, Cianchi R, Bullini L (1998) Allozyme and morphological identification of *Anisakis*, *Contracaecum* and *Pseudoterranova* from Japanese waters (Nematoda, Ascaridoidea). Syst Parasitol 40:81–92

Mattiucci S, Nascetti G, Dailey M, Webb SC, Barros NB, Cianchi R, Bullini L (2005) Evidence for a new species of *Anisakis* Dujardin, 1845: morphological description and genetic relationship between congeners (Nematoda: Anisakidae). Syst Parasitol 61:157–171

Mattiucci S, Paoletti M, Damiano S, Nascetti G (2007) Molecular detection of sibling species in anisakid nematodes. Parassitologia 49:147–153

Mattiucci S, Paoletti M, Webb SC (2009) *Anisakis nascetti* n. sp. from beaked whales of the southern hemisphere: morphological description, genetic relationships between congeners and ecological data. Syst Parasitol 75:199–217

McAlpine DF, Murison L, Hoberg E (1997) New records for the pygmy sperm whale *Kogia breviceps* (Physeteridae) from Atlantic Canada with notes on diet and parasites. Mar Mammal Sci 13:701–704

Moiseev SI (1991) Observation of the vertical distribution and behaviour of nektonic squids using manned submersibles. Bull Mar Sci 49:446–456

Mullin KD, Hoggard W, Roden CL, Lohoefener RR, Rogers CM, Taggart B (1994) Cetaceans on the upper continental slope in the north-central Gulf of Mexico. Fish Bull 92:773–786

Nikaido M, Matsuno F, Hamilton H, Brownell RL Jr, Cao Y, Ding W, Zuoyan Z, Shedlock AM, Fordyce RE, Hasegawa M, Okada N (2001) Retroposon analysis of major cetacean lineages: the monophyly of toothed whales and the paraphyly of river dolphins. Proc Natl Acad Sci USA 98:7384–7389

Palm HW (1999) Ecology of *Pseudoterranova decipiens* (Krabbe, 1878) (Nematoda: Anisakidae) from Antarctic waters. Parasitol Res 85:638–646

Palm HW, Damriyasa IM, Linda, Oka IBM (2008) Molecular genotyping of *Anisakis* Dujardin, 1845 (Nematoda: Ascaridoidea: Anisakidae) larvae from marine fish of Balinese and Javanese waters, Indonesia. Helminthologia 45:3–12

Panigada S, Pesante G, Zanardelli M, Oehen S (2003) Day and night-time behavior of fin whales in the western Ligurian Sea. In: Proceedings of the conference Ocean 2003, San Diego, California, USA, pp 466–471

Pauly D, Trites AW, Capuli E, Christesen V (1998) Diet composition and trophic level of marine mammals. ICES J Mar Sci 55:467–481

Perrin WF, Gilpatrick JW Jr (1994) Spinner dolphin–*Stenella longirostris* (Gray, 1928). In: Ridgway SH, Harrison SR (eds) Handbook of marine mammals. Volume 5: the first book of dolphins. Academic Press, London, pp 99–128

Perrin WF, Wursig B, Thewissen JGM (2009) Encyclopedia of marine mammals. Academic Press, London

Posada D, Crandall KA (1998) Modeltest: testing the model of DNA substitution. Bioinformatics 14:817–818

Post A (1986) Anoplogastridae. In: Whitehead PJP, Bauchot ML, Hureau JC, Nielsen J, Tortonese E (eds) Fishes of the north-eastern Atlantic and the Mediterranean. UNESCO, Paris, pp 767–768

Reyes JC (1991) The conservation of small cetaceans: a review. Report prepared for the secretariat of the convention on the conservation of migratory species of wild animals. UNEP/CMS Secretariat, Bonn

Ross GJB (1978) Records of pygmy and dwarf sperm whales, genus *Kogia*, from southern Africa, with biological notes and some comparisons. Ann Cape Prov Mus Nat Hist 11:259–327

Swofford DL (2003) PAUP* phylogenetic analysis using parsimony (*and other methods) version 4. Sinauer Associates, Sunderland

Tamura K, Dudley J, Nei M, Kumar S (2007) MEGA4: molecular evolutionary genetics analysis (MEGA) software version 4.0. Mol Biol Evol 24:1596–1599

Thompson JD, Higgins DG, Gibson TJ (1994) CLUSTAL W: improving the sensitivity of progressive multiple sequence alignment through sequence weighting, position specific gap penalties and weight matrix choice. Nucleic Acids Res 22:4673–4680

Valentini A, Mattiucci S, Bondanelli P, Webb SC, Mignucci-Giannone A, Cólon-Llavina MM, Nascetti G (2006) Genetic relationship among *Anisakis* species (Nematoda: Anisakidae) inferred from mitochondrial cox-2 sequences, and comparison with allozyme data. J Parasitol 92:156–166

Wang MC, Walker WA, Shao KT, Chou LS (2002) Comparative analysis of the diets of pygmy sperm whales and dwarf sperm whales in Taiwanese waters. Acta Zool Taiwan 13:53–62

West K, Walker W, Baird R, White W, Levine G, Brown E, Schofield D (2009) Diet of pygmy sperm whale (*Kogia breviceps*) in the Hawaiian Archipelago. Mar Mammal Sci 25:944–948

Westgate AJ, Read AJ, Bergren P, Koopman HN, Gaskin DE (1995) Diving behavior of harbor porpoises, *Phocoena phocoena*. Can J Fish Aqua Sci 52:1064–1073

Willis PM, Baird RW (1998) Status of the dwarf sperm whale, *Kogia simus*, with consideration of special reference to Canada. Can Field Nat 112:114–125

Yang XG (2009) Bayesian inference of cetacean phylogeny based on mitochondrial genomes. Biologia 64:811–818

Zhu X, Gasser RB, Jacobs DE, Hung GC, Chilton NB (2000) Relationship among some ascaridoid nematodes based on ribosomal DNA sequence data. Parasitol Res 86:738–744