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Author(s) :David R. Bryan, Kym C. Jacobson, and John C. Buchanan

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## RECENT INCREASE IN NYBELINIA SURMENICOLA PREVALENCE AND INTENSITY IN PACIFIC HAKE (*MERLUCCIUS PRODUCTUS*) OFF THE UNITED STATES WEST COAST

David R. Bryan, Kym C. Jacobson\*, and John C. Buchanan†

University of Miami, Rosenstiel School of Marine and Atmospheric Science, 4600 Rickenbacker Causeway, Miami, Florida 33149. e-mail: dbryan@rsmas.miami.edu

**ABSTRACT:** A larval marine cestode was found in 82.0% of 834 Pacific hake (*Merluccius productus*) stomachs collected from 341 trawl stations along the United States west coast during the summers of 2008 and 2009. Morphology and DNA sequencing was used to identify the cestode as *Nybelinia surmenicola*. In an examination of 131 Pacific hake stomachs collected from the same region in 1999, *N. surmenicola* prevalence was 35.1%. The results from a general linear model suggested that their prevalence is influenced by year and latitude, Pacific hake size, and sex. Mean intensity of *N. surmenicola* in 2008–2009 was 20.22 ( $\pm 1.13$  SE) and was positively related to Pacific hake length and the latitude of collection. Year-1 Pacific hake (<27 cm length) had significantly lower prevalence and intensity of *N. surmenicola* compared to older and larger fish. Pacific hake collected south of Point Conception, California (32.5 to 35°N) had lower prevalence and intensity of *N. surmenicola* compared to those collected in northern latitudes (35.1 to 48.4°N). Higher *N. surmenicola* prevalence in Pacific hake in recent years suggests food-web fluctuations in the northern California current ecosystem caused by changes in ocean transport of zooplankton or pelagic fish distributions and warrants future monitoring as a metric for ecosystem change.

Pacific hake, *Merluccius productus*, range from southern California (25°N) to the Haida Gwaii (Queen Charlotte Islands), Canada (55°N) along the continental shelf and slope. The population is comprised of a large migratory coastal stock, 2 smaller inshore stocks in the Strait of Georgia, British Columbia and Puget Sound, Washington, and a stock in the Gulf of California (Vrooman and Paloma, 1977; Bailey et al., 1982; Iwamoto et al., 2004). The coastal stock represents the largest groundfish biomass in the California current ecosystem (CCE), where Pacific hake are considered important predators as well as prey (Bailey et al., 1982; Livingston and Bailey, 1985). Pacific hake are not only an integral component of the CCE, but are also an extremely important species for the west coast groundfish fishery. Between 1966 and 2009, an average of 221,000 metric tons was landed annually (Stewart and Hamel, 2010). Juvenile and adult Pacific hake migrate from California northwards toward Oregon, Washington, and British Columbia during the spring and summer to feed (Bailey et al., 1982). Hake feed primarily on euphausiids during this migration, but their diet shifts toward fish as they grow larger (Bailey et al., 1982; Livingston and Bailey, 1985; Rexstad and Pikitch, 1986). In the fall and winter, mature hake migrate southwards to southern California to spawn (Bailey et al., 1982).

Pacific hake are known to harbor as many as 27 different species of marine parasites (Love and Moser, 1983; Sankurathri et al., 1983; Moles, 2007). Among these, larvae of the marine cestode *Nybelinia surmenicola* (Okada, 1929) have been previously described from Pacific hake in the northeast Pacific Ocean (Kovalenko, 1970) and in the Strait of Georgia, British Columbia (Sankurathri et al., 1983). Kovalenko (1970) reported a prevalence of 14.9% and a range of intensity of 1–20, whereas Sankurathri et al. (1983) recorded a prevalence of 2.1% with a range of intensity of 1–10. Oliva and Ballón (2002) found *N. surmenicola* in Peruvian hake (*Merluccius gayi peruanus*) and

Chilean hake (*Merluccius gayi gayi*), but in low prevalence and intensity (9.3% and 2.0% prevalence and mean intensities of 1.6 and 1.0, respectively). Sardella and Timi (2004) also found *Nybelinia* sp. plerocercoids in the mesenteries of Argentinean hake, *Merluccius hubbsi*, but only from a single location, and with a prevalence of 0.87% and a mean abundance of 0.9 ( $\pm 0.1$  SD).

*Nybelinia surmenicola* belongs to the order Trypanorhyncha and has a complex life cycle that includes crustacean, squid, and teleost, and ultimately elasmobranch final hosts (Shimazu, 1999). Shimazu (1999) described the euphausiid *Euphausia pacifica* as an intermediate host for *N. surmenicola*, squid and fish as the paratenic hosts, and salmon shark (*Lamna ditropis*) as the definitive host (Shimazu, 1975).

Despite the occurrence of *N. surmenicola* in the southern and northern Pacific Ocean, little is known about their abundance in the coastal stock of Pacific hake. In the present study, we provide the first report of *N. surmenicola* larvae in Pacific hake collected along the United States continental west coast shelf and slope and report high prevalence of the parasite in 2008 and 2009 in comparison to earlier reports from Kovalenko (1970) and Sankurathri et al. (1983), and to Pacific hake collected in 1999 in the CCE (this study). Our data suggest a recent expansion in prevalence and intensity of larval *N. surmenicola* in Pacific hake that could reflect environmental changes, or changes in host distributions, in the CCE (Lafferty, 1997; Marcogliese, 2001).

### MATERIALS AND METHODS

#### Pacific hake and parasite collection

Pacific hake stomachs were collected as part of an ongoing diet study in 2008 and 2009 during the NOAA Northwest Fisheries Science Center's (NWFS) West Coast groundfish bottom trawl survey (WCGBTS). Additional stomachs were collected in 2009 during the NOAA NWFS Pacific hake integrated acoustic and trawl (IAT) survey. Detailed descriptions of the WCGBTS and IAT survey can be found in Keller et al. (2008) and Fleischer et al. (2008). The WCGBTS uses an Aberdeen-style bottom trawl and trawl stations are selected by a stratified random sampling design. The WCGBTS runs annually from May until October and targets groundfish at depths of 55 to 1,280 m from the U.S. Mexican border (32.5°N) to Cape Flattery, Washington (48.2°N). Biological sampling during the IAT survey is conducted with an Aleutian wing trawl that is designed to fish off the bottom. Trawl stations are not randomly chosen, as they are used to classify observed backscatter layers from the acoustic survey. The 2009 IAT survey took place between 30

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\* Fish Ecology Division, Northwest Fisheries Science Center, NOAA Fisheries, 2030 South Marine Science Drive, Newport, Oregon 97365.

† Fisheries Resource Analysis and Monitoring Division, Northwest Fisheries Science Center, NOAA Fisheries, 2032 SE Oregon State University Drive, Newport, Oregon 97365.

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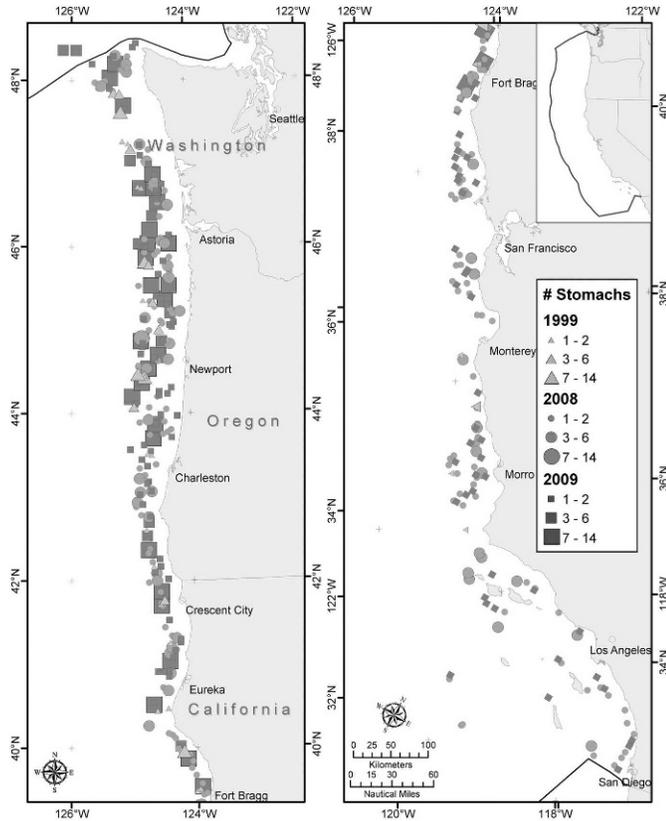


FIGURE 1. Trawl stations from which Pacific hake (*Merluccius productus*) were collected. Samples collected in 1999 are represented by triangles, those from 2008 are represented by circles, and those from 2009 by squares. Size of the symbol represents number of samples from each station.

June and 22 August at depths between 50 and 1,500 m from Point Piedras Blancas, California (35.7°N) to the northwest tip of Washington (48.4°N) (Fig. 1). Between 2008 and 2009 a total of 834 stomachs were examined from 341 separate trawl stations.

Pacific hake were randomly selected from each haul, but hake with signs of regurgitation (between 30 and 50%) were excluded from this study. Stomachs were immediately removed and placed in cloth bags with a fish identification tag. Stomachs were preserved in 10% buffered formalin on the research vessels and then rinsed and stored in 70% ethanol at the end of each cruise. Total length, weight, and sex of each fish were recorded at sea, along with trawl station information including location and depth.

A subsequent random sample of hake stomachs collected in 1999 during NOAA’s Alaska Fisheries Science Center’s west coast upper continental slope (WCUCS) groundfish bottom trawl survey were also examined. The 1999 WCUCS survey was conducted from the U.S./Canadian border (48.1°N) to Point Arguello, California (34.5°N) at depths between 183 and 1,280 m. The survey ran from October 14 until November 19 and was conducted with a poly Nor’eastern trawl. A more detailed description of the survey design can be found in Lauth (2000).

In the laboratory, stomachs were rinsed in water and contents were removed. The total number of *N. surmenicola* located at 3 different locations within the stomach were recorded; those embedded in the stomach wall, those partially embedded, and those that were loose inside the stomach. Parasite terminology follows Bush et al. (1997). For stomachs collected in 2008, only *N. surmenicola* prevalence was recorded. For 2009 and 1999, both prevalence and intensity were recorded.

**Cestode identification**

Specimens recovered from Pacific hake surveys were examined by light microscopy and initially identified as belonging to *Nybelinia* based upon Schmidt (1986). For taxonomic confirmation of larval cestodes, additional

Pacific hake were collected in March of 2010 by 2 commercial fishing vessels operating out of Newport, Oregon (44.6°N), and immediately frozen. Parasites were extracted from 10 thawed stomachs and placed in 90% ETOH. These plerocercoids were morphologically identical at 40× magnification to those recovered from the Pacific hake surveys. DNA extraction from cestode tissue was carried out with the use of a glass-fiber plate DNA extraction protocol (Ivanova et al., 2006). The larval cestodes were identified with PCR to amplify the D1–D3 region of the nuclear 28S (long) subunit of ribosomal DNA (rDNA) with the use of primers LSU-5 (5'-TAGGTCGACCCGCTGAAYTTA) and 1200R (5'-GCATAGTT-CACCATCTTTCGG) (Olson et al., 2003; Jensen and Bullard, 2010). PCR reactions had a final volume of 20 µl comprised of 2 µl of genomic DNA, 0.4 µM each primer, 0.40 mM of each deoxynucleoside triphosphate (dNTP), 2.5 mM MgCl<sub>2</sub>, 1X PCR buffer, and 1 unit of *Taq* DNA polymerase (Promega, Madison, Wisconsin). The temperature and cycling parameters included denaturation at 94 C for 2 min, followed by 32 cycles at 94 C for 30 sec, 55 C for 45 sec, 72 C for 2 min, followed by postamplification extension at 72 C for 10 min. PCR products were purified with the use of ExoSap-IT clean-up protocol (GE Healthcare, Piscataway, New Jersey). Cycle sequencing was performed with the use of Big Dye terminator reaction mix v3.1 (Applied Biosystems, Foster City, California), and excess dye terminators removed by ethanol precipitation. Sequence analysis took place on an ABI 3730xl DNA automated sequencer (Applied Biosystems). Sequence editing was conducted with the use of BioEdit 7.0.1 software (Hall, 1999) and aligned via ClustalW software (Thompson et al., 1994). Sequence data were deposited into GenBank under the accession number JN662466.

**Data analysis**

Intensity values were log transformed to meet assumptions of normal distribution. Linear regressions, *t*-tests and Pearson’s chi-square test were used to determine significant factors influencing parasite prevalence and intensity. Significant factors were then used to generate a suite of general linear models (GLM) to evaluate the significance and interactions between these factors on parasite prevalence. Akaike’s information criterion (AIC) values were calculated for all combinations of factors including main and interactive effects. The model with the lowest AIC value was considered to describe the relationship between prevalence and the suite of factors best. A chi-square test was used to test the significance of main and interactive effects for the chosen model. All statistical tests and GLM models were performed with the use of R 2.11.1 (R Development Core Team, 2010).

**RESULTS**

**Cestode identification**

Sequence data were obtained for a total of 51 individual worms, and an alignment was constructed with the use of a 79–base-pair (bp) region. A single haplotype was recovered, which, through a BLAST search, was found to be identical to the corresponding region in a specimen of *N. surmenicola* (GenBank accession no. FJ572929.1; Palm et al., 2009). The BLAST search found 98% similarity between our specimens and *Heteronybelinia* cf. *estigmena*; a total of 9 nucleotide sites differed across the 795 bp region between our sequence and this second best match (GenBank FJ572931.1; Palm et al., 2009).

**Pacific hake samples**

Stomach samples were taken from a wide range in size and spatial distribution of Pacific hake (Table I). There was no significant difference in mean length between 2008 and 2009 (*P* = 0.07, *n* = 834, *t*-test), but Pacific hake sampled in 1999 were significantly larger (*P* < 0.001, *t*-test) than both years. There was a significant difference in the mean length of hake between males (37.41 ± 0.40 SE, *n* = 429) and females (41.38 ± 0.46 SE, *n* = 548) collected during all years (*P* < 0.001, *t*-test). A total of 132 fish were sampled that were less than 27 cm and considered to be

TABLE I. Description of Pacific hake (*Merluccius productus*) samples collected in 1999, 2008, and 2009.

	Year		
	1999	2008	2009
Number of fish	131	391	443
Number of tows	34	190	151
Latitude range (°N)	34°28.8 47°51.0	32°20.1 48°18.0	32°39.5 48°27.1
Mean depth and range	397 m (193–753 m)	313 m (67–1,052 m)	314 m (65–1,077 m)
Mean fork length (cm)	44.15 ± 0.80 SE	39.21 ± 0.55 SE	37.92 ± 0.45 SE
Fork length range (cm)	30–73	10–72	13–70
Sex ratio (M:F)	0.51	0.70	0.95

year-1 fish. There was a small but significant positive relationship between Pacific hake length and latitude collected for all years (Pearson correlation 0.08,  $P = 0.01$ ) (Fig. 2).

### Prevalence

There was a significantly greater prevalence of *N. surmenicola* collected in 2009 (88.0%,  $n = 443$ ) than in 2008 (75.2%,  $n = 391$ ) and in 1999 (35.1%,  $n = 131$ ) (Pearson's chi-square test,  $P < 0.001$ ). *N. surmenicola* prevalence also increased with latitude (Fig. 3). Hake caught south of Point Conception, California (34.5°N) in 2008 and 2009 had a significantly lower prevalence of *N. surmenicola* (44.2%,  $n = 77$ ) compared to those collected north of Point Conception (85.9%,  $n = 757$ ) (Pearson's chi-square test,  $P < 0.001$ ,  $n = 834$ ). There was a slight trend of larger fish caught in northern waters, but the mean length of fish north of Point Conception (38.7 cm) was not significantly different than those south of Point Conception (36.8 cm) ( $P = 0.08$ ,  $t$ -test). There was

no spatial trend observed with the data from 1999 (data not shown).

*Nybelinia surmenicola* prevalence increased with fish length (Fig. 4). In 2008 and 2009, fish smaller than 27 cm (estimated to be year-1 fish) had significantly lower prevalence of *N. surmenicola* (58.3%,  $n = 32$ ) than those equal to or larger than 27 cm (86.5%,  $n = 702$ ) (Pearson's chi-square test,  $P < 0.001$ ,  $n = 834$ ). In 1999, no fish smaller than 37 cm ( $n = 29$ ) had *N. surmenicola* present in their stomach compared to 67.3% in 2008 and 2009 ( $n = 321$ ). There was also a significant difference in *N. surmenicola* prevalence between females (73.6%,  $n = 535$ ) and males (80.7%,  $n = 415$ ) for all years (Pearson's chi-square test,  $P = 0.01$ ,  $n = 950$ ).

Because of potential confounding influences of year, latitude, fish length, and host gender, independent (main) and interactive effects of these factors were investigated with multiple GLM models. Year and fish gender were treated as categorical covariates. Partial deviance residuals were plotted with a smoothing function for latitude and fish length (Fig. 5). These residuals show how the positive relationship between prevalence and latitude and prevalence and length is not linear and these covariates were, therefore, both fit with a second-degree polynomial in the GLM models. The residuals also show the uncertainty in the model regarding fish caught at low and high latitudes as well on both ends of the length spectrum. A model

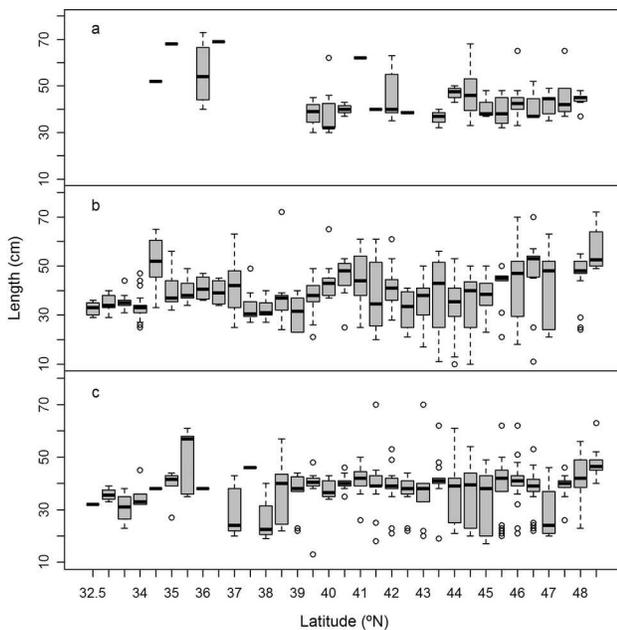


FIGURE 2. Box plots of Pacific hake (*Merluccius productus*) total length by latitude (rounded to 0.5°N bins) for (a) 1999, (b) 2008, and (c) 2009 samples. Information on median, quartiles, maximum, and minimum values are displayed. Open circles represent outliers or actual length values from latitudes with sample sizes of 5 or less.

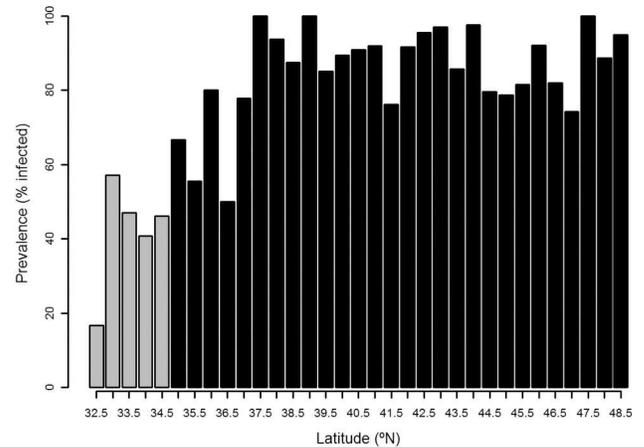


FIGURE 3. Prevalence of *Nybelinia surmenicola* in Pacific hake (*Merluccius productus*) by latitude with data rounded to 0.5°N bins from 2008 and 2009 combined. Gray bars represent latitudes south of Point Conception, California (34.5°N).

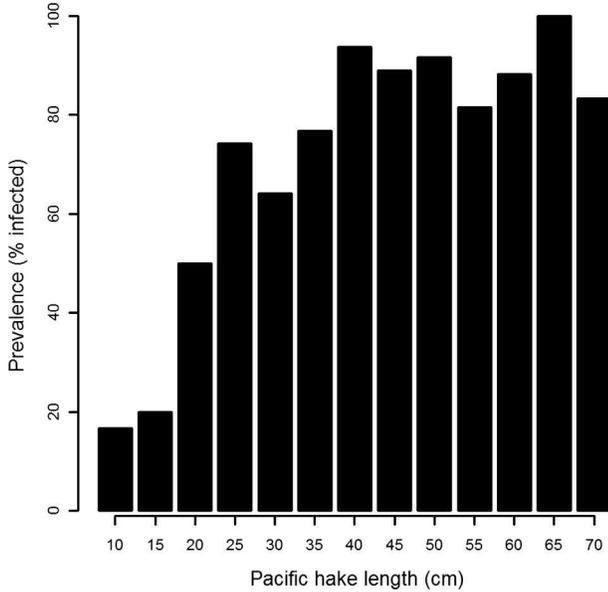


FIGURE 4. Prevalence of *Nybelinia surmenicola* in different size classes of Pacific hake (*Merluccius productus*). Data collected from 2008 and 2009 were combined.

that included all factors as main effects and an interactive effect between latitude and year, length and year, and latitude and length had the lowest AIC score (Table II). Fish gender as a main effect had the least influence on *N. surmenicola* prevalence and did not provide a significant reduction in deviance, but still improved the model fit. An interactive effect between latitude and length was significant and is explained by higher *N. surmenicola* prevalence in larger hake and those caught at higher latitudes.

**Intensity**

Mean intensity of *N. surmenicola* in 2009 (not recorded in 2008) was 20.22 ( $\pm 1.13$  SE,  $n = 390$ ) with a maximum intensity of 157. A majority (90.3%) of *N. surmenicola* was found embedded in the stomach wall; 7.6% were found loose within the stomach, and 2.1% were found halfway embedded in the stomach. Mean

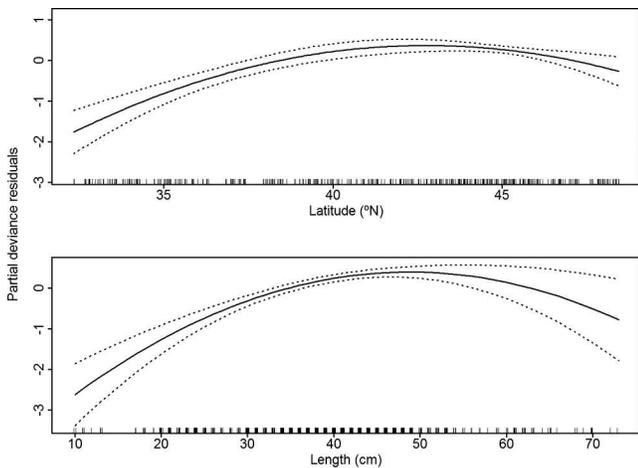


FIGURE 5. Partial deviance residuals for main effects of latitude and length on *Nybelinia surmenicola* prevalence in Pacific hake (*Merluccius productus*). Dotted lines represent 2 times standard error.

TABLE II. Selected GLM models used to test the effects of 4 factors on *Nybelinia surmenicola* prevalence in Pacific hake (*Merluccius productus*) with Akaike's information criterion (AIC) scores and delta AIC values that were used for model selection. Main effects are represented by (+) and interactive effects are represented by (:). Yr = year, Len = length, Lat = latitude, and S = sex.

Model tested	AIC score	$\Delta$ AIC
Yr + Len + Lat + S	750.98	61.80
Yr + Len + Lat + S + Yr:Len	717.40	28.26
Yr + Len + Lat + S + Yr:Lat	745.99	56.85
Yr + Len + Lat + S + Len:Lat	733.65	44.51
Yr + Lat + Len + S + Yr:Len + Yr:Lat	698.47	9.33
Yr + Lat + Len + S + Yr:Len + Len:Lat	722.34	33.20
Yr + Lat + Len + S + Yr:Lat + Len:Lat	725.03	35.89
Yr + Lat + Len + S + Yr:Len + Yr:Lat + Len:Lat	689.40*	0
Yr + Lat + Len + Yr:Len + Yr:Lat + Len:Lat	700.41	11.27

\* Indicates the lowest AIC score.

intensity of *N. surmenicola* in 1999 was 2.78 ( $\pm 0.62$  SE,  $n = 46$ ) with a maximum of 29 per stomach.

In 2009, there was a positive correlation between intensity and latitude (Pearson's correlation,  $P = 0.004$ ) but a very low *R* square value (*R*-squared = 0.018) (Fig. 6). There was no significant difference between intensity of *N. surmenicola* in males ( $21.26 \pm 1.42$  SE,  $n = 194$ ) versus females ( $19.37 \pm 1.78$  SE,  $n = 196$ ) (*t*-test,  $P = 0.62$ ,  $n = 390$ ). Mean *N. surmenicola* intensity was also significantly correlated with hake length (Pearson's correlation,  $P < 0.001$ , *R*-square = 0.358) (Fig. 7). Small fish estimated to be year-1 ( $< 27$  cm) had a mean intensity of 2.89 ( $\pm 0.32$  SE,  $n = 49$ ) *N. surmenicola* per stomach compared to a mean of 22.70 ( $\pm 1.24$  SE,  $n = 341$ ) for fish larger than 27 cm. All fish  $> 50$  cm were females, and there was a decrease in intensity for these larger fish (Fig. 8).

GLM models were not created to investigate intensity, because only latitude and length had significant effects. Pacific hake length and latitude collected were also correlated and together had an interactive effect on intensity. Larger fish and those collected in more northern latitudes had a greater intensity of *N. surmenicola*.

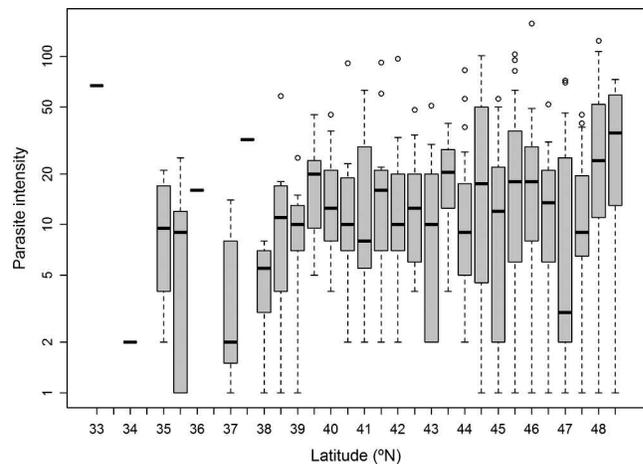


FIGURE 6. Box plot of *Nybelinia surmenicola* intensity in Pacific hake (*Merluccius productus*) and latitude (rounded to 0.5°N bins) in 2009 with information on median, quartiles, maximum, and minimum values. Intensity (*y*-axis) is shown on a logarithmic scale.

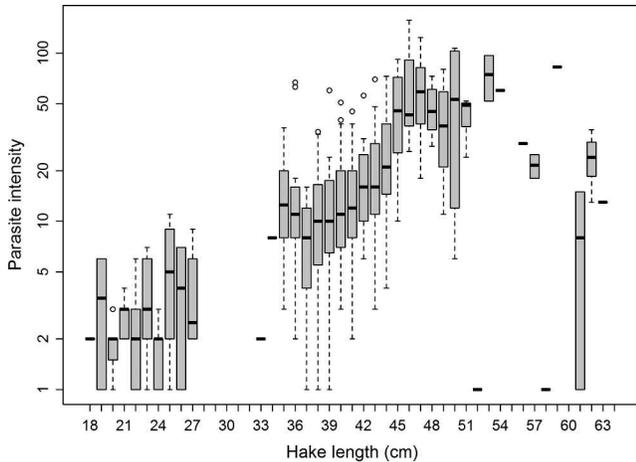


FIGURE 7. Box plot of *Nybelinia surmenicola* intensity and Pacific hake (*Merluccius productus*) length in 2009 with information on median, quartiles, maximum, and minimum values. Intensity (y-axis) is shown on a logarithmic scale.

## DISCUSSION

Despite the apparent ubiquity of *N. surmenicola* in the northern Pacific Ocean, to the best of our knowledge, this is the first report of *N. surmenicola* from Pacific hake caught in the CCE. Larval *N. surmenicola* have been recovered, often in high prevalence, from other fish species caught off Alaska and British Columbia (Moles, 2007). For example, it occurred in 8.3% of Alaskan pollock (*Theragra chalcogramma*) in the Strait of Georgia in 1972 and 70.2% of Alaskan pollock from the Queen Charlotte Sound in 1978 (Arthur et al., 1982). *Nybelinia surmenicola* prevalence in adult Pacific halibut (*Hippoglossus stenolepis*) ranged from 3% to 65% in 15 regions from northern California to the Bering Sea during the summers of 1990–1992, with higher prevalence recorded in Alaska (Blaylock et al., 2003). However, previous reports of *N. surmenicola* from Pacific hake caught in the Strait of Georgia (Sankurathri et al., 1983) and the northeast Pacific Ocean (Kovalenko, 1970), indicated prevalence less than 15%. Sankurathri et al. (1983) concluded that with a prevalence of 2.1%, a range of intensity of 1–10, and infections found only in fish larger than 41 cm, that *N. surmenicola* was not a common Pacific hake parasite in the Strait of Georgia. Our recent data of greater than 88% prevalence in the coastal stock sampled off California, Oregon, and Washington, shows that *N. surmenicola* is currently a very common parasite of this stock of Pacific hake. This prevalence is higher than what has been reported in Alaskan pollock (Arthur et al., 1982) and Pacific halibut (Blaylock et al., 2003). This is in contrast to our findings from a smaller sample of Pacific hake caught in 1999 that indicate a lower historical prevalence (35.1%).

The presence and intensity of *N. surmenicola* have increased significantly in the last decade and these measures of infection were also found to be positively related to Pacific hake length. An increase in prevalence with length was also noted in Alaskan pollock and Pacific halibut (Arthur et al., 1982; Blaylock et al., 1998) and has been well documented for other parasite–host relationships. Unless the Pacific hake population was aging (or average length was increasing), this relationship does not explain the temporal increase in prevalence. In contrast to previous

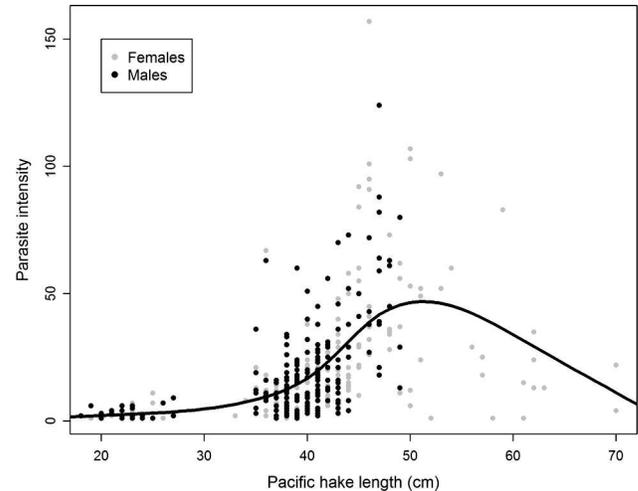


FIGURE 8. *Nybelinia surmenicola* intensity for female and male Pacific hake (*Merluccius productus*) by length in 2009. The data were fit with a general additive model that explained 42.6% of the deviance and had an *R*-square value of 0.42.

examinations of small Pacific hake (<41 cm [Sankurathri et al., 1983] and <37 cm in our 1999 samples), in which no larval *N. surmenicola* were recovered from the smaller fish classes, we found a prevalence of 67% in the smaller size classes of Pacific hake sampled in 2008–2009 (Fig. 3). Thus, it appears that *N. surmenicola* has increased in abundance in both adult and juvenile hake.

Although several factors influence *N. surmenicola* recruitment, once infected, Pacific hake length was the main influencing factor on intensity, with some minor influences of latitude. Mean intensity of *N. surmenicola* in hake is comparable to levels observed in Pacific halibut ( $15.8 \pm 54.3$ ), which, along with Alaskan pollock, also exhibited increased intensity with greater length (Arthur et al., 1982; Blaylock et al., 1998). Larger fish are older and have consumed more prey items, thereby increasing the number of *N. surmenicola* accumulated. An interesting caveat to this trend was the decrease in intensity in 2009 for fish larger than 50 cm, which were all females. Pacific hake diet shifts toward fish as they grow larger, and euphausiids become a smaller percentage of their diet (Buckley and Livingston, 1997). Given this ontogenetic shift in diet away from euphausiids, *N. surmenicola*'s first intermediate host species (Shimazu, 1999), an asymptote for intensity was expected. Instead, there was a decline in intensity for fish larger than 50 cm. There are many possible processes, single or in combination, that could lead to this observed age-intensity curve, including parasite mortality, parasite-associated host mortality, and acquired immunity (Duerr et al., 2003). With this specific host–parasite system, we have no information on the life span of *N. surmenicola* plerocercoids, and no reason to assume parasite–host associated mortality, or that acquired immunity takes place. In contrast, it is possible, that when these larger fish were younger, they either did not feed on euphausiids, *E. pacifica* was not as abundant, or *N. surmenicola* was not as prevalent, as our data have shown. However, this observed decrease in intensity with age also may have been an artifact of the smaller sample size of older hosts (Duerr et al., 2003).

Other studies that describe temporal changes in parasite prevalence in marine fish have suggested environmental changes

as a causal factor (MacKenzie, 1987; Olson et al., 2004; Khan, 2007, 2008). Temperature, for example, can affect the dynamics of host–parasite relationships in marine systems by acting directly on the hatching rate of parasites and changing the spatial distribution of intermediate and definitive hosts (Marcoligiese, 2001). Khan (2007, 2008) attributed declines in metazoan parasites of Atlantic cod (*Gadus morhua*) off coastal Labrador, Canada, to the affects of oceanic temperatures in the northwestern Atlantic Ocean on changes in the food web (specifically a loss of capelin [*Mallotus villosus*]). Large-scale climate changes such as the Pacific Decadal Oscillation and the El Niño Southern Oscillation have been shown to influence the distribution of a wide variety of organisms, including euphausiids (Mantua and Hare, 2002; Brinton and Townsend, 2003), and it is possible that these changes have affected *N. surmenicola* prevalence in Pacific hake.

An increase in *N. surmenicola* prevalence with latitude, especially the difference between Pacific hake caught south of Point Conception, California and those caught further north, suggests that there is an environmental or host species distribution factor influencing *N. surmenicola* transmission. Blaylock et al. (2003) also saw an increase in *N. surmenicola* prevalence in Pacific halibut with latitude from northern California to Alaska and defined it as a central and northern parasite species as he recorded prevalence at, or greater than, 50% at, and above, the Northern Haida Gwaii of Canada. Interestingly, the highest prevalence that Blaylock et al. (2003) recorded in Pacific halibut (65.4% off Kodiak Island, Alaska) was still less than what we recorded in 2008 and 2009 from Pacific hake in the CCE. The prevalence they recorded off Oregon and Washington was 17.4% and 14.3%, respectively.

Larvae of *N. surmenicola* have been reported from many fish species that serve as second intermediate hosts, but little has been documented regarding the other hosts required to complete the life cycle. Shimazu (1975, 1999) described krill (*Euphausia pacifica*) as a first intermediate host, fish as the paratenic host, and salmon shark (*Lamna ditropis*) as the definitive host. Euphausiids, including, *E. pacifica*, are a major dietary component of Pacific hake (Livingston and Bailey, 1985; Brodeur et al., 1987; Buckley and Livingston, 1997). *Euphausia pacifica* is an abundant species in the CCE and ranges south to latitudes of 25°N (Brinton, 1976). *Euphausia pacifica* abundance can vary annually with water temperature (Brinton, 1981) and Brodeur et al. (1987) also described yearly variations in the percentage of *E. pacifica* found in Pacific hake diet. It is possible that between 1999 and 2008, *E. pacifica* occurrence in Pacific hake diet increased, contributing to the increase in *N. surmenicola* in Pacific hake. Another possibility is that there has been an increase in the prevalence of *N. surmenicola* in *E. pacifica*.

Shimazu (1975) described salmon sharks as the definitive hosts for *N. surmenicola*. Although Palm and Caira (2008) list 74 species of hosts for larval *N. surmenicola*, we found only the 1 reference for the definitive host. Unfortunately, little is known about salmon shark ecology or their diet. Salmon sharks are thought to be concentrated between 50 and 60°N (Goldman and Musick, 2008), yet a tracking study indicates that they migrate along the entire U.S. west coast to southern California (Weng et al., 2005). Weng et al. (2008) identified the CCE as the second most important ecoregion, outside of Alaska, for salmon shark foraging; tagged salmon sharks were found to spend an average of

107 days, primarily in the winter and spring, in the CCE. Although we could not find any literature on the occurrence of Pacific hake in their diet, these species ranges overlap, and salmon sharks are known to consume other gadids (Goldman and Musick, 2008). A recent necropsy of an adult salmon shark caught in the Pacific hake fishery off the central Oregon coast revealed Pacific hake in the shark's stomach (B. Hanshumaker, pers. comm.). Pacific hake consume *E. pacifica* throughout their range, but more likely consume *E. pacifica* infected with *N. surmenicola* in regions where they have high spatial and temporal overlap with salmon sharks.

The relationship between salmon sharks, Pacific hake, *E. pacifica*, and *N. surmenicola* may be explained in terms of latitude, but the recent expansion of *N. surmenicola* in Pacific hake is more difficult to interpret. Despite their pervasiveness in northeastern Pacific marine fish species, 88% prevalence with a mean intensity of 20.2 per Pacific hake is noteworthy. This population growth of *N. surmenicola* in Pacific hake is remarkable and a possible signal of a larger environmental change. There have been recent environmental changes in the CCE (Chan et al., 2008) and Phillips et al. (2007) described a recent northward expansion of Pacific hake spawning grounds that occurred in 2006. Perhaps the underlying environmental effects that have caused this expansion have also positively affected *N. surmenicola* population biology. In addition, salmon shark populations appear to be rebuilding following the closing of open ocean gillnet fisheries in the eastern and west-central Pacific Ocean and are now among the few shark species listed with a Least Concern status by the IUCN Red List of Threatened Species (Goldman et al., 2008). The importance of the CCE as a foraging ecoregion for salmon sharks and the abundance of larval *N. surmenicola* in Pacific hake caught in the CCE suggest Pacific hake as an important prey item for salmon sharks that has not been previously recognized.

In summary, our data suggest that *N. surmenicola* has expanded within the CCE coastal stock of Pacific hake. Latitude appears to influence prevalence and intensity as fish collected at higher latitudes have greater prevalence and intensity of *N. surmenicola*. Larger fish also have greater prevalence and an elevated mean intensity of *N. surmenicola*. The cause of this increase of *N. surmenicola* is unknown, but is likely an expansion of overlap between different host species and may serve as an indicator of environmental and ecological change within the CCE. Future evaluations of Pacific hake ecology in the CCE should include monitoring of plerocercoids of *N. surmenicola* to help determine stability of recently identified high abundances.

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