

Abstract—Northern rock sole (*Lepidopsetta polyxystra* Orr and Matarese, 2000) and southern rock sole (*L. bilineata* Ayres, 1855) from the Gulf of Alaska and northern rock sole from the Aleutian Islands were examined for gill parasites. Four species of copepod parasites were identified: *Naobranchia occidentalis* and *Nectobranchia indivisa* were the most common. Both parasites were more prevalent on northern rock sole (22% and 15%, respectively) than on southern rock sole (5% and 1%, respectively) in the Gulf of Alaska samples. Northern rock sole tended to have a greater mean intensity of *Naobranchia occidentalis* than southern rock sole but there was not a significant difference because of the high variance about the means; too few southern rock sole were infested by *Nectobranchia indivisa* for comparison. Northern rock sole from the Aleutian Islands region had a significantly greater prevalence (36%) and mean intensity (10.2/infested fish) of *Naobranchia occidentalis* than northern rock sole from the Gulf of Alaska (22%, and 4.4, respectively) but did not differ significantly in prevalence and mean intensity of *Nectobranchia indivisa*. Parasitized male northern rock sole from the Gulf of Alaska had a significantly reduced weight at length, indicating a possible effect of parasitism. *Naobranchia occidentalis* selectively infested larger northern rock sole and only the largest southern rock sole. *Nectobranchia indivisa* also were found on larger northern rock sole but did not infest enough southern rock sole to describe a trend. Southern rock sole males were not infested by either parasite. *Naobranchia occidentalis* preferred to infest the middle gill arches of hosts and *Nectobranchia indivisa* preferred to infest the exterior gill arches of hosts.

Differential parasitism by *Naobranchia occidentalis* (Copepoda: Naobranchiidae) and *Nectobranchia indivisa* (Copepoda: Lernaeopodidae) on northern rock sole (*Lepidopsetta polyxystra* Orr and Matarese, 2000) and southern rock sole (*L. bilineata* Ayres, 1855) in Alaskan waters

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The rock soles (*Lepidopsetta* spp.) are important commercial flatfish species that inhabit the continental shelf of the north Pacific Ocean (Hart, 1973). Stock assessment bottom trawl surveys conducted by the Alaska Fisheries Science Center (AFSC) historically recognized only one species of rock sole occurring in four survey areas: eastern Bering Sea, Aleutian Islands, Gulf of Alaska, and western U.S. coast. Recent larval morphometrics by Matarese et al. (1989) and a generic revision by Orr and Matarese (2000) have demonstrated that there are actually two species of rock sole that overlap in the AFSC survey areas. The northern rock sole (*L. polyxystra* Orr and Matarese, 2000) ranges throughout the Bering Sea and Aleutian Islands to Puget Sound, whereas the southern rock sole (*L. bilineata* Ayres, 1855) ranges from the Islands of Four Mountains in the eastern Aleutian Islands to Mexico (Orr and Matarese, 2000). With the knowledge of this recent research, field biologists began separating the two rock sole species in AFSC bottom trawl surveys starting in 1996. The northern rock sole is distinguished by higher gill-raker counts and a whiter blind side than southern rock sole occurring in the same trawl hauls (Orr and Matarese, 2000).

While examining gill rakers to identify specimens of rock soles captured

near the Shumagin Islands during the 1996 Gulf of Alaska survey, we noticed that several live, apparently healthy, northern rock soles had pink or white gill filaments, a condition normally associated with dead fish. On close examination, we found small copepod parasites attached to the gill filaments of these fish. Southern rock soles from the same trawl hauls usually had red, apparently healthy gill filaments and were less frequently parasitized. Therefore we surveyed northern and southern rock soles in selected hauls from the Gulf of Alaska in 1996 for the presence of these parasites and saved infested heads for parasite identification and enumeration in the laboratory. In 1997, we conducted the same parasite investigation in several hauls in the Aleutian Islands region. Our main objective was to quantify differences in the prevalence (percent fish infested) and mean intensity (average number of parasites per infested fish) of gill parasites infesting the northern and southern rock soles (see Margolis et al., 1982; Bush et al., 1997, for complete definitions of ecological terms in parasitology). Secondary objectives were to test for regional differences in prevalence and mean intensity, to describe and compare site preferences of the parasites, and to determine if parasites influenced weight at length for parasitized fish.

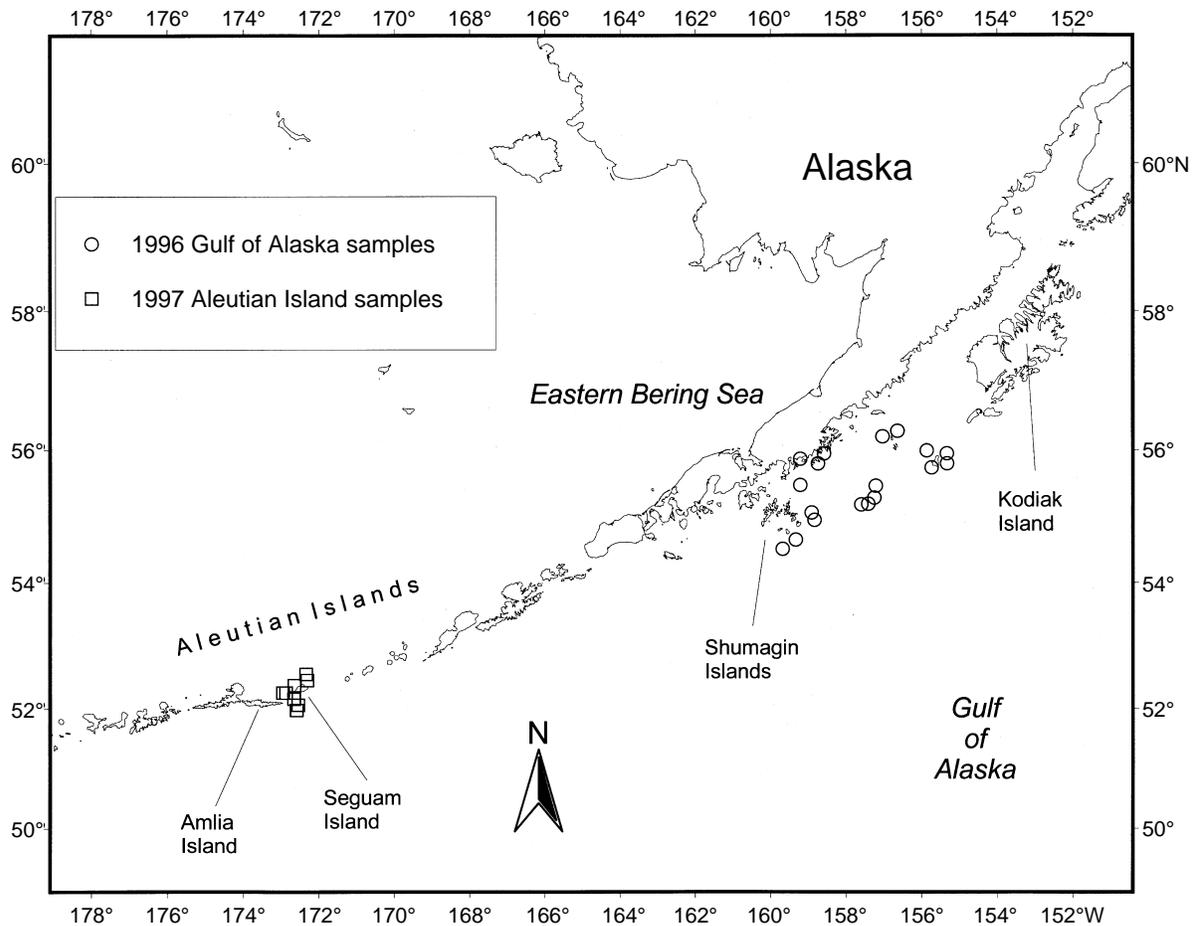


Figure 1

Location of trawl hauls in the Gulf of Alaska and Aleutian Islands where northern and southern rock sole were examined for gill parasites.

Materials and methods

Between 8 and 18 June 1996 (Table 1), northern and southern rock soles captured in a series of trawl hauls from the western Gulf of Alaska were examined for parasites (Fig. 1). Between 25 and 27 June 1997 (Table 1), we examined northern rock soles from a series of trawl hauls around Seguam Island and the east end of Amlia Island in the central Aleutian Islands. The two sampling areas are approximately 850 km apart. We scanned the interior and exterior surfaces of gill filaments on all gill arches for parasites. All rock soles were examined in hauls with few fish ($n \leq 50$), and a random selection of fish in larger hauls were subsampled in a manner similar to that used for obtaining a random subsample for lengths (see Martin, 1997, for Gulf of Alaska bottom trawl survey methods). For each parasitized fish, we measured the fork length (FL) in centimeters, weight (± 2 grams), determined the sex, and removed and froze the entire head, including gill arches, at sea. Lengths and weights were also collected from uninfested northern and southern rock soles in the Gulf of Alaska survey for comparisons with parasitized fish.

Frozen heads were thawed slowly in a refrigerator; thawing heads quickly in warm water produced gill filaments with an excess of mucus, making it difficult to locate parasites. Host species identification was confirmed by examining the gill rakers on the first gill arch on the blind side, and by counting supraorbital pores (Orr and Matarese, 2000). The internal and external surfaces of all gill filaments were examined for parasites with a dissecting microscope. The parasites were removed from gill filaments by washing with water into a filter, or pulling with tweezers, or by removing the gill filament if the parasite was well-anchored. All parasites were preserved in 10% formalin for 3–5 days and stored in 70% ethanol with a small amount of glycerol (Kabata and Cousens, 1972). Fish heads were fixed in 10% formalin for up to one week and stored in 70% ethanol.

We identified the parasites by using the key of Kabata (1988), and Kabata verified our identifications. Generally, only female parasites, which measured at least 2 millimeters in length, were enumerated. Males were found occasionally, sometimes attached to females. However, males were too small (< 0.3 mm in length) to identify and quantify; therefore males were not included in any summaries or

Table 1

Summary of field collection information for northern and southern rock sole from the two sampling areas of the western Gulf of Alaska and the central Aleutian Islands.

Area	Dates	Hauls	Depth range (m)	Temperature range (Celsius)
Gulf of Alaska	8 to 18 Jun 1996	18	46–149	4.0–7.4
Aleutian Islands	25 to 27 Jun 1997	8	143–232	3.9–4.5

Table 2

Summary of fish examined at sea and parasite collections. Mean intensity = average number of parasites for each infested fish. Range is from minimum to maximum numbers of parasites for each infested fish.

Area and rock sole species	Fish examined at sea for gill parasites	Fish infested with either gill parasite	<i>Naobranchia occidentalis</i>			<i>Nectobranchia indivisa</i>		
			Prevalence (%)	Mean intensity	Range	Prevalence (%)	Mean intensity	Range
Gulf of Alaska								
Northern	225	58	22	4.4	1–22	15	3.8	1–21
Southern	282	15	5	2.9	1–13	1	2.0	1–3
Aleutian Islands								
Northern	237	89	36	10.2	1–45	9	3.1	1–8

analyses. Differences in parasite prevalence between the northern and the southern rock sole were determined with chi-square tests, and differences in mean intensity were determined with Welch's approximate *t*-test (Zar, 1984).

To test for significant differences in the length-weight relationship between parasitized (containing *Naobranchia occidentalis* or *Nectobranchia indivisa*, or both) and unparasitized fish, natural log-transformed length and weight data were compared by linear regression. The slopes and *Y*-intercepts were compared by using *F*-ratios.

Results

Parasite species

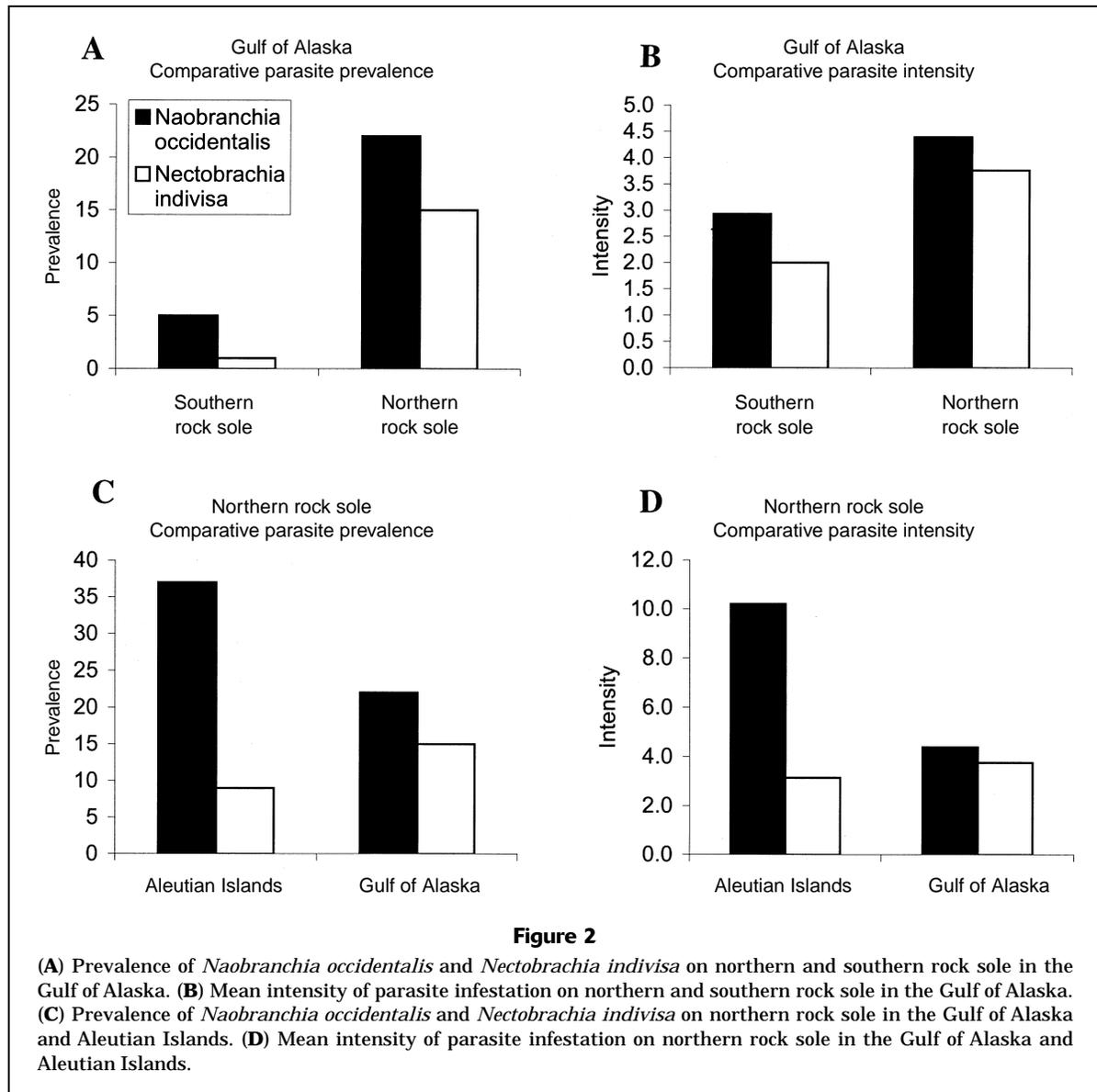
Four species of copepod parasites were identified from the gills of the infested fish. The most common parasite was *Naobranchia occidentalis* Wilson, 1915, which attaches to the gill filaments by its modified second maxillae (Kabata, 1988). This parasite was easily removed in the laboratory; freezing and thawing the specimens may, therefore, have loosened the parasite's grip. The next most common parasite, *Nectobranchia indivisa* Fraser, 1920, firmly anchors in the filament and could only be removed by cutting the filament or breaking off the bulla. *Nectobranchia indivisa* was almost always found attached to the tips of the gill filaments. Two specimens of *Acanthochondria vancouverensis* were found unattached in the gill chambers of two Gulf of Alaska northern rock sole, constituting the

first record of parasitism in wild rock sole for this species (Kabata¹). A single specimen of *Haemobaphes diceraus* was found attached on the third gill arch, eyed side, of a Gulf of Alaska northern rock sole (Kabata²). Kabata (1988) reported that all of these parasites occur on rock sole, except for *A. vancouverensis*. Small, highly mobile leeches were also frequently noted on the gills of fish caught in the Gulf of Alaska survey, but because of their mobility, their presence could not be reliably documented. We did not attempt to enumerate or identify this species.

Gulf of Alaska A total of 225 northern and 282 southern rock soles were visually examined for parasites at sea during the 1996 Gulf of Alaska survey, and 78 rock sole heads were collected because they appeared to have at least one copepod gill parasite (Table 2). *Naobranchia occidentalis* or *Nectobranchia indivisa* (or both) were found on 73 of the collected heads during laboratory dissection (58 northern and 15 southern rock sole). Only one juvenile female or

¹ Kabata, Z. 1998. Personal commun. Department of Fisheries and Oceans, Pacific Biological Station, Nanaimo, British Columbia, Canada, V9R 5K6. Kabata suggested that we consider this incidence of parasitism by *A. vancouverensis* to be the first record of parasitism in wild rock sole by this species. A former record of parasitism by this species was for aquarium fish only.

² Kabata, Z. 1998. Personal Commun. Department of Fisheries and Oceans, Pacific Biological Station, Nanaimo, British Columbia, Canada, V9R 5K6. Kabata confirmed our tentative identification of *Haemobaphes* and identified it with fair certainty as *H. diceraus*.



postreproductive adult *Naobranchia occidentalis* was found in the Gulf of Alaska samples. The original at-sea identification of the two rock sole species was confirmed for all but one fish in the laboratory (a northern rock sole was incorrectly identified at sea as a southern rock sole).

Both *Naobranchia occidentalis* and *Nectobranchia indivisa* were more prevalent (chi square test, $\alpha=0.05$, $P<0.001$) on the northern rock sole (22% and 15% of the 225 fish examined, respectively) than on the southern rock sole (5% and 1% of the 282 fish examined, respectively, Fig. 2A). Mean intensity was not significantly different between the northern (4.4/fish, range 1–22) and southern rock sole (2.9/fish, range 1–13) for *Naobranchia occidentalis* (Welch's approximate *t*-test, $\alpha=0.05$, $df=28$, $P=0.08$, Fig. 2B) owing to a single southern rock sole with 13 parasites. Mean intensity also was not significantly different between the northern and the southern rock sole for

Nectobranchia indivisa (Welch's approximate *t*-test, $\alpha=0.05$, $df=2$, $P>0.05$); however only two southern rock soles were infested with *N. indivisa*. A chi-square test showed that infestation of northern rock sole by *N. indivisa* was not independent of infestation by *Naobranchia occidentalis* ($\alpha=0.05$, $P<0.001$). Thus, northern rock sole infested by one species of parasite had an increased likelihood of also being infested by the other. However, infestation of southern rock sole by *Nectobranchia indivisa* was independent of infestation by *Naobranchia occidentalis* ($P>0.05$).

Aleutian Islands Only northern rock soles were identified at sea in sampled hauls from the Aleutian Islands region, and laboratory analysis confirmed their species identification. A total of 237 northern rock soles from 8 trawl hauls was examined at sea for gill parasites: 90 fish appeared to have at least one gill parasite and their heads were frozen

at sea (Table 2). None of the fish had abnormally pale gill filaments. *Naobranchia occidentalis* or *Nectobranchia indivisa* (or both) were found on all but one of the northern rock soles examined in the laboratory. No other parasite species were observed. Approximately 17% of the *Naobranchia occidentalis* were juvenile females. Northern rock soles infested by one species of parasite had an increased likelihood of also being infested by the other species of parasite (chi square test, $\alpha=0.05$, $P<0.001$), similar to our observations for northern rock soles from the Gulf of Alaska.

Area and species infestation comparisons

Naobranchia occidentalis was more prevalent (chi square test, $\alpha=0.05$, $P<0.01$) on the northern rock soles in the Aleutian Islands (36%) than on fish from the Gulf of Alaska (22%) (Fig. 2C). The northern rock soles from the Aleutian Islands also had a significantly higher mean intensity of *N. occidentalis* (Welch's approximate *t*-test, $\alpha=0.05$, $df=127$, $P<0.001$; 10.2/fish) than northern rock soles from the Gulf of Alaska (4.4/fish, Fig. 2D). There were no differences in either prevalence (chi-square test, $\alpha=0.05$, $P>0.05$) or mean intensity (Welch's approximate *t*-test, $\alpha=0.05$, $df=50$, $P>0.05$) of *Nectobranchia indivisa* on the northern rock soles from the Aleutian Islands and Gulf of Alaska.

Trends in parasite infestations—arches and sides

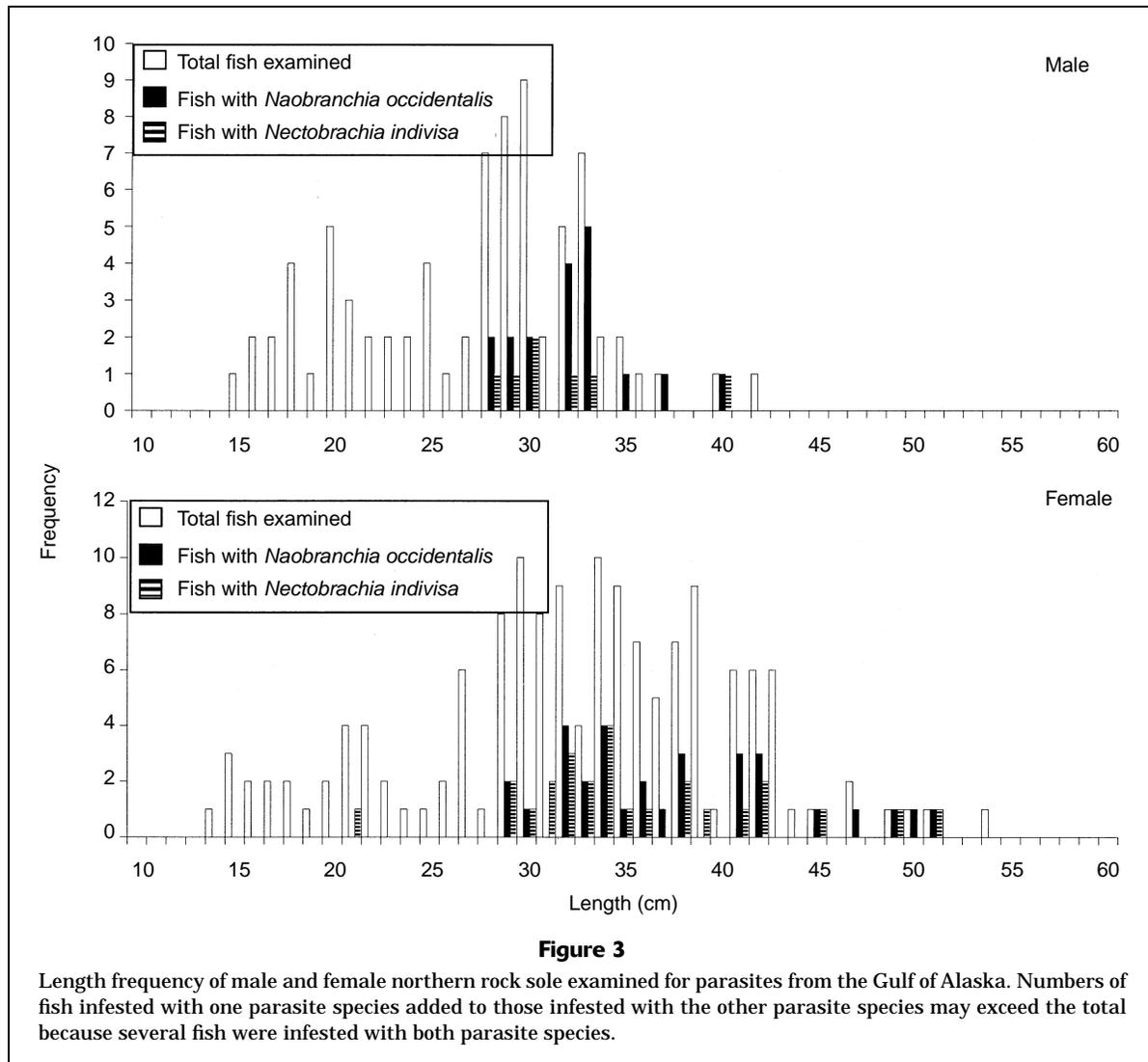
Heads of fish from the 1996 Gulf of Alaska survey had been frozen for a year before examination and the gill filaments were in poor condition. As a result, only a small percentage of *Naobranchia occidentalis* were still attached to a gill arch, and it was not possible to detect preferences of *N. occidentalis* for individual gill arches, or for eyed-side or blind-side arches, on northern rock sole (Table 3). Ninety-one percent of the observed *Nectobranchia indivisa* were still firmly anchored in the gill filaments on northern rock sole, were evenly distributed per side (60), and showed a preference for the outer arches over the inner arches on both sides of the fish (Table 3). All *Naobranchia occidentalis* on the southern rock sole from the Gulf of Alaska were unattached. Four *Nectobranchia indivisa* were found still attached on the blind side of southern rock sole from the Gulf of Alaska, but this small sample was insufficient for analysis.

Aleutian Islands samples were frozen for only a few weeks prior to examination in the laboratory and were in much better condition than samples from the Gulf of Alaska survey. The infested gill arch was determined for 83% of the *Naobranchia occidentalis* and for 97% of the *Nectobranchia indivisa* (Table 3). For northern rock sole from the Aleutian Islands, the total number of *Naobranchia occidentalis* was higher on the blind side (452) than the eyed side (414) and equal on both sides for *Nectobranchia indivisa* (33); these results nearly duplicated those observed for northern rock sole from the Gulf of Alaska. *Naobranchia occidentalis* showed a strong preference for the middle and inner gill arches on both eyed and blind sides (Table 3). The results were mixed for *Nectobranchia indivisa*; parasites on the blind side showed a preference for the outer arches, whereas parasites on the eyed side showed

Table 3

Counts of female parasites by gill arch attachment (1st=exterior arch, 4th=interior arch). Unattached parasites (U.) were on or in the area of the eyed-side or blind-side gill arches. Loose parasites were not associated with either set of gill arches. Male parasites were too small to be reliably enumerated and are not included in this summary. Juvenile female parasites are included in the totals and are also listed separately.

Area and rock sole species	Parasite species	Eyed side gill arches					Blind side gill arches					Grand total	Juvenile				
		1st	2nd	3rd	4th	U.	Subtotal	1st	2nd	3rd	4th			U.	Subtotal	Loose	
Gulf of Alaska	Northern	<i>Naobranchia occidentalis</i>	0	0	1	0	99	100	0	0	3	0	106	109	6	215	1
		<i>Nectobranchia indivisa</i>	23	16	16	1	4	60	60	26	14	12	5	60	4	124	0
	Southern	<i>Naobranchia occidentalis</i>	0	0	0	0	11	11	11	0	0	0	30	30	0	41	0
		<i>Nectobranchia indivisa</i>	0	0	0	0	0	0	0	3	0	1	0	4	0	4	0
Aleutian Islands	Northern	<i>Naobranchia occidentalis</i>	27	119	139	62	67	414	414	22	97	181	73	452	2	868	146
		<i>Nectobranchia indivisa</i>	5	10	12	5	1	33	33	15	8	5	4	33	0	66	0



a preference for middle gill arches, and overall, there was a slight preference for outer arches (Table 3). Although there were numerous juvenile *Naobranchia occidentalis* parasites on northern rock soles from the Aleutian Islands, their individual positions were not recorded separately from the adults.

Trends in parasite infestations—species, sex, and size

Gulf of Alaska A wide size range of northern rock sole males (15–42 cm FL) and females (14–54 cm FL) were examined for parasites during the Gulf of Alaska survey (Fig. 3), but *Naobranchia occidentalis* was found only on larger males (28–40 cm FL) and females (29–51 cm FL). Similarly, *Nectobranchia indivisa* was found only on larger males (28–40 cm FL) and females (29–51 cm FL), with the exception of a single, small (21 cm FL) infested female.

None of the male southern rock soles (19–40 cm FL) were infested with either parasite species, but male southern rock soles were uncommon in our survey catches and

only 28 fish were examined (Fig. 4). A total of 254 female southern rock soles (14–58 cm FL) were examined for parasites during the survey and *Naobranchia occidentalis* infested only 14 of the larger females (42–52 cm FL). Only two relatively large (37 and 47 cm FL) female southern rock soles were infested with *Nectobranchia indivisa*.

Aleutian Islands Male (19–37 cm FL) and female (20–46 cm FL) northern rock soles from the Aleutian Islands were examined, and *Naobranchia occidentalis* was found only in larger individuals (24–37 cm FL males and 28–44 cm FL females, Fig. 5). The size range of fish infested with *Nectobranchia indivisa* was slightly more restricted (24–33 cm FL males and 28–43 cm FL females) than the size range of fish infested with *Naobranchia occidentalis*.

Length-weight relationships

Parasitized (range 28–40 cm FL) and unparasitized (range 18–36 cm FL) male northern rock soles from the Gulf of

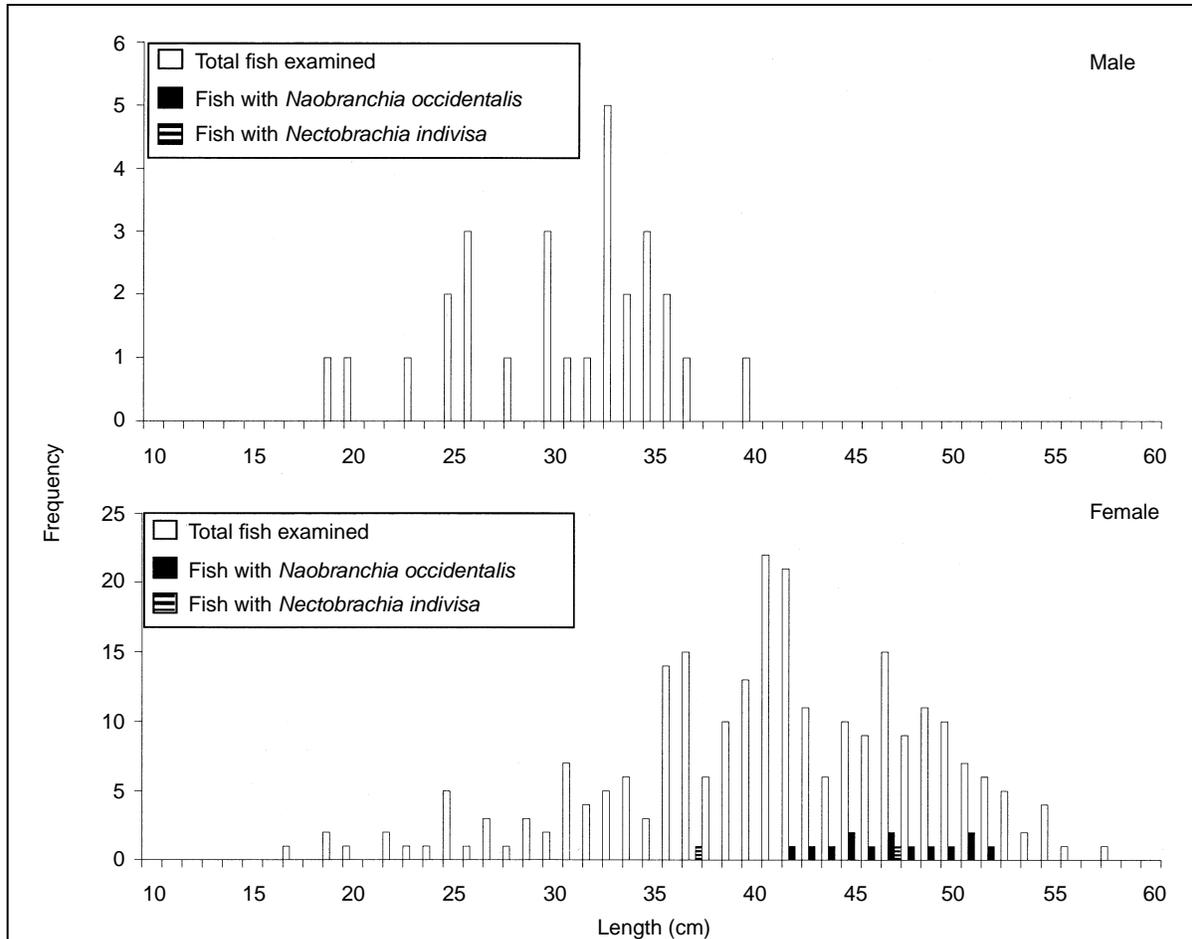


Figure 4

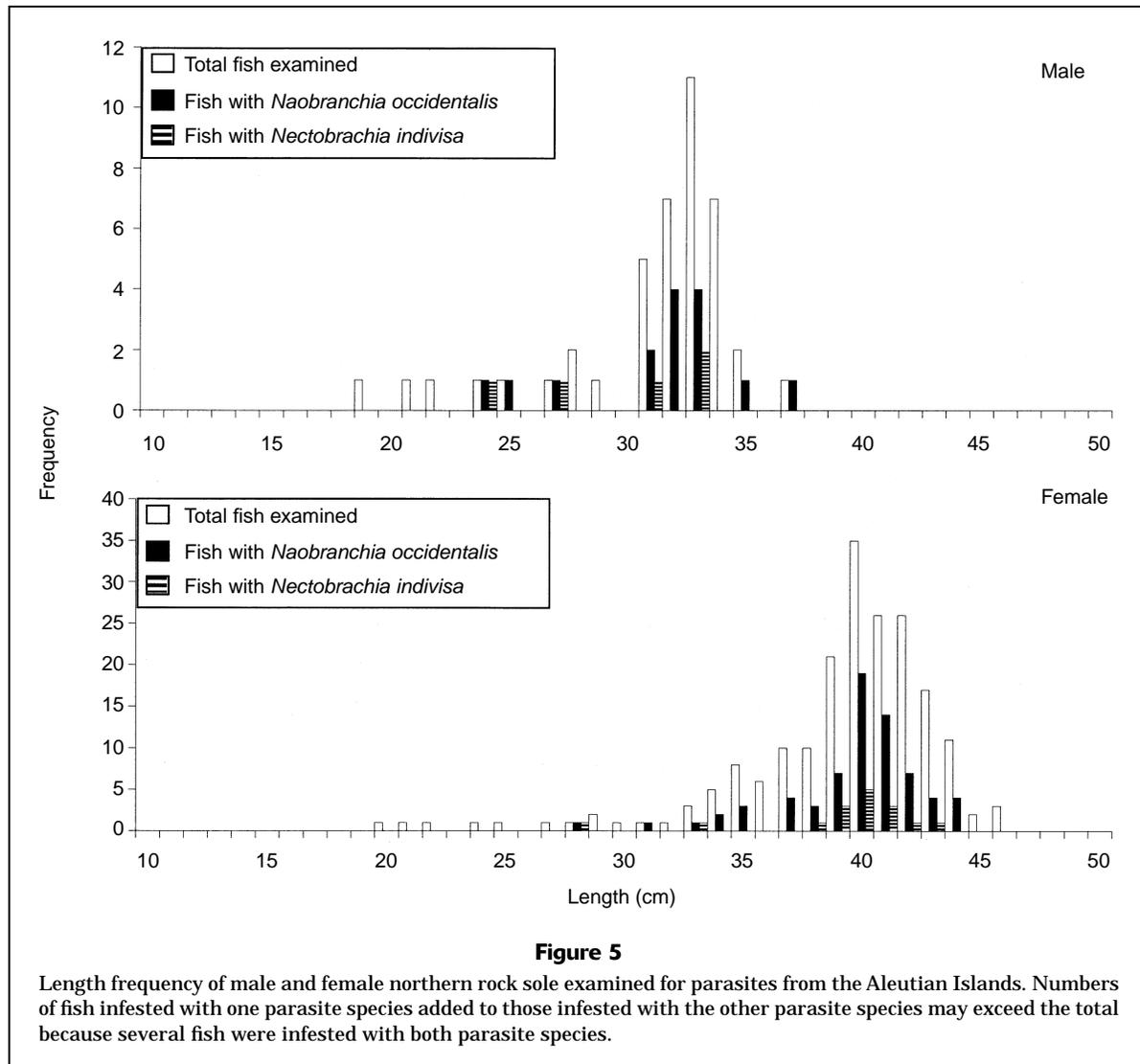
Length frequency of male and female southern rock sole examined for parasites from the Gulf of Alaska. Numbers of fish infested with one parasite species added to those infested with the other parasite species may exceed the total because several fish were infested with both parasite species.

Alaska did not have significantly different length-weight slopes ($df=1$, F -ratio=0.29, $P>0.05$) but had significantly different intercepts ($df=1$, F -ratio=13.74, $P<0.001$). For example, a 33-cm-FL parasitized male northern rock sole from the Gulf of Alaska had an estimated weight of 407.5 grams, whereas an unparasitized fish of the same length weighed an estimated 451.4 grams, a difference of more than 10%. The length-weight slopes and intercepts were not significantly different for female northern or southern rock soles from the Gulf of Alaska. No comparison could be made between parasitized and unparasitized Aleutian Islands fish because individual weights were not taken for unparasitized fish.

Discussion

Laboratory examination confirmed our original observations that copepod parasites were more prevalent on the northern rock soles from the Gulf of Alaska than on south-

ern rock soles. There could also be a higher mean intensity for both species of parasites on the northern rock sole, but our analysis was limited by a small sample size and high variability within the sample. Of the two gill parasites examined in detail, *Naobranchia occidentalis* was more prevalent and caused more intense infestations than did *Nectobranchia indivisa*. Our sampling efforts in the Aleutian Islands occurred beyond the geographic range of southern rock sole and indicated that the northern rock sole had a higher prevalence and greater mean intensity of *Naobranchia occidentalis* than the northern rock sole in the Gulf of Alaska. Differences in parasite prevalence and mean intensity between the Gulf of Alaska and Aleutian Island samples were confounded by sampling in different years, limited areal coverage, limited temperature range, and greater depths in the Aleutian samples. Also, the significance of the large number of juvenile *N. occidentalis* in the Aleutian Island samples is not known. Despite these limitations, it is noteworthy that none of the northern rock soles heavily infested with *Naobranchia occidentalis*



from the Aleutian Island samples had white gill filaments. Because of this observation and the apparent preference of *Nectobranchia indivisa* for northern rock sole, we speculate that the white gill filaments in the northern rock soles from the Gulf of Alaska survey may have been caused by heavy infestation with *N. indivisa*.

The decreased weight at length of parasitized male northern rock soles from the Gulf of Alaska indicates a possible effect of infestation. It is interesting to note that northern rock soles from both areas, which were infested with one parasite, had an increased chance of also being infested by the other parasite. Either some northern rock soles are more susceptible to infestation by both parasites, or infestation by one parasite increases the likelihood of infestation by the other species. Because infestation of southern rock soles by *Nectobranchia indivisa* was independent of infestation by *Naobranchia occidentalis*, it is possible that southern rock sole may be resistant to infestation by both parasite species.

Apparently *Naobranchia occidentalis* infests smaller northern than southern rock sole; thus, much of the southern rock sole population may be unavailable to successful infestation by this parasite. This size-dependent prevalence may be related to the grasping method of attachment of *N. occidentalis*; thus, its ability to infest rock sole may be related to the diameter of the gill filaments. Cressey et al. (1983) proposed a similar mechanical limitation for female pseudocycnids that grasp the gill filament in scombrids by partially encircling it with the lateral lobes of their cephalon. They suggested that hosts must reach a minimum size before the gill filament is large enough for the parasite to achieve a firm grip. Roubal and Graham (1999) noted that the smallest fish in their study were not infested with *Naobranchia variabilis*, which attaches to gill filaments in a similar manner as *N. occidentalis*, and suggested it was because those fish simply had not been encountered by a parasite. They did not suggest any sort of mechanical limitations to successful infestation because the

parasite larvae are apparently sufficiently small (Roubal³). Both Cressey et al. (1983) and Roubal and Graham (1999) noted that the largest adult parasites were found on the largest fish—a finding that suggests that the gill filaments of smaller fish may be less suitable for infestation.

Nectobranchia indivisa also selectively infested larger northern rock sole but rarely infested southern rock sole, suggesting an apparent species preference. Because *N. indivisa* attaches by means of a bulla permanently embedded near the end of a gill filament, it seems less likely that this parasite would be limited by mechanical restrictions such as the diameter of the gill filament. The parasite *Salmincola californiensis*, which also attaches to its host by means of a bulla (Kabata and Cousens, 1972), seemed to be dependent on its sockeye salmon (*Oncorhynchus nerka*) host reaching a large size before the gill filaments became the preferred site of attachment (Kabata and Cousens, 1977). Perhaps *N. indivisa* is able to infest northern rock sole successfully only after the fish reach a certain size.

We did not perform histological analysis of gill filaments to determine differential damage caused by infestation of *Naobranchia occidentalis* and *Nectobranchia indivisa*. Roubal (1999) determined that damage caused by *Naobranchia variabilis* was restricted to the infested gill filament and was minor. Kabata (1984) noted that naobranchids only partially compress the gill filament, do not completely restrict blood flow, and do not cause whitening of gill filaments. Roubal (1999) also determined that *N. variabilis* live by feeding on the blood supply and not by grazing the tissue, as do lernaepodids. Kabata and Cousens (1977) reported macroscopic observations of significant atrophy and tissue reaction to as much as one-third of the gill filament surface area of juvenile sockeye salmon due to the presence of *S. californiensis*. This type of damage is consistent with our macroscopic observations of the white gills of northern rock soles seen early in the Gulf of Alaska survey. Kabata and Cousens (1977) also reported on microscopic observations of gill filament damage, sometimes including proliferation of the gill epithelium, hypertrophy of epithelial cells, fusion of adjacent filaments, thickening of filament walls, blood blisters, and erosion of epithelial cells as the oral apparatus of the *S. californiensis* scrapes them for ingestion.

Margolis and Arthur (1979), Kabata and Whitaker (1984), and Kabata (1988) all reported that both *Naobranchia occidentalis* and *Nectobranchia indivisa* occurred on rock soles in Pacific Canadian waters, prior to the determination that there are two species of rock sole in this area (Orr and Matarese, 2000). Neither Moles (1982) nor Love and Moser (1983) reported these parasites from rock soles from Alaskan waters and U.S. west coast waters, respectively. Our study reported new host records for *Acanthochondria vancouverensis* and *Haemobaphes diceraus* on northern rock sole.

The apparent preference of both parasites for the northern rock soles is supported by the conclusion of Orr and

Matarese (2000) that northern and southern rock soles are two distinct species. Possible differences in the ecology of these newly described rock sole species, such as food habits, growth rates, habitats, spawning seasons and locations, nursery grounds, and seasonal and ontogenetic migrations might also account for the differential parasitism that we observed. It is not known if parasite prevalence and intensity is related to differences in the ecology and behavior of these closely related species, or related to differences in their anatomy or physiology. As more research is done on these species, based on the work of Orr and Matarese (2000), more potential differences will be determined.

Acknowledgments

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Literature cited

- Bush, A. O., K. D. Lafferty, J. M. Lotz, and A. W. Shostak. 1997. Parasitology meets ecology on its own terms: Margolis et al. revisited. *J. Parasitol.* 83(4):575–583.
- Cressey, R. F., B. B. Collette, and J. L. Russo. 1983. Copepods and scombrid fishes: a study in host-parasite relationships. *Fish. Bull.* 81(2):227–265.
- Hart, J. L. 1973. Pacific fishes of Canada. *Fish. Res. Board Can. Bull.* 180, 740 p.
- Kabata, Z. 1984. Diseases caused by metazoans: crustaceans. *In Diseases of marine animals. Vol IV, part 1: Introduction: Pisces* (Kinne, ed.), p. 321–399. *Biologische Anstalt Helgoland, Hamburg.*
1988. Copepoda and Branchiura. *In Guide to the parasites of fishes of Canada. Part II: Crustacea* (L. Margolis and Z. Kabata, eds.), p. 3–127. *Can. Spec. Publ. Fish. Aquat. Sci.* 101.
- Kabata, Z., and B. Cousens. 1972. The structure of the attachment organ of *Lernaepodidae* (Crustacea: Copepoda). *J. Fish. Res. Board Canada* 29: 1015–1023.
1977. Host-parasite relationships between sockeye salmon, *Oncorhynchus nerka*, and *Salmincola californiensis* (Co-

³ Roubal, F. R. 1999. Personal commun. Department of Parasitology, The University of Queensland, Brisbane 4072, Queensland, Australia.

- pepoda: Lernaepodidae). J. Fish. Res. Board Can. 34:191–202.
- Kabata, Z., and D. J. Whitaker.
1984. Results of three investigations of the parasite fauna of several marine fishes of British Columbia. Fish. Res. Board Can., Tech. Rep. 1303, 19 p.
- Love, M. S., and M. Moser.
1983. A checklist of parasites of California, Oregon, and Washington marine and estuarine fishes. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-777, 576 p.
- Margolis, L., and J. R. Arthur.
1979. Synopsis of the parasites of fishes of Canada. Fish. Res. Board Can. Bull. 199, 269 p.
- Margolis, L., G. W. Esch, J. C. Holmes, A. M. Kuris, and G. A. Schad.
1982. The use of ecological terms in parasitology (report of an ad hoc committee of the American Society of Parasitologists). J. Parasitol., 68(1):131–133.
- Martin, M. H.
1997. Data report: 1996 Gulf of Alaska bottom trawl survey. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-AFSC-82, 235 p.
- Matarese, A. C., A. W. Kendall Jr., D. M. Blood, and B. M. Vinter.
1989. Laboratory guide to early life history stages of North-east Pacific fishes. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 80, 651 p.
- Moles, A.
1982. Parasite-host records of Alaskan fishes. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-760, 41 p.
- Orr, J. W., and A. C. Matarese.
2000. Revision of the genus *Lepidopsetta* Gill, 1862 (Teleostei: Pleuronectidae) based on larval and adult morphology, with a description of a new species from the North Pacific Ocean and Bering Sea. Fish. Bull. 98:539–582.
- Roubal, F. R.
1999. Extent of gill pathology in the toadfish *Tetractenos hamiltoni* caused by *Naobranchia variabilis* (Copepoda: Naobranchiidae). Dis. Aquat. Org. 35:203–211.
- Roubal, F. R., and D. Graham.
1999. Monthly variation in recruitment, infection, size, fecundity and mating of *Naobranchia variabilis* (Copepoda: Naobranchiidae) parasitic on the gills of toadfish *Tetractenos hamiltoni* from Moreton Bay, Australia. Mar. Freshwater Res. 50:291–298.
- Zar, J. H.
1984. Biostatistical analysis, second ed. Prentice-Hall Inc., Englewood Cliffs, NJ, 718 p.