

PREVALENCE, INTENSITY, AND DIFFERENTIAL DEVELOPMENT OF *PSEUDODELPHIS OLIGOCOTTI* (NEMATODA: DRACUNCULOIDEA) IN SYMPATRIC FISH HOSTS OF THE NORTHEASTERN PACIFIC COAST

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ABSTRACT: Counter to expectations of coevolved parasite–host relationships, parasites frequently infect hosts that never contribute to their reproduction, making the identification of a parasite’s true host-specificity problematic. *Pseudodelphis oligocotti* (Nematoda: Dracunculoidea) infects several coastal Pacific fishes, but its course of development appears highly variable, suggesting that incidence does not reflect effective host range. To determine the host range of *P. oligocotti* and describe its relationship to various potential hosts, 24 fish species were examined from several British Columbia localities for prevalence, intensity, and extent and tissue location of parasite development. *Pseudodelphis oligocotti* infects 9 species of fishes from 5 orders, of which penpoint gunnel, *Apodichthys flavidus*, showed the highest prevalence and intensity, up to 80% and 19 (± 17.1 SD) worms per host, respectively. Although subadult and adult *P. oligocotti* occurred in all 9 fishes, larvigerous *P. oligocotti* only occurred in *A. flavidus* and rarely in the northern clingfish, *Gobiesox maeandricus*. Infective first-stage larvae were recovered from gill tissue of *A. flavidus*. Thus, at most only 2 of the 9 host species infected by *P. oligocotti* actually contribute to its transmission. The occurrence of *P. oligocotti* in diverse hosts may be accounted for by the parasite’s indiscriminate mode of transmission via ingestion of free-living intermediate copepod hosts, where highly exposed or more suitable fishes (or both) are closely related by diet and microhabitat. This study demonstrates how parasite transmission and host ecology can greatly affect observed host range and ultimately its potential for expansion.

When characterizing parasite host specificity, it is desirable to distinguish between hosts that are regularly infected and contribute to parasite transmission versus those that are incidentally infected and may or may not contribute to ongoing transmission, i.e., accidental hosts (Poulin, 1992). Although we might intuitively assume that parasites have coevolved with their hosts to optimize efficiency of such a critical life history step, it is in fact not unusual for parasites to frequently infect hosts that are reproductive dead ends. Targeted transmission to particular hosts would be constrained by ecological relationships to the other hosts in the life cycle. Ultimately, the number of different host taxa infected and their suitability for transmission is not only a reflection of a parasite’s physiological specificity but of ecological factors that relate to method of parasite transmission and host exposure (Kennedy, 1975; Noble et al., 1989; Adamson and Cairns, 1994; Roberts and Janovy, 1996). Leong and Holmes (1981) indicated that of 20 metazoan salmonid parasites, 10 regularly infected nonsalmonid hosts, but only 2 of these matured in such hosts. Bennett et al. (1998) reported that 2 of the 3 dominant helminth species infecting sockeye salmon never mature, instead being maintained by sympatric freshwater fish hosts. Such phenomena challenge our ability to identify those observed hosts that actually contribute to parasite transmission and that can, therefore, be considered elements of a parasite’s effective host range (Lymbery, 1989). Comparative parasite host-specificity studies are becoming increasingly common and to be informative must rely on accurate assessments of host range (Poulin and Mouillot, 2003). In spite of this, studies that acknowledge or address helminthic intraspecific variation across hosts are few (Maizels and Kurniawan-Atmadja, 2002; Rohde, 2002) and are outnumbered by those that examine host use, e.g., parasite species richness, at the community level (reviewed by Poulin, 1997). In fact, parasite diversity, so much higher than that of free-living species (Poulin and Morand,

2000), has been associated with transfers to novel hosts particularly among marine vertebrates, which, in turn, is linked to parasite transmission along trophic networks (Hoberg and Klassen, 2002).

Pseudodelphis oligocotti Adamson and Roth, 1990 (Nematoda: Dracunculoidea) is a parasite found in several northeastern Pacific coastal fishes, in which it infects a variety of organs and appears to follow a variable course of development. As with most dracunculoid nematodes, *P. oligocotti* is transmitted between fish hosts by ingestion of a copepod intermediate host, which ingests free-swimming L1 parasite larvae, which become infective to fish after approximately 30 days (as third-stage larvae, L3) (Bennett, 1999; Anderson, 2000). In the case of *P. oligocotti*, L1s exit the fish host via the gills, immediately upstream from larvigerous adults (stage L5) residing in the heart (Bennett, 1999). However, in some fishes, *P. oligocotti* appears to migrate to organs other than the heart, and mature forms are not always found, suggesting that not all fish hosts actually contribute to successful parasite transmission. For example, although *P. oligocotti* was first described from the body cavity of tidepool sculpin (*Oligocottus maculosus* Girard, 1856), gravid adult parasites were never found (Adamson and Roth, 1990). Fishes infected by *P. oligocotti* form diverse communities in rocky intertidal zones of intermediate wave exposure, subtidal eelgrass beds, or both. Thus, the frequency with which *P. oligocotti* infects various hosts, its abundance, and even extent of development observed in those hosts may reflect not only physiological compatibility but also potential host exposure rate. Because *P. oligocotti* is transmitted through the food chain, we expect it to be distributed to fishes in proportion to overlap in diet and microhabitat.

The goal of the present study was to characterize the host distribution and developmental variation of trophically transmitted *P. oligocotti*, to identify the principle definitive host(s) that contributes to its transmission in nature, and to better understand the biology of, or preceding, the expansion of parasite host range by host capture. Toward this end, we surveyed fishes throughout the parasite’s geographic range for infection, the ex-

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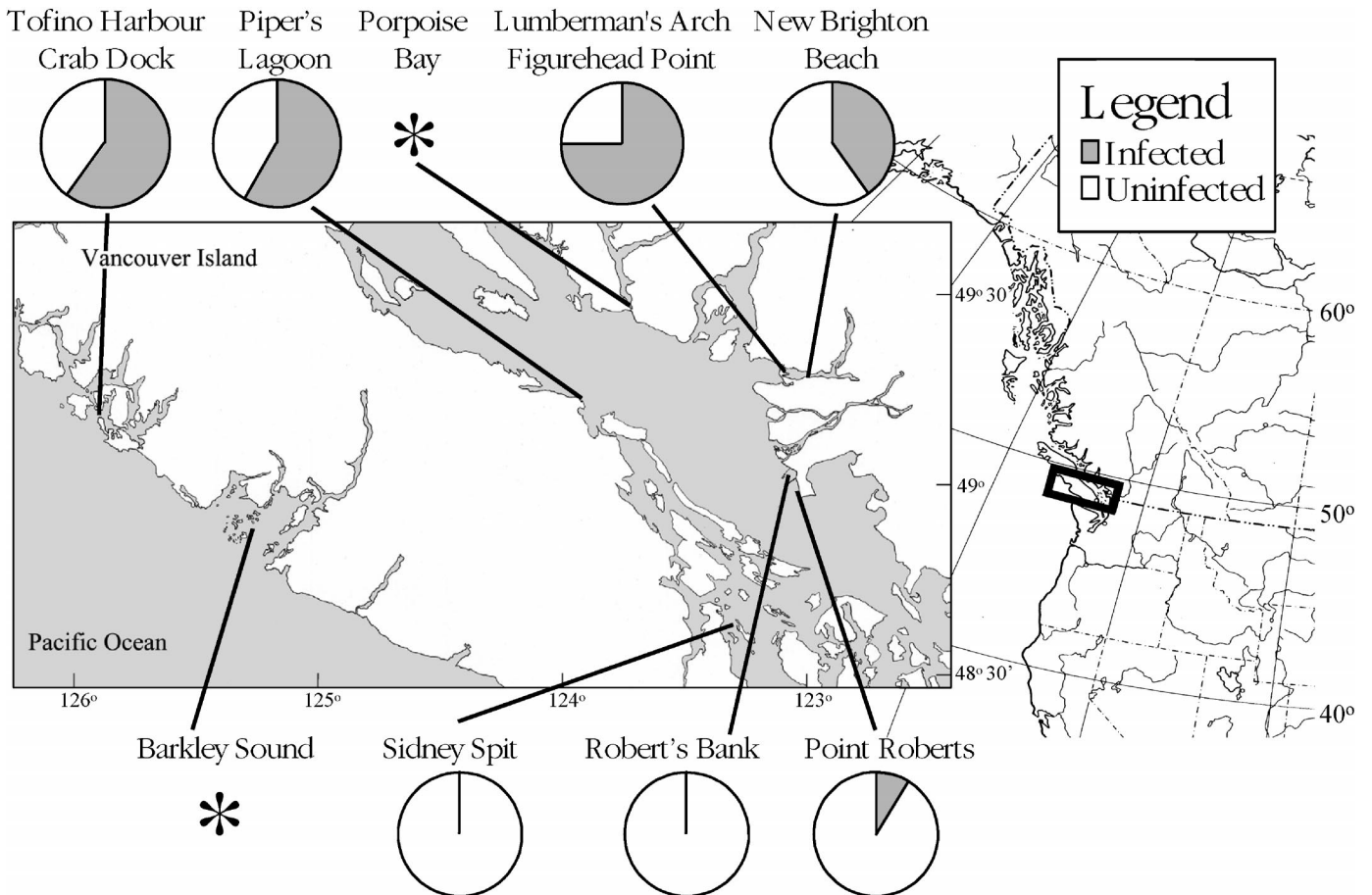


FIGURE 1. Map of British Columbia localities surveyed for *Pseudodelphis oligocotti*. Proportion of infected *Apodichthys flavidus* is indicated by shaded portion of pies. Empty pies mean that *A. flavidus* was uninfected with *P. oligocotti*. Localities marked with an asterisk indicate that sites were sampled, but no *A. flavidus* was captured; *P. oligocotti* did not occur at these sites in any fish surveyed.

tent of development achieved by *P. oligocotti*, and tissue location of infection by stage and host species. Results provide important information on the relative impact of host ecology and host–parasite physiological compatibility on perceived and actual parasite host specificity.

MATERIALS AND METHODS

Field collections

Potential *P. oligocotti* host fish species were collected from 2 main coastal habitats in southern British Columbia: subtidal eelgrass (*Zostera marinus*) beds and rocky intertidal flats. The former were sampled with a pole seine (length 2 m, height 1.5 m, diagonal mesh size 11 mm), typically covering approximately 16–136 m² of substrate per sampling event. Rocky intertidal sites were sampled by overturning exposed rocks at low tide. Although we sampled up to 10 localities throughout coastal British Columbia at least once to determine parasite geographic range (Fig. 1), we focused primarily on sites: Lumberman's Arch and Figurehead Point, Vancouver, British Columbia; Point Roberts, Washington; and Roberts Bank, British Columbia. Rocky Figurehead Point and the adjacent eelgrass beds of Lumberman's Arch were sampled on spring tides from spring to midwinter in 1991, 1992, and 1995, throughout the year in 1993 and 1994, sporadically in spring, summer, and fall 1996–1997, and in spring 1998. Point Roberts and Roberts Bank were sampled on spring tides, twice in the spring of 1993, throughout the year in 1994, and sporadically from 1995 to 1997. Fish nomenclature and taxonomic information were updated from FishBase (<http://www.fishbase.org/home.htm>).

Dissections

Fish were necropsied within 72 hr of capture for intensity, developmental stage, and tissue location of *P. oligocotti*, giving rise to derived statistics on prevalence and mean intensity by species, location, and season (terminology from Bush et al., 1997). *Pseudodelphis oligocotti* was identified by morphological examination of adults (L5) using microscopy, based on the description by Adamson and Roth (1990). Voucher specimens from the various host species are available at the University of Nebraska State Museum (accession numbers HWML 45531–45556).

We killed fishes before dissection with tricaine methanesulfonate (MS222) as an anesthetic, identified them to species, measured (total length, to caudal tip), and sexed them. A ventral incision along the entire body length exposed body cavity, gills, and other internal organs (liver, hepatic sinus, heart, common cardinal vein, and gonads) for examination. Liver and heart were reserved for further histological examination. Gills were divided for examination by either dissecting microscope (at $\times 4$ magnification) or histology. Live nematodes were isolated and maintained in 0.67% sodium chloride solution for determination of stage and sex (see below). Dead worms, often encapsulated within host tissue, were removed to a solution of 70% ethanol and 5% glycerine with phenol (70% EtOH–5% glycerine–phenol).

Determination of stage and sex of *Pseudodelphis oligocotti*

We identified stage and sex of nematodes with the aid of a compound microscope (under $\times 4$ to $\times 200$ objectives). A dorsal cephalic swelling and little cellular differentiation distinguish first-stage larvae. Older larvae (third to fourth developmental stage) have developing gonads that

TABLE I. Potential hosts of *Pseudodelphis oligocotti*: number of hosts sampled, prevalence (percent infected), and, if infected, the number of hosts that contained mature stages (females with either embryos or first-stage larvae in utero) of *P. oligocotti*.

	Sample size	Prevalence	No. containing females with	
			embryos	larvae
Batrachoidiformes				
<i>Porichthys notatus</i>	1	0		
Gobiesociformes				
<i>Gobiesox maeandricus</i>	15	47	0	1
Gasterosteiformes				
<i>Aulorhynchus flavidus</i>	1	0		
<i>Syngnathus leptorhynchus</i>	653	22	10	0
<i>Gasterosteus aculeatus</i>	1	100	0	0
Perciformes				
<i>Cymatogaster aggregata</i>	2	0		
<i>Anoplarchis purpurescens</i>	15	0		
<i>Xiphister mucosus</i>	1	0		
<i>Lumpenus sagitta</i>	2	0		
<i>Apodichthys flavidus</i>	402	45	67	95
<i>Pholis laeta</i>	105	54	1	0
<i>Ph. ornata</i>	63	44	0	0
Scorpaeniformes				
<i>Hexagrammus stelleri</i>	1	0		
<i>H. decagrammus</i>	4	0		
<i>Leptocottus armatus</i>	45	9	0	0
<i>Artedius fenestralis</i>	9	0		
<i>A. lateralis</i>	3	33	0	0
<i>Oligocottus maculosus</i>	1	100	0	0
<i>Enophrys bison</i>	8	0		
<i>Blepsias cirrhosus</i>	1	0		
Pleuronectiformes				
<i>Platichthys stellatus</i>	1	0		
<i>Hippoglossoides elassodon</i>	11	0		
Salmoniformes				
<i>Oncorhynchus nerka</i>	1	0		
Rajiformes				
<i>Raja binoculata</i>	1	0		

may range from a few cells to a complete organ short of a patent vulva (in the case of a female) or short of a coiled tail with spicules (in the case of a male). The fifth, adult, stage was designated if either the vulva was patent (in the case of a female) or the tail was coiled (in the case of a male) (Adamson and Roth, 1990). For larger gravid females we determined whether the uterus contained either developing embryos (ovigerous) or first-stage larvae (larvigerous). Nematodes were fixed in hot (50–55 C) 70% EtOH–5% glycerine–phenol and stored according to fish host, tissue site in the host, sex, and stage.

RESULTS

We examined 1,386 marine fish belonging to 24 species for *P. oligocotti* (Table I). *Pseudodelphis oligocotti* infected up to 9 of these species (426 individuals, Table I) at 7 of the 10 British Columbia localities surveyed between 1991 and 1998 (Table II). Overall, *P. oligocotti* was most prevalent in the pholids penpoint gunnel (*Apodichthys flavidus* Girard, 1854), crescent gunnel (*Pholis laeta* Cope, 1873), and saddleback gunnel

(*Ph. ornata* Girard, 1854), and the gobiesocid northern clingfish (*Gobiesox maeandricus* Girard, 1858, Table I).

Locality differences in the distribution of *Pseudodelphis oligocotti*

Fishes from 7 of the 10 surveyed sites (Lumberman's Arch and Figurehead Point, Point Roberts, Roberts Bank, Piper's Lagoon, New Brighton Beach, and Tofino Harbour Crab Dock) were infected with *P. oligocotti*. However, *P. oligocotti* varied by site in prevalence and host species infected (Table II). *Apodichthys flavidus* was always among the infected host species at all sites positive for *P. oligocotti* with the exception of Roberts Bank, where *P. oligocotti* occurred in fish species other than *A. flavidus*, i.e., bay pipefish *Syngnathus leptorhynchus* Girard, 1854, *Ph. ornata*, and *Ph. laeta* (Fig. 1; Table II). For a given species, *A. flavidus* was also the most prevalently infected host

TABLE II. Prevalence (followed by fish sample size), in addition to mean intensity (followed by range of intensity) in italics, of *Pseudodelphis oligocotti* for each infected fish species at each locality positive for *P. oligocotti*. Number of times a locality was surveyed is included. In cases where only a single infected individual was recovered for a given host species, intensity is provided.

	Lumberman's Arch	Figure-head Point	Point Roberts	Roberts Bank	Piper's Lagoon	New Brighton	Tofino Harbour
No. surveys		72*	11	10 0 (68)	3	2	1
<i>Apodichthys flavidus</i>	0.75 (213), 19 (1-84)	0.80 (5), 18.5 (7-36)	0.09 (78), 1.4 (1-3)		0.58 (12), 4.7 (2-9)	0.40 (5), 1 (1-1)	0.60 (5), 5.7 (2-12)
<i>Gobiosox maeandricus</i>	1 (2), 6.5 (4-9)	0.36 (11), 1.3 (1-2)			1 (1), 1 (1)	0 (1)	
<i>Syngnathus leptorhynchus</i>	0.24 (599), 5.5 (1-40)		0 (6)	0.02 (46), 0.20 (5), 2		0 (2)	
<i>Pholis laeta</i>	0.65 (74), 4.8 (1-47)	0.78 (9), 3.7 (1-7)	0.13 (8), 1	0.14 (7), 1			
<i>Ph. ornata</i>	0.77 (30), 3.9 (1-15)		0.25 (16), 1.5 (1-3)				
<i>Leptocottus armatus</i>	0.15 (27), 1.8 (1-3)		0 (3)	0 (8)			
<i>Artedius lateralis</i>	0.5 (2), 1		0 (1)				
<i>Oligocottus maculosus</i>	1 (1), 6						
<i>Gasterosteus aculeatus</i>	1 (1), 1						

* Sum of surveys from either site, which lie adjacent to each other and together constitute main study site.

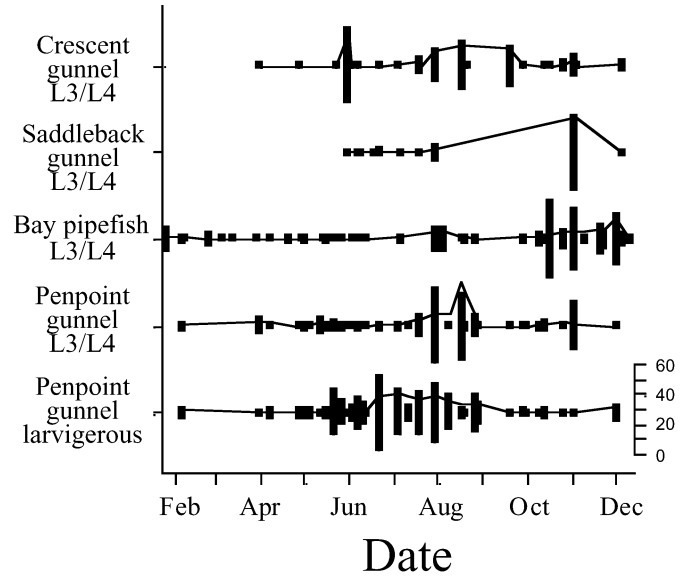


FIGURE 2. Seasonal relationship between total number of larvigerous *Pseudodelphis oligocotti* recovered from *Apodichthys flavidus* caught at particular time of year and total number of larval stages of *P. oligocotti* (L3 or L4) in *A. flavidus*, bay pipefish (*Syngnathus leptorhynchus*), saddleback gunnel (*Pholis ornata*), and crescent gunnel (*Ph. laeta*) caught at a particular time. Vertical bars represent number of worms (scale bar in far right corner applies to all categories). Lines represent robust (3 iterations) estimates of each point using the nearest 0.1625 points of the data set to generate the estimate (lowess function, Mathssoft 1997).

at any 1 site, i.e., 80% at Figurehead Point (Table II). Three sites did not support *P. oligocotti*, i.e., Porpoise Bay, Sidney Spit, and Barkley Sound; however, of these, *A. flavidus* was only recovered from Sidney Spit (Fig. 1).

Prevalence and intensity of *Pseudodelphis oligocotti* in hosts recovered from primary study sites

At the main study sites (Lumberman's Arch and Figurehead Point), *P. oligocotti* was most prevalent (>65%) in the 3 pholids (*Ph. laeta*, *Ph. ornata*, and *A. flavidus*); it also frequently infected *S. leptorhynchus* (24%), *G. maeandricus* (46%), and *Leptocottus armatus* Girard, 1854, or staghorn sculpin (15%) (Table II). In addition, *P. oligocotti* was recovered occasionally from threespine stickleback (*Gasterosteus aculeatus* Linnaeus, 1758), smoothhead sculpin (*Artedius lateralis* Girard, 1854), and tidepool sculpin (*O. maculosus*) (Table II). Intensity of *P. oligocotti* at the main study sites was highest in *A. flavidus* (mean intensity of 19 worms, Table II), by 3-fold the next most intensely infected host *S. leptorhynchus* (5.5). Mean intensities were 3.9 and 4.7 in *Ph. ornata* and *Ph. laeta*, respectively (Table II).

Seasonal fluctuations in prevalence and intensity at primary study sites did occur, with larvigerous *P. oligocotti* reaching peak levels in *A. flavidus* throughout June to August and larval stages (third or fourth) reaching peak abundances in August to September, with another pulse in November (Fig. 2). In other words, there was 1.5- to 2-mo time lag between peaks in larvigerous adults and the stage infective to fishes, corresponding to experimental findings that development in copepod intermediate hosts requires approximately 1 mo under laboratory

TABLE III. Summary of intensities by developmental stage of *Pseudodelphis oligocotti* and tissue site of infection for fishes caught at all study sites.

	Tissue site	Stage				Total no. worms*
		L3/L4	L5	Gravid (eggs)	Gravid (larvae)	
<i>Apodichthys flavidus</i>	Body cavity	283	1,517			1,800
	Circulatory system†	2	126	256	460	844
	Gills					40
	Other‡		1			1
<i>Gobiesox maeandricus</i>	Body cavity		17			17
	Circulatory system†				1	1
<i>Syngnathus leptorhynchus</i>	Body cavity	191	424	8		623
	Circulatory system†	15	44	1		60
	Other§	4	35	1		40
<i>Pholis laeta</i>	Body cavity	123	93			216
	Circulatory system†		2	1		3
<i>Ph. ornata</i>	Body cavity	26	60			86
	Circulatory system†		1			1
<i>Oligocottus maculosus</i>	Body cavity		6			6
<i>Leptocottus armatus</i>	Body cavity		7			7
<i>Artedius lateralis</i>	Body cavity		1			1
<i>Gasterosteus aculeatus</i>	Body cavity		1			1

* Totals do not include the small percentage of worms that were encysted or otherwise not developmentally staged.

† Heart and associated blood vessels, e.g., sinus venosus, hepatic sinus, common cardinal vein.

‡ Ovaries.

§ Ovaries and swim bladder.

conditions (Bennett, 1999). The abundance of *P. oligocotti* larval stages in other fish hosts peaked somewhat later than in *A. flavidus*, by anywhere from 2 to several months (Fig. 2).

Development of *Pseudodelphis oligocotti* according to host species

Parasites were recovered from host body cavity, ovaries, heart, including associated blood vessels, i.e., circulatory system, and gills, depending on the host species. All infected hosts supported fifth-stage adults and, in many cases, earlier stages of infection (third- to fourth-stage larvae) in the body cavity. However, *A. flavidus* was the only fish species to consistently support the larvigerous stage of *P. oligocotti* (Table III), where 14.4% of all *P. oligocotti* in *A. flavidus* from the main study sites (Lumberman's Arch and Figurehead Point) were females containing infective first-stage larvae. Larvigerous females were recovered from the heart (including sinus venosus) through to the hepatic sinus and occasionally the common cardinal vein of *A. flavidus*. In addition, first-stage larvae (the transmitting stage) were recovered from gill filaments, downstream of larvigerous females. Many subgravid adults (primarily females) were recovered from the heart and associated vessels, although most (92%) were found in the body cavity (Table III). One specimen of *G. maeandricus* also contained a larvigerous *P. oligocotti* female in the heart but was not examined for first-stage larvae (Table III).

Advanced stages of *P. oligocotti* were infrequently found in *S. leptorhynchus*, *Ph. laeta* (Table III), and *O. maculosus* (Adamson and Roth, 1990); in these instances, parasites were short of full maturation, e.g., female nematodes with developing embryos but not L1 larvae in utero. Of the 723 worms develop-

mentally staged from *S. leptorhynchus*, females with developing embryos in utero were found in the body cavity (8), ovary (1), and once in the heart. Of 503 subgravid adults (L5) in this potential host, 44 (~9%) were recovered from the heart or associated blood vessels, indicating that tissue migration to site of transmission, if not complete maturation, does occur in this host. Only 1 of 219 *Ph. laeta* worms contained developing embryos and was also found in the heart. The remaining 5 infected potential host species (*Ph. ornata*, sculpins *O. maculosus*, *L. armatus*, and *A. lateralis*, and stickleback *G. aculeatus*) never supported *P. oligocotti* individuals with developing embryos or first-stage larvae in utero. In most cases, parasites were found exclusively in the body cavity, except for 1 L5 recovered in the heart of *Ph. ornata* (Table III). Adamson and Roth (1990) reported *P. oligocotti* females with developing embryos recovered from the body cavity of *O. maculosus*.

DISCUSSION

We surveyed a diverse group of temperate inter- and subtidal fishes to identify and characterize effective host range of *P. oligocotti*, a tropically transmitted dracunculoid nematode. Based on the extent and tissue location of parasite development, *A. flavidus* was the only suitable host for *P. oligocotti*, even though the parasite frequently infected up to 8 other species of fishes. With the possible exception of *G. maeandricus*, these fishes all appeared to be dead ends with respect to transmission because the maturation of *P. oligocotti* occurred in inappropriate tissues or was ultimately curtailed. The importance of *A. flavidus* to *P. oligocotti* transmission is further indicated by the parasite's absence in intertidal fish communities without pen-point gunnel. The single exception, muddy-bottomed Roberts

Bank, had no mature *A. flavidus*. Infrequently infected Roberts Bank fishes may acquire their infections from nearby rocky Point Roberts (Bennett, 1999).

On the surface, *P. oligocotti*'s occurrence in 9 fish species, spanning 5 different orders, gives the false impression that it has broad host specificity, when in fact it is a host specialist in a single species. Confusion between *P. oligocotti*'s observed and actual host range is further indicated by its erroneous type host, *O. maculosus*, from which researchers never in fact recovered gravid (with larvae) females from 76 infected fish of 344 examined (Adamson and Roth, 1990). Moravec et al. (2001) described a very similar parasite from the heart of *S. leptorhynchus* from California or British Columbia but never recovered males, again suggesting abnormal transmission. Leong and Holmes (1981) observed that many of the diverse fish hosts infected by helminths in Cold Lake, Alberta, appeared to be unsuitable for successful transmission. Thus, infection records from superficial host surveys are often misleading in assessing host specificity (Poulin, 1992). Disparity between observed and effective host range might be expected to be broader in trophically transmitted parasites, especially of marine fishes, which are characterized by broad generalized diets (Marcogliese, 2002).

The relative importance of ecological opportunity and phylogenetic host relatedness in determining host specificity is indicated from patterns of parasite distribution and development among potential hosts. *Pseudodelphis oligocotti* showed considerable variation in prevalence and development across fishes it infected, suggesting differences among fishes in both exposure probability and host suitability. Other members of Pholidae (to which *A. flavidus* belongs) were infected as frequently as, and at some sites more frequently than, *A. flavidus*, whereas *G. maeandricus* and *S. leptorhynchus* were infected less frequently. Marcogliese (2002) observed that trophically transmitted parasites are useful indicators of ecological relationships among hosts. Although detailed ecological data for the various potential host species are sporadic, coastal waters inhabited by *A. flavidus* generally act as feeding, nursery, breeding, or spawning grounds (or all) for all the fish species surveyed (Jones, 1962). Those infected by *P. oligocotti* eat mainly small crustaceans, including harpacticoid copepods (Clemens and Wilby, 1961; Miller et al., 1980; Barton, 1982; Goodson, 1988; MacDonald and Chang, 1993), *P. oligocotti*'s intermediate host (Bennett, 1999). All 3 pholids are broadly sympatric in rocky intertidal breeding grounds (Clemens and Wilby, 1961; Barton, 1982; Gibson, 1982; Marliave, 1986; Bennett, 1999). The clingfish, *G. maeandricus*, is also found under intertidal cobble with *A. flavidus* (Hart, 1973; Yoshiyama, 1981; Marliave, 1986). Pipefish, *S. leptorhynchus*, is a dominant species in eelgrass beds where *A. flavidus* overlaps with it during nonbreeding season (Clemens and Wilby, 1961; Hart, 1973; Goodson, 1988).

The relative suitability of potential host species also varied as indicated by maximum stage of development and tissue location of *P. oligocotti* recovered, ranging from *G. maeandricus* that supported larvigerous *P. oligocotti* in the appropriate tissue (the heart) to those that supported advanced stages (gravid females with developing embryos) in the heart (*S. leptorhynchus*, *Ph. laeta*) or another nontarget tissue (*O. maculosus*, Adamson and Roth, 1990) to those that supported at best subgravid adults (L5) either in the heart at least (*Ph. ornata*) or never beyond

the body cavity. The frequency distribution of parasite stage by tissue within a fish species (Table III) indicated that migration to the appropriate tissue and maturation are closely linked, although in an unsuitable host species, *P. oligocotti* sometimes migrates to the final tissue site but never fully develops, or its development may advance regardless of tissue site, even without the preceding event of migration. Failure to migrate, mature, or both may indicate that tissue sites lack the appropriate biochemical cues, essential nutrients, or both (Sukhdeo, 1990; Read and Skorping, 1995). Counter to most experimental findings that good potential hosts are those most closely related (reviewed by Perlman and Jaenike, 2003), phylogenetic relatedness did not account for variation in extent of *P. oligocotti* development observed in a given fish species because both nontarget pholids appeared to be even less suitable than either *G. maeandricus* or *S. leptorhynchus*.

The mode of parasite transmission and the opportunity for exposure to diverse hosts greatly affect parasite host specificity and ultimately patterns of parasite speciation. Passive or trophically transmitted parasites have broader host specificities than do active transmitters (Noble et al., 1989), a pattern partially upheld among other dracunculoids, many of which are transmitted by ingestion of a copepod intermediate host and whose final host specificities include multiple orders (reviewed by Anderson, 2000). Conversely, anguillicolids (also Dracunculoidea), whose members are consistently host specific, are transmitted by an arthropod hematophagous vector rather than trophically (for review, see, Anderson, 2000). Parasites with indiscriminate transmission have evolutionary histories marked by host switching (as opposed to tight coevolution with hosts) (Poulin, 1992), particularly noted among marine vertebrate parasites (Hoberg and Klassen, 2002). Perlman and Jaenike (2003) demonstrated that large potential host ranges in a *Drosophila* sp.–parasitic nematode transmitted at multispecies breeding sites are associated with rampant host switching throughout the group's evolutionary history. Parasites with exposure to many hosts (and therefore a larger heterogeneous environment) are themselves more diverse (de Meeüs, 1998; Poulin and Morand, 2000).

The present study sheds further light on the biology of expansion of host range by a trophically transmitted parasite. Although *P. oligocotti* appears to be physiologically restricted to a host range of one, ongoing exposure to novel hosts occasionally produced pairings of parasite and potential host that approached successful transmission, as in the case of the *G. maeandricus* infection producing a larvigerous female. In addition, intense parasite exposure under laboratory conditions produced an infection in *Ph. ornata* leading to the development of a larvigerous female (Bennett, 1999). Overall, our results emphasize the importance, particularly in specificity studies, of in-depth host–parasite surveys on significant spatial or temporal scales (or both) to encompass parasite developmental variation and transmission success. Thus, we can begin to accurately assess whether observed infected “hosts” are in fact, from the parasite's perspective, true hosts (regularly infected, successful transmitters, e.g., *A. flavidus*) versus commonly infected nontarget hosts (that may occasionally prove capable of transmission, e.g., *G. maeandricus*), commonly infected accidentals (that never prove capable of transmission, e.g., *S. leptorhynchus* and *Pholis* spp.), or, finally, rarely infected accidentals. With

new tools for comparative parasite host-specificity studies available (Caira et al., 2003; Poulin and Moullot, 2003), an accurate assessment of host use by parasites is increasingly important.

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