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Heavy infestation by endoparasitic copepod crustaceans (Poecilostomatoida: Splanchnotrophidae) in Chilean opisthobranch gastropods, with aspects of splanchnotrophid evolution

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Abstract

Copepods of the family Splanchnotrophidae are very significant parasites of shell-less opisthobranchs, but little information exists on their occurrence, infection frequencies, and local or seasonal abundances. Using a quantitative faunistic approach, 2257 potential hosts belonging to 47 opisthobranch species were collected from 1991 to 1996 off the Chilean and Argentinian coasts, mainly by SCUBA. Endoparasitic splanchnotrophids of the genus *Ismaila* were found in 303 host specimens, corresponding to a 13% prevalence of infection. The opisthobranch hosts were one sacoglossan, three doridoidean and four aeolidoidean nudibranch species. In total, 12 Chilean opisthobranch species are known to be infected with splanchnotrophids. This amounts to about 20% of all shell-less opisthobranch species from Chile, and a remarkable 26% of all splanchnotrophid hosts worldwide. Infection frequencies are low in most host species, but reached 89–100% in certain populations of *Thecacera darwini, Okenia luna, Flabellina* sp. 1 and *Elysia patagonica*, representing the highest rates of infestation by splanchnotrophids ever documented. In *Thecacera darwini*, the prevalence was very low in northern Chile, consistently high in central Chile, and low in the south. High infestation coupled with a high number of sympatric but host-specific species indicate the coast of central Chile is a centre of *Ismaila* evolution. The biogeography of splanchnotrophid genera is discussed, and a hypothesis on their distributional history is presented.

Key words: Chile, Opisthobranchia, parasite, Splanchnotrophidae, *Ismaila*, biogeography, evolution

See also Electronic Supplement (Parts 1 and 2) at **http://www.senckenberg.de/odes/02-03.htm**

Introduction

Already in the 19th century, considerable attention was paid to endoparasitic copepods associated with opisthobranch gastropods (i.e. Hancock & Norman 1863; Bergh 1867, 1876, 1879, 1898; Hecht 1895), and all these poecilostomatoid copepods were regarded as belonging to (or possibly related with) the family Splanchnotrophidae (see review of Jensen 1987). Members of the genera *Micrallecto* Stock, 1971, *Nannallecto* Stock, 1973, and *Megallecto* Gotto, 1986 were known as being rare ectoparasites of gymnosome pteropods (Ho 1981, Gotto 1986). All others – *Chondrocarpus* Bassett-Smith, 1903, *Briarella* Bergh, 1876, *Ismaila* Bergh, 1867, and *Splanchnotrophus* Hancock & Norman, 1863 – live endoparasitically and, in relation to their hosts, may be considerably large (see Bassett-Smith 1903, Ho 1981, Jensen 1987). The scattered knowledge on the occurrence of endoparasitic copepods associated with opisthobranch hosts was reviewed by Jensen (1987, 1990) who reported 38 host species worldwide. Most hosts are nudibranchs, along with two sacoglossan and two (one not identified) notaspidean species.

However, most recently the taxonomy of Splanchnotrophidae has changed radically. Huys (2001) excluded all the above-mentioned genera but the endoparasitic *Ismaila* and *Splanchnotrophus* (the latter split into *Splanchnotrophus* s.s. and *Lomanoticola*) from the family Splanchnotrophidae. Additionally, Huys (2001) established two new splanchnotrophid genera, *Arthurius*

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(type species *Splanchnotrophus elysiae* Jensen, 1990) and *Ceratosomicola* (type species *Splanchnotrophus sacculatus* O'Donoghue, 1924), comprising western Australian, New Caledonian and possibly Japanese specimens.

Host preferences of splanchnotrophid genera were suspected to be related to systematic groups or, in the case of *Splanchnotrophus* and *Ismaila*, to the presence of cerata within hosts of various subgroups (Jensen 1987). Recorded infestations by splanchnotrophids, especially *Ismaila* and *Ceratosomicola*, mainly derive from single host specimens (e.g. Bergh 1867, 1898; Ho 1981; Jensen 1987; Huys 2001), indicating generally low rates of splanchnotrophid parasitism (Ho 1987b). In contrast, numerous infections by some *Splanchnotrophus* spp. were reported from the Mediterranean Sea and around the British Isles (e.g. Hecht 1895, Laubier 1964), but never quantified in terms of percentage of hosts infected. Belcik (1981) was the first to document a massive splanchnotrophid infection quantitatively: in Oregon, a parasitological examination of several thousand opisthobranchs showed that only a single species (*Janolus fuscus* O'Donoghue, 1924; as *Antiopella*) out of 26 potential host species was infected. Within that host species, however, the prevalence of infection by *Ismaila belciki* Ho, 1987 (as *I. monstrosa* Bergh, 1867; Ho 1987a) was high (62%). No information was given on seasonal or local variations so this may or may not have been a sporadic or local phenomenon.

Although splanchnotrophids have been relatively poorly studied on the Chilean coast, a considerable number of species are reported from there. Single specimens assigned to *Ismaila monstrosa* Bergh, 1867 parasitized the nudibranch *Archidoris incerta* Bergh, 1898 and *Aeolidia papillosa serotina* Bergh, 1873 (Bergh 1898). Marcus (1959) mentioned endoparasitic copepods, certainly splanchnotrophids, from *Rostanga pulchra* MacFarland, 1906, *Acanthodoris falklandica* Eliot, 1907 and from the aeolid *Eubranchus agrius* Marcus, 1959. More recently, splanchnotrophids have been found in a variety of other Chilean host species, of which several appeared to be heavily infected (Millen et al. 1994; Schrödl 1996b, 1997; Haumayr & Schrödl in press).

The present study investigated the occurrence of endoparasitic splanchnotrophids in over 2000 opisthobranch specimens from Chile and Argentina. Levels of infestation were studied, as well as seasonal and local variations. The central and southern Chilean coast is discussed as a "hot spot" of nudibranch infection by splanchnotrophid copepods, in particular by members of the genus *Ismaila*. Information on host preferences and actual geographical distributions of splanchnotrophids led to some conclusions on their evolution and distributional history.

Material and methods

This study uses data from relevant studies on Chilean, Argentinian and Peruvian opisthobranchs (e.g. Bergh 1898; Marcus 1959; for full citation lists see Schrödl 1996b, 1999a), recently published results (e.g. Millen et al. 1994; Schrödl 1996a, b, 1997, 1999a, b, 2000) and new data. Between 1991 and 1996, shell-less opisthobranchs were collected from localities distributed along the coasts of Chile and Argentina (Fig. 1). Using SCUBA, search time ranged from five to ten hours per site. In the Bay of Coliumo it reached a total of 100 hours. Specimens were examined externally, most whilst still alive under a dissecting microscope, for the presence of endoparasitic splanchnotrophids. Mature male or female endoparasites, the latter usually possessing a pair of conspicuous egg sacs, penetrate the body wall of their hosts with their posterior body segments and thus were clearly detectable (see Figs 2A, B). In addition, juvenile stages freely migrating in the body cavities of their hosts were often (but not quantitatively) recog-

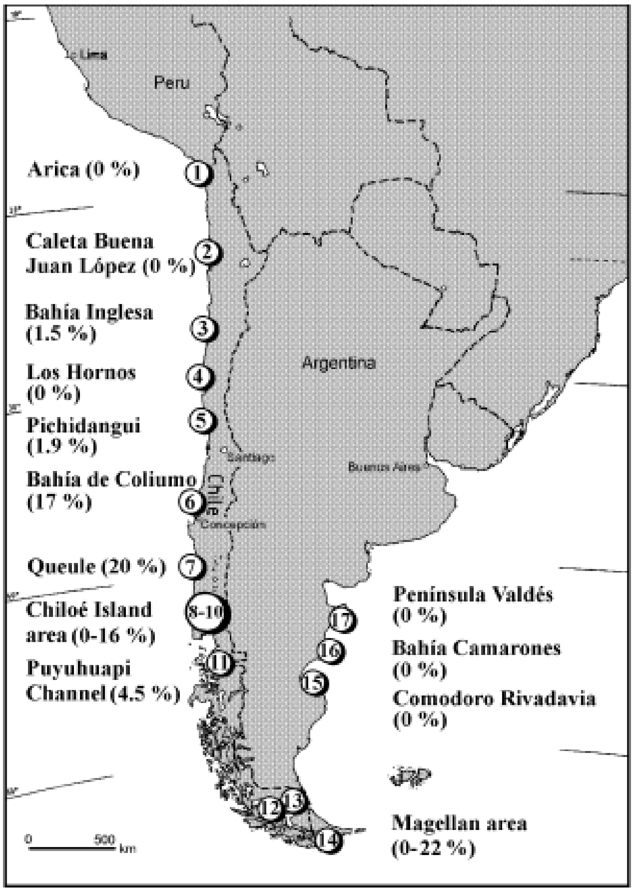

Fig. 1. Collecting areas in southern South America (for details see Electr. Suppl. 02–03, Part 1). Local percentage incidences of infection of opisthobranchs shown in brackets.

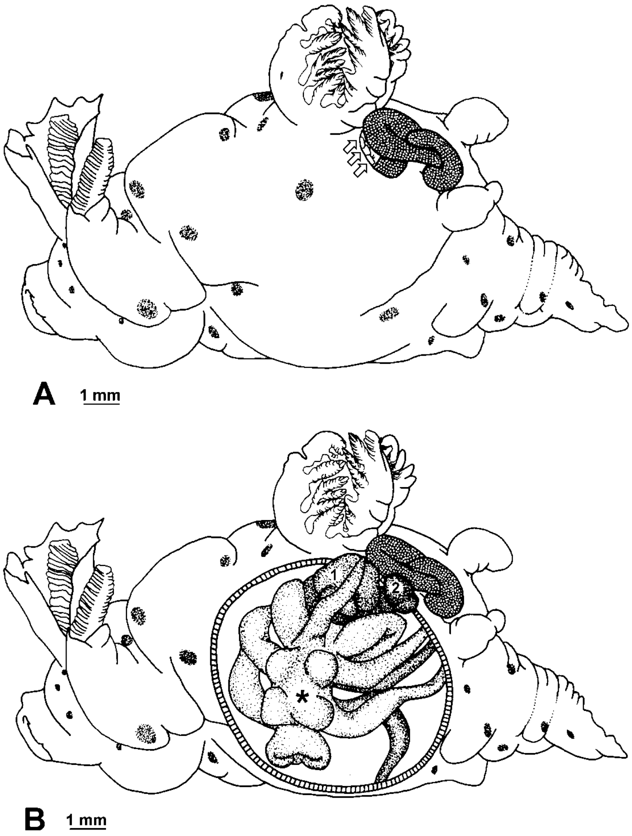

Fig. 2. Preserved *Thecacera darwini* infected by endoparasitic splanchnotrophids. **A.** Undissected host. Note the abdomina of the male and female copepods protruding from the host body wall (arrows), and the pair of copepod egg sacs. **B.** Host with left body wall removed, showing one large female copepod (asterisk) and two dwarf males (1, 2).

nized, shining through their hosts' body tissue or causing deformations. Opisthobranch specimens were narcoticised using a 7–10% $MgCl_2$ solution, and fixed with 70% alcohol or 4% formalin-seawater solutions. Depending on the material available, one to many specimens of each host species were dissected. Only one (*Corambe lucea* Marcus, 1959; see Electr. Suppl. 02–03, Part 1) was found to be infected by a (juvenile) parasite which had not been detected previously by external examination. Complete dissection of 133 specimens of the primary hosts, *Thecacera darwini* Pruvot-Fol, 1950, *Okenia luna* Millen, Schrödl, Vargas & Indacochea, 1994, and *Flabellina* sp. 1 (Millen & Schrödl, submitted), revealed either no infection or infection by at least one mature (i.e. externally detectable) female. Therefore, the infection rates given in this study are conservative in referring to mature parasites, but appear to be close to reality. Parasites were removed from the hosts and identified microscopically. Depending on specimens available, 1 to 15 mature females and generally even more males of each host species were examined using SEM. Results are given within a detailed taxonomic revision by Haumayr & Schrödl (in press).

Results

2257 notaspidean, sacoglossan and nudibranch specimens belonging to 47 different species were collected (Electr. Suppl. 02–03, Parts1 and 2). An additional 13 specimens from the Magellan Strait and the Beagle Channel area came from the International Magellanic "Victor Hensen" Expedition, 1994 (see Schrödl 1996a). Endoparasitic copepods of the family Splanchnotrophidae were detected in 303 host specimens. Using Jensen's (1987) and Huys's (2001) reviews of the Splanchnotrophidae, all parasites were identified as members of the genus *Ismaila* Bergh, 1867 due to both males and females having well developed thoracic appendages (i.e. legs). Females have a single postero-dorsal process (see Fig. 2B) which is characteristic of the genus *Ismaila*. Parasites from different host species can be clearly distinguished from each other, and have been described as new species within a detailed revision of the genus *Ismaila* separately (Haumayr & Schrödl, in press). The hosts belonged to eight different species (Electr. Suppl. 02–03, Parts 1 and 2), seven nudibranchs (four Aeolidoidea, three Doridoidea) and one shell-less sacoglossan.

The total frequency of infection was 13%, but this varied geographically (Fig. 1; Electr. Suppl. 02–03, Part 1). At northern Chilean collecting sites, only four of 444 (0.9%) potential hosts were infected, and all were *Thecacera darwini* (Fig. 2B). In central Chile, at the Bay of Coliumo and Queule, 245 of 1432 (17%) and 29 of 142 (20%) hosts belonging to several species were parasitized (Electr. Suppl. 02–03, Part 1). Further south, Chilean localities yielded 28 of 317 (12%) potential hosts infected. The 17 hosts from the Magellan Strait (Electr. Suppl. 02–03, Part 1) all belonged to the sacoglossan *Elysia patagonica* Muniaín & Ortea, 1997. No parasites were found within any of the 83 Argentinian specimens.

Prevalence of infection clearly varies between the different host species (see Electr. Suppl. 02–03, Part 2). Examination of all specimens of *Corambe lucea*, *Flabellina falklandica* Eliot, 1907 and *Aeolidia papillosa serotina* Bergh, 1873 revealed only single infected animals. Infestation levels reached up to 10% in *A. papillosa serotina* (Electr. Suppl. 02–03, Part 2), but due to the small numbers of specimens available these values may change after examining more material. *Phidiana lottini* (Lesson, 1831) was found in high numbers (n = 243) at several southern, central and northern Chilean localities, but with only three specimens from the Bahía de Coliumo infected it has only 1.2% prevalence. Seventeen of the 19 specimens of *Elysia patagonica* from the Magellan Strait were parasitized, resulting in nearly 90% infection. *Thecacera darwini*, *Flabellina* sp. 1, and *Okenia luna* reached 28 to 70% total infection (Electr. Suppl. 02–03, Part 2).

Infection frequencies of primary host species showed little variation during different seasons and years in the Bahía de Coliumo. *Okenia luna* was found only during the southern summer, with infection rates of 50% in January 1994 (n = 8 specimens) and 70% in March to April 1992 (n = 122). *Flabellina* sp. 1 was collected in higher numbers in January 1994, April 1992 and September 1996 (40, 14 and 31 specimens, respectively), with 16, 3, and 15 specimens infected, corresponding to 21–48% prevalence. None of the three specimens from March 1994 was infected. Populations of *Thecacera darwini* showed consistently high infection levels (70–100%) in Bahía de Coliumo (Fig. 3A). All 20 specimens collected in January 1994 were infected, as well as 21 of 24 from February 1995, 17 of 18 from March 1994, 54 of 77 found in April 1992, and 5 of 6 specimens from September 1996.

Geographical differences in the level of infection were evident for the widespread *Thecacera darwini* (Fig. 3B). During March 1994, 96% of hosts were infected (n = 24 specimens) in the central Chilean Bahía de Coliumo, but these rates were very low in the northern Chilean localities Pichidangui (2%; n = 150), Los Hornos (0%; n = 6), Bahía Inglesa (1.6%; n = 61), and Juan López (0%; n = 18). From central Chile southwards

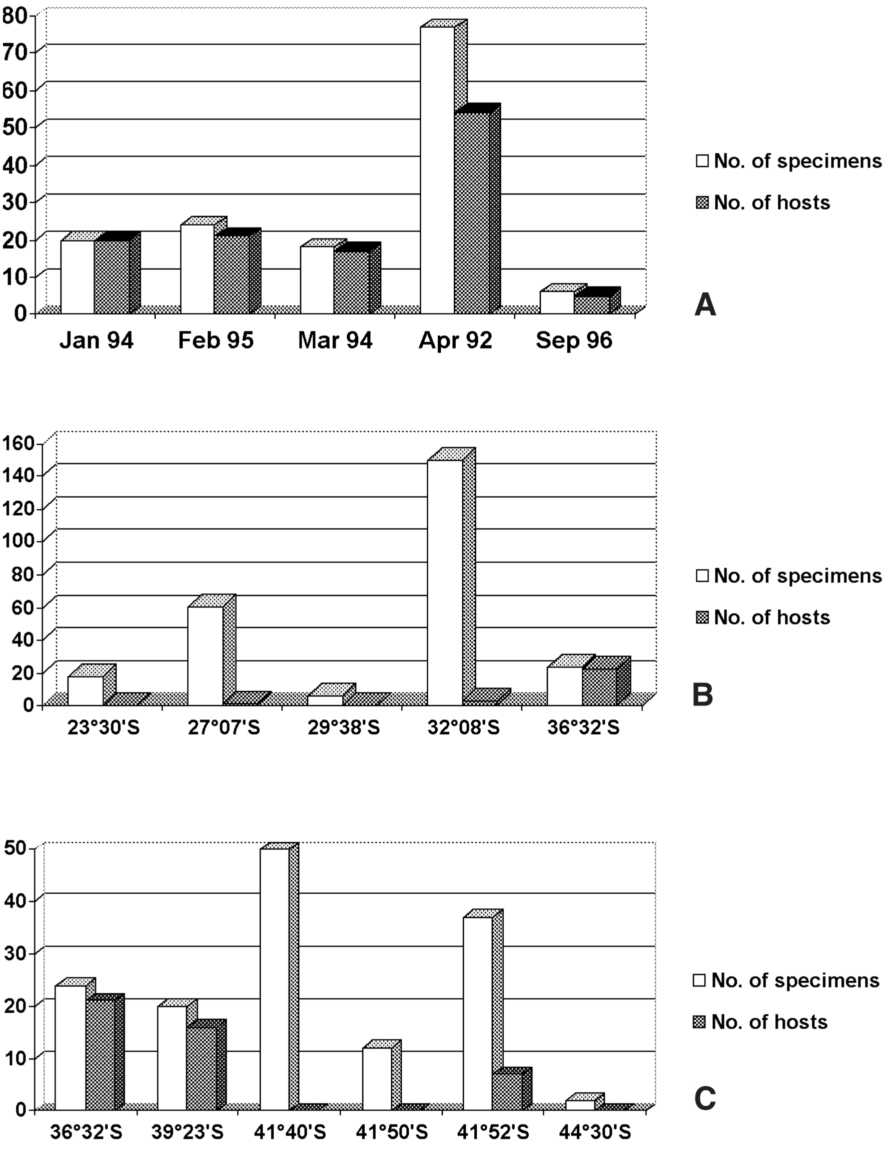

Fig. 3. Temporal and geographical variation in the rate of infection of *Thecacera darwini*. **A.** Bay of Coliumo during different seasons and years. **B.** Northern and central Chilean localities (see Electr. Suppl. 02-03, Part 1) during March 1994. **C.** Central and southern Chilean localities during 24 December 1994 to 5 February 1995.

there also was a trend towards lower infection levels, although the data are more limited and extend over a longer period (six weeks) (Fig. 3C). On 5 February 1995, 21 of 24 (88%) *T. darwini* were infected in the Bay of Coliumo. In late January 1995 the infestation was 80% (n = 20) in Queule. In late December 1994, infection was low (0–19%) at three localities near Chiloé Island, with 12, 37 and 50 specimens examined. Only two specimens were found at Seno Ventisquero, Puyuhuapi Channel (January 1995), both without parasites.

Discussion

Hosts

According to Huys's (2001) revision, there are 10 named and some unnamed splanchnotrophid species with 43 host species. The present study reports eight Chilean opisthobranch species as hosts for *Ismaila* spp. (see Electr. Suppl. 02–03, Part 2). An additional *Ismaila* specimen was previously found by Bergh (1898) in the Chilean cryptobranch *Anisodoris fontaini* (D'Orbigny, 1837) (as *Archidoris incerta* Bergh, 1898; Schrödl 2000), and Marcus (1959) detected splanchnotrophids in three further host species from Chiloé Island. In all, 12 Chilean opisthobranch species are now known to be infected with endoparasitic splanchnotrophids, nine of them certainly with *Ismaila* species. Adding four host species to Huys's (2001) list (Marcus 1959, this study), the number of hosts known worldwide increases to 47. Thus, a surprising 26% of all species known to be infected with splanchnotrophid copepods, and at least nine of the 14 (64%) known *Ismaila* hosts occur in Chilean waters. With a total of only about 65 valid nudibranch, notaspidean and sacoglossan species in Chile (Marcus 1959; Schrödl 1996, 1999a,b; 2000; author's unpublished data), in relation to well over 3000 opisthobranch species known worldwide (Boss 1971, Gosliner & Draheim 1996), the percentage of infected opisthobranch species in Chile is more than 10 times higher than the worldwide average. Collecting bias can largely be excluded since many regions of the world's oceans have been investigated much more thoroughly over the last centuries than the Chilean coast, and most opisthobranch researchers with a worldwide activity (e.g. Bergh, Marcus) would have mentioned the findings of endoparasites not only from Chilean but from any material studied. In Oregon (USA), the location of the only comparable study in which several thousand opisthobranchs were examined for parasites, only one (*Janolus fuscus*) of 26 potential host species was parasitized by splanchnotrophids (Belcik 1981).

With present knowledge (Huys 2001, this study), the rate of opisthobranch species infected divided by the total number of opisthobranch species is zero in polar waters, and very low (<< 1%) in tropical waters, possibly with some spots of higher infection levels such as western Australia, New Caledonia and the Caribbean (see also Fig. 4). Higher prevalences are found in certain, but not all temperate areas: there are three adequately documented splanchnotrophid host species –

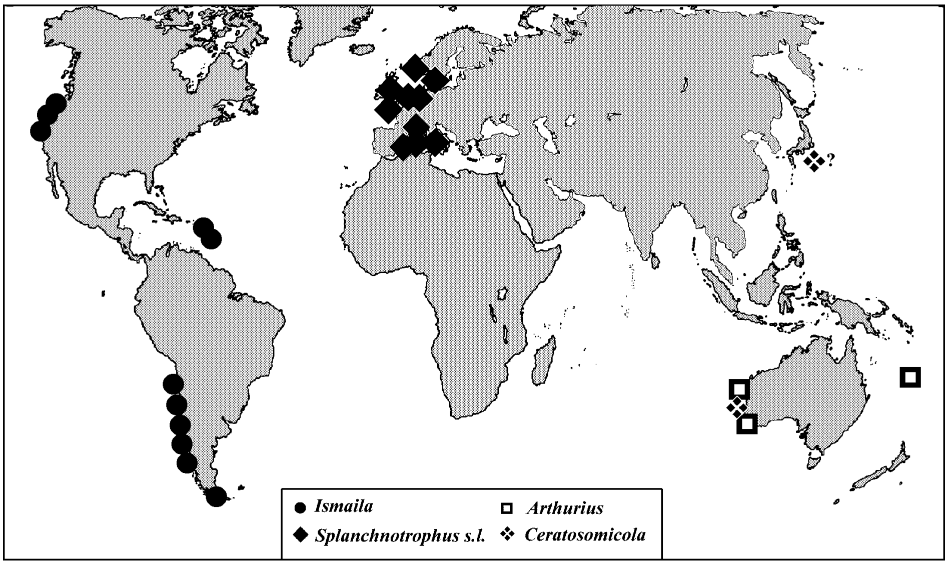

Fig. 4. Geographical distribution of endoparasitic splanchnotrophid genera (data from Jensen 1987, 1990; Huys 2001; this study). Note the geographical separation of *Ismaila* (eastern Pacific and Caribbean), *Splanchnotrophus* s.l. (northeastern Atlantic, Mediterranean), and *Arthurius* and *Ceratosomicola* (a few records from the Indo-West Pacific and, possibly, Japan).

other records by Monod & Dollfus (1934) and Belcik (1981: "Illg, in lit.") require confirmation – from the entire Pacific coast of North America (Jensen 1987), comprising less than 2% of the corresponding nudipleuran (Pleurobranchoidea plus Nudibranchia; see Wägele & Willan 2000) and sacoglossan fauna (see Behrens 1991). Highest levels of infection occur on the Mediterranean and northeastern Atlantic coasts, as well as in Chile where about 20% of nudibranch species, and one of the six sacoglossan species (see Schrödl 1996, 1999a), are at least occasional hosts of splanchnotrophids (this study).

Prevalence

The total infection level (13%) of Chilean opisthobranchs examined was exceptionally high. Prevalences do, however, depend strongly on the species involved: in each of the six Chilean host species only a single specimen was parasitized (Bergh 1898; Odhner 1926; Marcus 1959; this study, Electr. Suppl. 02–03, Part 2). Rates were also low for *Phidiana lottini* (Electr. Suppl. 02–03, Part 2) and *Acanthodoris falklandica* (Marcus 1959; this study, Electr. Suppl. 02–03, Part 2). Infection of a single or very few specimens also appears to be the norm in most other known splanchnotrophid host species (see Ho 1987b, Jensen 1987). This is in contrast to Hecht's (1895) observation that splanchnotrophid parasites are seasonally frequent in *Aeolidia papillosa* in Europe. The only quantitatively documented information on higher infection rates within opisthobranch populations is that of a 62% prevalence (no numerical data) of *Ismaila belciki* (as *I. monstrosa*) found in the northeastern Pacific *Janolus fuscus* by Belcik (1981). More recently, infection prevalences in Chilean populations of *Okenia luna* and *Flabellina* sp. 1 were shown to be high (70% and 43%, respectively; see Millen et al. 1994, Schrödl 1997). The present study summarizes these infection data collected in Chile over six years, resulting in 1.2% to 89.5% total infection for eight opisthobranch host species (Electr. Suppl. 02–03, Part 2). These are the highest prevalences documented.

Infection rates might vary seasonally or geographically. The limited data available from the primary host species within the Bay of Coliumo indicate relatively constant and high infection prevalence in *Okenia luna* (50–70%) and *Thecacera darwini* (70–100%; Fig. 3A) over different seasons and years, but a lower and more variable level in *Flabellina* sp. 1 (0–48%). Further studies on this seasonality aspect are required.

Remarkable geographical differences in the rate of infection are evident in the wide ranging *Thecacera darwini*. Figures 3B, C show very high prevalences (88% and 96%) in the central Chilean Bay of Coliumo, in contrast to 0% or 2% at northern and 0–19% at southern Chilean localities. The total infection of *Okenia luna* was high in the Bahía de Coliumo (50–70%), but no parasites were mentioned from any of eight specimens from Peru (Millen et al. 1994). The northernmost record of splanchnotrophids from the South American Pacific coast (Fig. 4) is a female *Ismaila* sp. which was present in the single *O. luna* specimen from Iquique (northern Chile) but not recognized as a copepod by Muñoz et al. (1996: Fig. 2B).

From the Chilean coast south of Chiloé Island and from the South American Atlantic coast the only records of splanchnotrophids are a single infected *Flabellina falklandica* from the Puyuhuapi Channel (44°30´S), and a frequently infected population of *Elysia patagonica* in the Magellan Strait (Fig. 4), while Argentinian populations do not show any infection (Muniaín, pers. comm.). Thus, the high incidence of splanchnotrophid parasites in Chilean nudibranchs refers almost exclusively to the central Chilean coast south to Chiloé Island. Possible reasons, e.g. a high density of potential hosts, special hydrographic conditions such as frequent upwellings, or even human impact in this comparatively densely populated and industrialized zone, remain speculations until more is known about the biology of splanchnotrophids and their hosts. High parasite abundances coupled with the high number of species specialized on certain hosts (see Haumayr & Schrödl, in press) suggest that central Chile may be a centre of speciation for the genus *Ismaila*.

Biogeography and evolution

Jensen (1987) suspected splanchnotrophid genera to have host preferences amongst the different groups of shell-less Opisthobranchia. This might indicate an evolutionary adaptation to certain host clades as is already known from several other parasitic copepod groups (Gotto 1979). However, *Ismaila* and *Splanchnotrophus* s.l. (including *Lomanoticola*) are the only genera of Jensen's (1987) list still recognized as Splanchnotrophidae by Huys (2001). Chilean *Ismaila* hosts, beside four aeolidoidean species, also include one sacoglossan and four doridoidean species (Bergh 1867; this study). Together with the record from the "arminoidean" *Janolus fuscus* (see Belcik 1981), *Ismaila* thus occurs in all major traditional nudibranch subgroups and in Sacoglossa. *Splanchnotrophus* (s.l.) species parasitize a similar array of hosts including Sacoglossa and major nudibranch groups except for "Arminoidea" (see Huys 2001). Two splanchnotrophid genera recently established by Huys (2001) are known from a few records: *Arthurius* (one named and one unnamed species) was found in two *Elysia* species (Sacoglossa), and *Ceratosomicola* (one named and, possibly, one unnamed species) was mentioned from two chromodorid nudibranch hosts. Since the copepod parasitizing a pleurobranchid specimen (*Berthellina citrina*) from the Red

Sea (see Jensen 1987) was considered to belong to the Philoblennidae by Huys (2001), there are no records of notaspideans infected by splanchnotrophids. In summary, all Splanchnotrophidae appear to be limited to Sacoglossa and Nudibranchia. The major splanchnotrophid groups thus either split early (no data available), prior to the times of the last common ancestor of Nudibranchia and Sacoglossa, or they gained the ability to parasitize these different shell-less opisthobranch host groups later and independently from each other.

With present data (Huys 2001, this study), the splanchnotrophid genera are geographically disjunct, each displaying certain areas of high incidence (Fig. 4): *Splanchnotrophus* s. l. (with two sympatric subgroups, *Splanchnotrophus* and *Lomanoticola*) has been exclusively reported from the temperate northeastern Atlantic and the Mediterranean, *Arthurius* from western Australia and New Caledonia, and *Ceratosomicola* from the Houtman Abrolhos Islands and, possibly, Japan (see Huys 2001). *Ismaila* specimens have generally been found in temperate northeastern and southeastern Pacific waters, but only twice in the Caribbean (Jensen 1987, 1990; this study, Fig. 4). Thus, with our present knowledge, the ranges of splanchnotrophid genera do not overlap. Since at least the better known genera, *Splanchnotrophus* and *Ismaila*, comprise species parasitizing a similar array of cosmopolitan clades of opisthobranchs (Sacoglossa and Nudibranchia, and many different subgroups of the latter), it is concluded that the *Splanchnotrophus* and *Ismaila* clades evolved independently from their host opisthobranch clades. It appears that relatively eurytrophic (i.e. not host-specific) common ancestors might have become geographically isolated (in the Atlantic?), and have both undergone parallel radiation since, becoming specialized on a variety of host species which are not necessarily closely related. The continuing geographic isolation of *Splanchnotrophus* and *Ismaila* is both evident and surprising, because members of both genera occur within temperate and tropical waters. Splanchnotrophids have pelagic larvae (Belcik 1981, Ho 1987b, author's observations) and thus a considerable dispersal potential. Relatively strict host preferences may, however, have hindered successful colonization of areas without an adequate host. On the other hand, the consistently high rates of infection of central Chilean populations of *Thecacera darwini* by *Ismaila* sp. 1, coupled with the near absence of parasites in northern and southern host populations, indicate the existence of splanchnotrophid parasite requirements other than the abundant presence of appropriate hosts.

The occurrence of *Ismaila* species on both sides of the Isthmus of Panama suggests a common ancestor of this clearly monophyletic group (Huys 2001, Haumayr & Schrödl in press) older than 2–5 million years – before the closing of the eastern Pacific-Caribbean connection. Assuming dispersal from the Caribbean and subsequent geographical separation by vicariance it seems likely that the ancestor(s) of temperate northeastern and southeastern Pacific *Ismaila* species were adapted to tropical waters. At present (see Fig. 4), the temperate species appear isolated from each other by the tropics and thus may have radiated in parallel. Phylogenetic analyses confirming this scenario would be desirable and could give valuable insights into the evolutionary processes and time scales of marine invertebrate host-parasite associations.

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References

Bassett-Smith, P. W. (1903): On new parasitic Copepoda from Zanzibar and East Africa, collected by Mr. Cyril Crossland, B.A., B.Sc. Proc. Zool. Soc. London (1903): 104–109.

Behrens, D. W. (1991). Pacific Coast Nudibranchs. 107 pp, Sea Challengers, Monterey.

Belcik, F. P. (1981): The male of *Ismaila monstrosa* Bergh, 1867 (Copepoda, Splanchnotrophidae). Crustaceana 40: 16–25.

Bergh, L. S. R. (1867): *Phidiana lynceus* og *Ismaila monstrosa*. Videnskab. Meddr. Dansk. Naturh. Foren. (1866): 97–130, pls. 3–4.

Bergh, L. S. R. (1876): Malacologische Untersuchungen. Pp. 10–14 in: Semper, C. (ed.) Reise im Archipel der Philippinen 2: 377–645, pls. 49–68.

Bergh, L. S. R. (1879): Beiträge zur Kenntniss der Aeolidiaden, VI. Verh. Kaiserl.-königl. zool.-bot. Ges. Wien (1878): 553–584, pls. 6–8.

Bergh, L. S. R. (1898): Die Opisthobranchier der Sammlung Plate. Zool. Jahrb., Suppl. 4: 481–582.

Boss, K. J. (1971): Critical estimate of the number of recent Mollusca. Occas. Pap. Moll. 3: 81–135.

Gosliner, T. M. & Draheim, R. (1996): Indo-Pacific opisthobranch gastropod biogeography: how do we know what we don't know. Amer. Malacol. Bull. 12: 37–43.

Gotto, R. V. (1979): The association of copepods with marine invertebrates. Adv. Mar. Biol. 16: 1–109.

Gotto, R. V. (1986): A new parasitic copepod crustacean of uncertain affinities: *Megallecto thirioti* n. gen. n. sp.. Bull. Zoöl. Mus. Univ. Amsterdam 10: 185–189.

Hancock, A. & Norman, A. M. (1863): On *Splanchnotrophus*, an undescribed genus of Crustacea, parasitic in nudibranchiate Mollusca. Trans. Linn. Soc. Lond. 24: 49–60, pls. XV–XVI.

Haumayr, U. & Schrödl, M. (in press): Revision of the endoparasitic copepod genus *Ismaila* Bergh, 1867 (Poecilostomatoida: Splanchnotrophidae), with description of eight new species. Spixiana.

Hecht, E. (1895): Contributions a l'étude des nudibranches. Mem. Soc. Zool. France 8: 539–711.

Ho, J.-S. (1981): *Ismaila occulta*, a new species of poecilostomatoid copepod parasitic in a dendronotid nudibranch from California. J. Crust. Biol. 1: 130–136.

Ho, J.-S. (1987a): Reconsideration of *Ismaila monstrosa* Bergh, 1867 (Copepoda, Splanchnotrophidae) from Oregon. Crustaceana 52: 109–111.

Ho, J.-S. (1987b): Larval stages of *Ismaila occulta* Ho, 1981 and the affinity of Splanchnotrophidae (Copepoda: Poecilostomatoida). Res. Crust. 16: 67–83.

Huys, R. (2001): Splanchnotrophid systematics: a case of polyphyly and taxonomic myopia. J. Crust. Biol. 21: 106–156.

Jensen, K. R. (1987): *Ismaila monstrosa* Bergh (Copepoda: Splanchnotrophidae) found parasitizing in *Ercolania funerea* (Costa) (Gastropoda: Ascoglossa). Ophelia 28: 75–84.

Jensen, K. R. (1990): *Splanchnotrophus elysiae* n. sp. (Copepoda; Splanchnotrophidae) found parasitizing in the sacoglossan opisthobranch *Elysia australis* (Quoy and Gaymard, 1832). Proceedings of the Third International Marine Biological Workshop: the Marine Flora and Fauna of Albany, Western Australia. Western Australian Museum, Perth 1: 291–296.

Laubier, L. (1964): La morphologie des pieces buccales chez Splanchnotrophidae (copépodes parasites de mollusques). Crustaceana 7: 167–174.

Marcus, E. (1959): Lamellariacea und Opisthobranchia. Reports of the Lund University Chile Expedition 1948–49, No. 36. Lunds Univ. Arssk. (2) 55: 1–133.

Millen, S. V. & Schrödl, M. (submitted): The genus *Flabellina* Voigt, 1834 (Opisthobranchia: Aeolidacea) from the Pacific Coast of South America. Zool. J. Linn. Soc.

Millen, S. V., Schrödl, M., Vargas, N. & Indacochea, A. (1994): A new species of *Okenia* (Nudibranchia: Doridacea) from the Peruvian Faunal Province. Veliger 37: 312–318.

Monod, T. & Dollfus, R.-P. (1934): Des copépodes parasites de mollusques. Ann. Parasit. 12: 309–321.

Muñoz, M. A., Valdés, A. & Ortea, J. (1996): The genus *Okenia* Menke, 1830 (Nudibranchia: Goniodorididae) in Chile. Haliotis 25: 101–106.

Odhner, N. H. (1926): Die Opisthobranchien. Further Zool. Res. Swed. Antarct. Exped. 1901–1903, 2: 1–100, pls. 1–3.

Schrödl, M. (1996a): Opisthobranchs (Gastropoda) collected by the research vessel "Victor Hensen". Rep. Polar Res. 160: 52–54.

Schrödl, M. (1996b): Nudibranchia y Sacoglossa de Chile: Morfología exterior y distribución. Gayana Zool. 60: 17–62.

Schrödl, M. (1997): Aspects of Chilean nudibranch biology: effects of splanchnotrophid copepod parasitism on *Flabellina sp*.1. Opisthobranch Newsletter 23: 45–47.

Schrödl, M. (1999a): Zoogeographic relationships of Magellan Nudibranchia (Mollusca: Opisthobranchia), with special reference to species of adjacent regions. In: Arntz, W. E. & Ríos, C. (eds.) Magellan–Antarctic. Ecosystems that drifted apart. Scientia Marina 63 (Supl. 1): 409–416.

Schrödl, M. (1999b): The genus *Berthella* Blainville, 1825 (Notaspidea: Pleurobranchidae) from Magellanic waters. J. Moll. Stud. 65: 399–409.

Schrödl, M. (2000): Taxonomic revision of the common South American nudibranch *Anisodoris fontaini* (D'Orbigny, 1837) (Gastropoda: Opisthobranchia), with discussion of its systematic placement. J. Moll. Stud. 66: 49–61.

Wägele, H. & Willan, R. C. (2000): Phylogeny of the Nudibranchia. Zool. J. Linn. Soc. 130: 83–181.