

Occurrence and effect of the parasitic isopod, *Lironeca ovalis* (Isopoda: Cymothoidae), on young-of-the-year bluefish, *Pomatomus saltatrix* (Pisces: Pomatomidae)

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Abstract: The bluefish, *Pomatomus saltatrix*, is often a preferred host for infection by the isopod, gill ectoparasite *Lironeca ovalis*. Here we quantify the occurrence of infection by *L. ovalis* on young-of-the-year bluefish in the Hudson River estuary and evaluate whether there is a significant reduction in growth or foraging as a result of infection. Prevalence of *L. ovalis* on bluefish was high (25.4%) but small (<75 mm) and large fish (>175 mm) exhibited significantly lower prevalences than intermediate-sized fish. Parasite size increased with bluefish size, and a significant but small effect of parasitism on the bluefish mass-length relationship was found; parasitized fish weighed 3% less than nonparasitized fish at a given length. Infection did not have a significant effect on the mass of stomach contents at capture. Although there remain many questions regarding the host-parasite relationship between *P. saltatrix* and *L. ovalis*, the physiological cost associated with infection appears to be small and probably does not constitute a serious threat to individual bluefish survival.

Résumé : Le tassergal (*Pomatomus saltatrix*) est souvent un hôte privilégié de l'isopode (*Lironeca ovalis*), ectoparasite des brachies. Nous avons mesuré la fréquence d'infection par le *L. ovalis* chez les jeunes tassergals de l'année, dans l'estuaire du fleuve Hudson, et évalué dans quelle mesure cette infection entraîne une réduction significative de la croissance ou de la recherche de nourriture. La fréquence du parasite était globalement élevée (25,4%), mais significativement moindre chez les tassergals de taille petite (<75 mm) ou grande (>175 mm) que chez ceux de taille intermédiaire. La taille des parasites augmentait avec celle de l'hôte, et le parasitisme avait un effet significatif, bien que léger, sur le rapport masse-longueur : pour une longueur donnée, les sujets parasités pesaient 3 % de moins que ceux qui ne l'étaient pas. L'infection n'avait pas d'effet significatif sur la masse du contenu stomacal au moment de la capture. De nombreux aspects de la relation hôte-parasite entre le *P. saltatrix* et le *L. ovalis* restent à élucider, mais le coût physiologique de l'infection semble faible et ne constitue sans doute pas une menace grave pour la survie individuelle des tassergals.

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Introduction

Lironeca ovalis (Crustacea: Isopoda: Cymothoidae) is a proandrous, hermaphroditic, gill parasite (Brusca 1981; Kabata 1984). The bluefish, *Pomatomus saltatrix* (Pisces: Pomatomidae) is a pelagic teleost that spawns in continental shelf waters along the east coast of the United States (Kendall and Walford 1979). Larval and pelagic juvenile bluefish are trans-

ported from offshore spawning grounds to estuarine nursery habitat (Kendall and Walford 1979; Hare and Cowen 1996) where they spend a majority of their first year (Kendall and Walford 1979; McBride and Conover 1991). While in estuaries, young-of-the-year (YOY) bluefish grow rapidly (McBride and Conover 1991; Juanes and Conover 1994). *Lironeca ovalis* frequently parasitize YOY bluefish (Richardson 1905; Fowler 1912; Lindsay and Moran 1976; Sandifer and Kerby 1983) and may affect individual survival by reducing foraging ability and (or) growth.

The physiological effects of cymothoid infection are not clearly understood. Deleterious effects on host finfish have been reported in several studies citing tissue damage; host behavioral changes; decreases in mean weight, size, and growth; and, in some instances, death (Kroger and Guthrie 1972; Sadzikowski and Wallace 1974; Lindsay and Moran 1976; Brusca 1978; Romestand and Trilles 1979; Brusca 1981; Kabata 1984; Moser and Sakanari 1985; Segal 1987). Other research has concluded that individual fish infected with a single parasite were not significantly "less healthy" than nonparasitized fish (Brusca 1981; Ruiz and Madrid 1992; Landau et al. 1995) and, only in cases of multiple infection or stress, would an effect on condition and (or) behavior of hosts be realized (Keys 1928; Lanzing and

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O'Connor 1975; Brusca 1981). Similarly, Weinstein and Heck (1977) suggested that host damage, if any, due to cymothoid infection is minimal.

The objective of this study was to quantify the occurrence and evaluate the effect of infection by *L. ovalis* on YOY bluefish in the Hudson River Estuary. The infection rate (prevalence) relative to bluefish length was elucidated, as was the parasite mass – bluefish length relationship. The effect of parasitism on bluefish growth and feeding was also examined through analysis of the bluefish mass–length relationship and weight of stomach contents.

Materials and methods

Young-of-the-year, spring-spawned bluefish ($n = 768$) were collected from the lower 40–65 km of the Hudson River. Collections were made biweekly from mid-July to early November in 1989 and 1990 using a beach seine (61 × 3 m with 13 mm mesh wings and a 6 mm mesh bag) set from a boat. Bluefish and isopods were killed and preserved in 10% buffered formalin. In the laboratory, stomachs were emptied, and in 1989, the contents were weighed to the nearest 0.001 g. Bluefish, minus their stomach contents, were wet weighed to the nearest 0.01 g and measured for total length (hereafter length) to the nearest 1 mm. This work was part of a larger studying examining the diet of YOY bluefish (see Juanes et al. 1993).

The number of *L. ovalis* on each bluefish was enumerated. Isopods were then removed from their host and weighed to the nearest 0.001 g. The gills of nonparasitized bluefish were examined for the presence of scars that would imply previous parasitism. None were found.

The relationship between prevalence of the isopod and host size was evaluated using nonparametric regression based on splines (see Schluter 1988; Anderson 1995). The method, as developed by Anderson (1995), estimates relative survival with regard to a quantitative trait based on cross-sectional data (before–after comparisons). Nonparametric regression based on splines was used in this study to estimate the rate of parasitism relative to bluefish length. Rather than a before–after comparison, lengths of parasitized and nonparasitized bluefish were compared. The 95% confidence limits were calculated with 10 bootstrapped replications. This method assumes parasitism is a smoothly changing function of bluefish length, makes no a priori assumption as to a parametric model, does not require grouping of data, and allows calculation of confidence intervals about the function (see Schluter 1988; Anderson 1995).

A randomization procedure was used to evaluate the estimated prevalence relative to bluefish length. In the actual data, 195 out of 768 bluefish were infected with *L. ovalis*. The randomization procedure used the actual lengths of bluefish and randomly classified 195 of these 768 lengths as being parasitized fish. The nonparametric regression procedure was then used to estimate the function of parasitism rate relative to bluefish length based on the randomly generated data set. Randomization was repeated 10 times, and for each bluefish length, the average estimated parasitism rate (if parasitism was a random function of bluefish length) was calculated, as were the 95% confidence limits. If the estimated function based on the actual data fell outside the 95% confidence limits of the estimated function based on random data, then it was concluded that parasitism was not independent of bluefish length (see Sokal and Rohlf 1981).

The relationship between parasite mass – host length was analyzed with linear regression (Sokal and Rohlf 1981) using the multiple general linear hypotheses module of SYSTAT (Wilkinson 1990). Bluefish length and isopod mass were log transformed before calculation of the regression.

To evaluate the effect of parasitism on bluefish growth, the log-transformed bluefish mass–length relationship was analyzed using an ANCOVA model (Sokal and Rohlf 1981). First, data from the

2 years were compared for bluefish between 100 and 150 mm length ($n = 484$) with the model: $\log(\text{mass}) = a + b \times \log(\text{length}) + c \times \text{year} + d \times \log(\text{length}) \times \text{year}$. The interaction term was not significant ($p > 0.05$) and the reduced ANCOVA model: $\log(\text{mass}) = a + b \times \log(\text{length}) + c \times \text{year}$ was calculated. The year term was not significant ($p > 0.05$), and thus, the data from the 2 years were pooled. An ANCOVA model was then used to determine the effect of parasitism on the mass–length relationship. The significance of the interaction term was first determined with the model: $\log(\text{mass}) = a + b \times \log(\text{length}) + c \times \text{parasitized} + d \times \log(\text{length}) \times \text{parasitized}$. The significance of the parasitism term was then determined with the model: $\log(\text{mass}) = a + b \times \log(\text{length}) + c \times \text{parasitized}$. Calculations were made with the multiple general linear hypotheses module of SYSTAT (Wilkinson 1990). In addition, the allometric coefficient b ($W = aL^b$) describing the rate of isopod mass increase relative to bluefish length and bluefish mass increase relative to bluefish length were compared (Sokal and Rohlf 1981).

The effect of parasitism on bluefish feeding was analyzed with an ANCOVA model (Sokal and Rohlf 1981) using the stomach content mass data collected in 1989. Bluefish length and stomach content weight were log transformed; because many bluefish had no prey items in their guts, a $\log(\text{stomach content mass} + 1)$ transformation was used. The significance of the interaction term was first determined with the model: $\log(\text{stomach content mass} + 1) = a + b \times \log(\text{length}) + c \times \text{parasitized} + d \times \log(\text{length}) \times \text{parasitized}$. The significance of the parasitism term was then determined with the model: $\log(\text{stomach content mass} + 1) = a + b \times \log(\text{length}) + c \times \text{parasitized}$.

Results

Of 768 bluefish collected, 25.4% (195) were infected with a single *L. ovalis*. All isopods were attached to the host either on the antero-ventral portion of the gill chamber ($n = 192$) or in the buccal cavity ($n = 3$). Bluefish were 45–278 mm in length and weighed 0.96–220.26 g. Isopods weighed 0.030–0.880 g.

The estimated function of isopod prevalence in relation to bluefish length was complex with a steep increase at about 75 mm, a broad but varying plateau (~30%) between 75 and 175 mm, and a gradual decrease at sizes greater than 175 mm (Fig. 1). Fewer fish were parasitized at sizes <75 mm and >175 mm than expected if parasitism was a random function of length (Fig. 1).

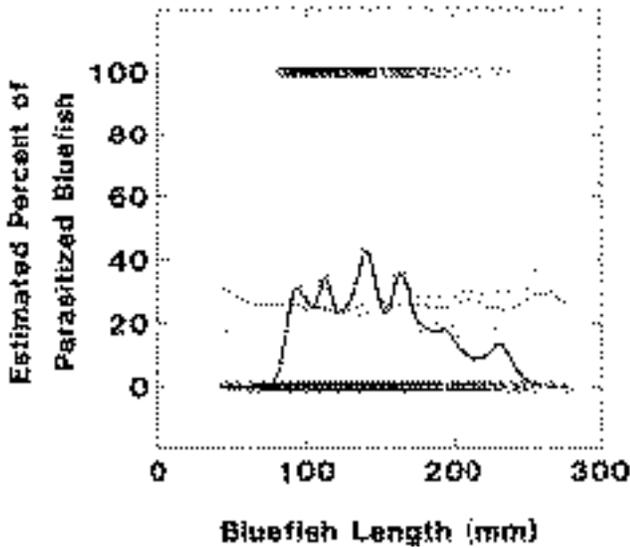
Parasite mass increased with increasing bluefish length (Fig. 2). The linear regression model ($\log(\text{parasite mass}) = a + b \times \log(\text{length})$) was significant ($p < 0.001$, $r^2 = 0.41$) as were both terms of the model ($a = -5.61$, $SE = 0.40$, $p < 0.001$; $b = 2.29$, $SE = 0.19$, $p < 0.001$).

Although there was a significant effect of parasitism on the bluefish mass–length relationship, this effect was very small. Parasitized fish weighed only 3% less than nonparasitized fish at a given length (Fig. 3). Using the full ANCOVA model, the interaction term was nonsignificant (Table 1). However, without the interaction term, a significant but small parasite effect was found (Table 1).

Bluefish mass increased more rapidly with bluefish length than did isopod mass. The allometric coefficient b ($W = aL^b$) for the isopod mass – bluefish length relationship ($b = 2.29$, $SE = 0.19$) differed from that for the bluefish mass–length relationship ($b = 3.15$, $SE = 0.01$) ($MSD_{\alpha=0.05} = 0.383$).

Parasitism did not affect stomach content mass of bluefish. Using the full ANCOVA model with length as a covariate, the interaction term was not significant (Table 2). Without the

Fig. 1. Nonparametric regression estimates of prevalence relative to bluefish length. The estimated function based on the actual data is denoted by the thick line, and the estimated function based on the randomly generated data is denoted by the thin line. 95% confidence limits around each function are shown as broken lines. Individual lengths for all bluefish, both parasitized and nonparasitized, are denoted by open circles.



interaction term, the parasite effect was also nonsignificant (Table 2).

Discussion

During estuarine residency, young bluefish are often preferred hosts for cymothoid infection (Thomas et al. 1974; Lindsay and Moran 1976; Brusca 1981; Rokicki 1985). In this study, overall prevalence of *L. ovalis* on YOY bluefish from the Hudson River Estuary was high (25.4%). This generally high level of infection, as compared with other species (Table 3), suggests that the bluefish is a uniquely suitable host for *L. ovalis*. The tendency of bluefish to school (Van der Elst 1976), combined with an estuarine-dependent early life history (McBride and Conover 1991) and one of the highest specific growth rates reported for temperate fishes (1–2 mm · day⁻¹, McBride and Conover 1991; Juanes and Conover 1994), may partially explain the relationship.

The decreasing prevalences at larger host sizes that we observed is consistent with other reports of infection on larger juveniles and offshore adults (Anderson 1970; Sadzikowski and Wallace 1974; Thomas et al. 1974; Lanzing and O'Connor 1975; Brusca 1981). The rapid increase in prevalence at smaller sizes has not been reported previously. Future studies should examine the ecological causes of size dependency in the host–parasite relationship.

A positive, significant host–parasite size relationship was found in this study (Fig. 2) and in other studies on bluefish (Landau et al. 1995), lutjanids (Weinstein and Heck 1977), *Citharichthys* spp. (Robinson 1982), and carangids (Menzies et al. 1955). Despite the significance of this relationship, the correlation coefficient ($r^2 = 0.41$) indicates substantial variability that may reflect differences in host size at the time of infection.

Fig. 2. Isopod mass – bluefish length relationship with the fitted allometric function ($W = aL^b$) based on the linear regression of the log-transformed data ($\log(W) = \log(a) + b \log(L)$).

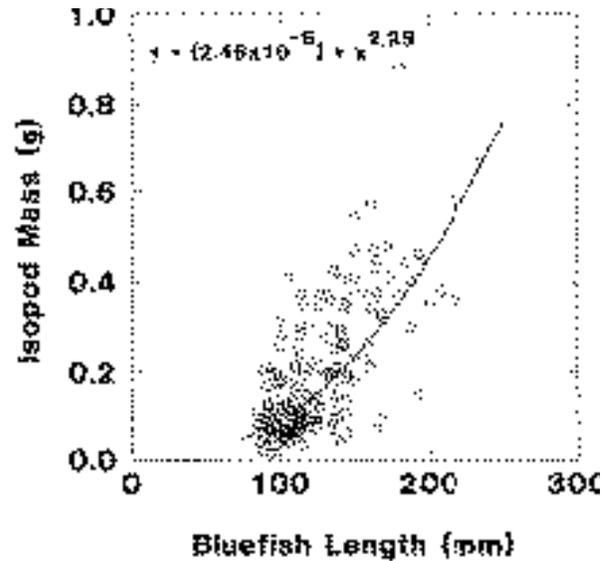
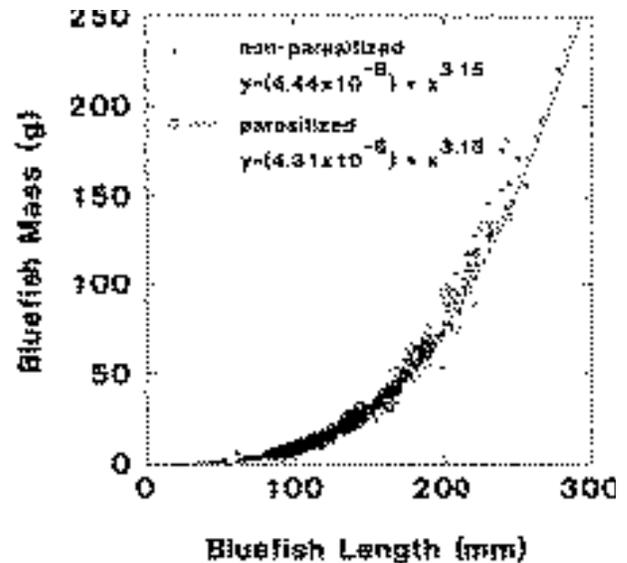


Fig. 3. Mass–length relationship for both parasitized and nonparasitized bluefish. The fitted allometric functions ($W = aL^b$) based on the reduced ANCOVA model for both parasitized and nonparasitized bluefish are also shown ($\log(W) = \log(a) \pm \text{parasitism effect} + b \log(L)$).



Keys (1928) and Brusca (1981) suggested that only in stressful environmental situations will a deleterious, parasite-induced influence on host vitality be realized. Hence, one might expect evidence of a serious negative effect on condition in the polluted environment of the lower Hudson River (Limburg et al. 1986). We found no evidence of a serious effect due to parasitism. Although there was a significant effect of parasitism on the host mass–length relationship (Table 2), infected fish weighed only 3% less than nonparasitized individuals for a given length (Fig. 3).

Table 1. Summary of the ANCOVA analysis of the effect of parasitism on the bluefish mass–length relationship.

(A) Full ANCOVA model ($\log(\text{mass}) = a + b \times \log(\text{length}) + c \times \text{parasitized} + d \times \log(\text{length}) \times \text{parasitized}$).

Source	df	MS	F	p
Log(length)	1	61.571	29 142.979	<0.001
Parasitized	1	0.001	0.545	ns
Log(length) × parasitized	1	0.001	0.317	ns
Error	764	0.002		

(B) Reduced ANCOVA model ($\log(\text{mass}) = a + b \times \log(\text{length}) + c \times \text{parasitized}$).

Source	df	MS	F	p
Log(length)	1	122.430	58 001.140	<0.001
Parasitized	1	0.027	12.649	<0.001
Error	765	0.002		

Table 2. Summary of the ANCOVA analysis of the effect of parasitism on the bluefish stomach content mass – bluefish length relationship.

(A) Full ANCOVA model ($\log(\text{stomach content mass} + 1) = a + b \times \log(\text{length}) + c \times \text{parasitized} + d \times \log(\text{length}) \times \text{parasitized}$).

Source	df	MS	F	p
Log(length)	1	6.038	120.246	<0.001
Parasitized	1	0.004	0.769	ns
Log(length) × parasitized	1	0.006	0.727	ns
Error	367	0.050		

(B) Reduced ANCOVA model $\log(\text{stomach content mass} + 1) = a + b \times \log(\text{length}) + c \times \text{parasitized}$.

Source	df	MS	F	p
Log(length)	1	11.607	231.685	<0.001
Parasitized	1	0.053	1.061	ns
Error	368	0.050		

Other studies have found that parasitic infection may reduce or interfere with the ability of the host to feed (Menzies et al. 1955; Weinstein and Heck 1977). However, our data indicate that infection by *L. ovalis* had little effect on the mass of bluefish stomach contents. While infected bluefish may weigh slightly less for a given length, infection does not appear to impair feeding. This result implies that the difference in the infected versus noninfected bluefish mass–length relationships was not due to differential feeding ability or behavioral changes affecting foraging success; the basis of this difference remains to be resolved. We conclude that infection by *L. ovalis* probably does not constitute a serious threat to YOY bluefish survival.

According to Nikolsky (1978), teleost–parasite interactions are defined in two ways: those where parasites benefit from host survival and those where parasite fitness is enhanced by death of the host. In relationships where survival of the host

fish is important, parasitic species may consume tissues or fluids in a manner that does not cause serious harm to the host (Nikolsky 1978). Several aspects of isopod life history support the concept that cymothoids may parasitize in a manner that does not constitute a serious threat to host well-being. In the case of *Lironeca* spp., swimming ability is vestigial in adults (Menzies et al. 1955; Brusca 1978; Keusink 1979; Sandifer and Kerby 1983). Thus, it may be critical for a young, mobile isopod to attach to a host and then mature as the host grows. *Lironeca* spp. also exhibit self-regulating behavior regarding the maximum number of individual parasites allocated to any one host (Keusink 1979). Finally, cymothoids produce a small number of eggs per adult female (approx. 300–400). This combination of life-history traits may result in cymothoids being adapted to semi-enclosed habitats where host density is high (Brusca 1981; Rokicki 1985) and where continued host survival is beneficial to the parasite.

Table 3. Summary of *Lironeca ovalis* prevalence for several teleost species, including *Pomatomus saltatrix*, in nearshore habitats of the Middle Atlantic Bight.

Species	Study site	Prevalence (%)	Reference
<i>Pomatomus saltatrix</i>	Hudson River	25.0	This study
<i>P. saltatrix</i>	Great South Bay	7–16.0	R.E. Marks (personal observation)
<i>P. saltatrix</i>	Great Bay	6.0	R.E. Marks (personal observation)
<i>P. saltatrix</i>	Delaware River	20.0	Lindsay and Moran (1976)
<i>P. saltatrix</i>	Sandy Hook Bay	10.0	Breder (1925)
<i>P. saltatrix</i>	Great Bay	2–38.0	Thomas et al. (1974)
<i>P. saltatrix</i>	Jersey Shore	22.0	Landau et al. (1995)
<i>Morone saxatilis</i>	Delaware River	2.0	Lindsay and Moran (1976)
<i>M. saxatilis</i>	Long Island	2.0	Alperin (1966)
<i>M. saxatilis</i>	Chesapeake Bay	7.0	B.H. Young (personal communication) ^a
<i>M. saxatilis</i>	Long Island Sound	12.0	B.H. Young (personal communication) ^a
<i>Morone americana</i>	Delaware River	2.0	Sadzikowski and Wallace (1974)
<i>M. americana</i>	Delaware River	4.0	Lindsay and Moran (1976)
<i>Bairdiella chrysura</i>	Delaware River	6.0	Lindsay and Moran (1976)
<i>Cynoscion regalis</i>	Delaware River	3.0	Lindsay and Moran (1976)
<i>Leiostomus xanthurus</i>	Delaware River	0.4	Lindsay and Moran (1976)
<i>Micropogonius undulatus</i>	Delaware River	0	Lindsay and Moran (1976)
<i>Menticirrhus saxatilis</i>	Delaware River	0	Lindsay and Moran (1976)
<i>Pogonias cromis</i>	Delaware River	0	Lindsay and Moran (1976)

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References

- Alperin, I.M. 1966. A new parasite of striped bass. N.Y. Fish. Game J. **13**: 121–123.
- Anderson, C.S. 1995. Calculating size-dependent relative survival from samples taken before and after selection. In *Edited by* D.H. Secor, J.M. Dean, and S.E. Campana. Recent developments in fish otolith research. Belle W. Baruch Library Mar. Sci. No. 19. University of South Carolina Press, Columbia, S.C. pp. 455–466.
- Anderson, H.G., Jr. 1970. Annotated list of parasites of the bluefish *Pomatomus saltatrix*. Tech. Rep. No. 54. U.S. Department of the Interior, Bureau of Sport Fisheries and Wildlife, Washington, D.C. pp. 3–15.
- Breder, C.M., Jr. 1925. Growth of young bluefish. N.Y. Zool. Soc. **28**: 181–183.
- Brusca, R.C. 1978. Studies on the cymothoid fish symbionts of the eastern Pacific (Crustacea: Isopoda: Cymothoidae). II. Systematics and biology of *Lironeca vulgaris* Stimpson 1857. Occas. Pap. Allan Hancock Found. New Ser. No. 2. pp. 1–19.
- Brusca, R.C. 1981. A monograph on the Isopoda: Cymothoidae (Crustacea) of the eastern Pacific. Zool. J. Linn. Soc. **73**: 117–199.
- Fowler, H.W. 1912. Report of the New Jersey State Museum — 1911. Part II. The Crustacea of New Jersey. New Jersey State Museum, Trenton, N.J.
- Hare, J.A., and Cowen, R.K. 1996. Transport mechanisms of larval and pelagic juvenile bluefish (*Pomatomus saltatrix*) from South Atlantic Bight spawning grounds to Middle Atlantic Bight nursery habitats. Limnol. Oceanogr. **41**: 1264–1280.
- Juanes, F., and Conover, D.O. 1994. Rapid growth, high feeding rates, and early piscivory in young-of-the-year bluefish (*Pomatomus saltatrix*). Can. J. Fish. Aquat. Sci. **51**: 1752–1761.
- Juanes, F., Marks, R.E., McKown, K.A., and Conover, D.O. 1993. Predation by age-0 bluefish on age-0 anadromous fishes in the Hudson River Estuary. Trans. Am. Fish. Soc. **122**: 348–356.
- Kabata, Z. 1984. Diseases caused by metazoans: crustaceans. In O. Kinne. Diseases of marine animals. Vol 4. Part 1. Introduction, Pisces. *Edited by* Biologische Anstalt Helgoland, Hamburg, Germany. pp. 321–347.
- Kendall, A.W., and Walford, L.A. 1979. Sources and distributions of bluefish, *Pomatomus saltatrix*, larvae and juveniles off the east coast of the United States. Fish. Bull. U.S. **77**: 213–227.
- Keys, A.B. 1928. Ectoparasites and vitality. Am. Nat. **62**: 279–282.
- Keusink, C.R. 1979. Biology and natural history of the fish parasite *Lironeca vulgaris*. (Crustacea; Isopoda; Cymothoidae) M.S. thesis, San Jose State University, San Jose, Calif.
- Kroger, R.L., and Guthrie, J.F. 1972. Incidence of the parasitic isopod, *Olencira praegustator*, in juvenile Atlantic menhaden. Copeia, 1972: 370–374.
- Lanzing, W.J.R., and O'Connor, P.F. 1975. Infestation of luderick

- (*Girella tricuspidata*) populations with parasitic isopods. Aust. J. Mar. Freshwater Res. **26**: 355–361.
- Landau, M., Danko, M.J., and Slocum, C. 1995. The effect of the parasitic cymothoid isopod (*Lironeca ovalis*) (Say) on growth of young-of-the-year bluefish (*Pomatomus saltatrix*). Crustaceana, **68**: 397–400.
- Limburg, K.E., Moran, M.A., and McDowell, W.H. (Editors). 1986. The Hudson River ecosystem. Springer-Verlag, New York, N.Y.
- Lindsay, J.A., and Moran, R.L. 1976. Relationships of parasitic isopods *Lironeca ovalis* and *Olencira praegustator* to marine fish hosts in Delaware Bay. Trans. Am. Fish. Soc. **105**: 327–332.
- McBride, R.S., and Conover, D.O. 1991. Recruitment of young-of-the-year bluefish, *Pomatomus saltatrix*, to the New York Bight: variation in abundance and growth of spring- and summer-spawned cohorts. Mar. Ecol. Prog. Ser. **78**: 205–216.
- Menzies, R.J., Bowman, T.E., and Alverson, F.G. 1955. Studies of the fish parasite *Lironeca convexa* Richardson (Crustacea, Isopoda, Cymothoidae). Wasmann J. Biol. **13**: 277–295.
- Moser, M., and Sakanari, J. 1985. Aspects of host location in the juvenile isopod *Lironeca vulgaris* (Stimpson, 1857). J. Parasitol. **71**: 464–468.
- Nikolsky, G.V. 1978. The ecology of fishes. T.F.H. Publications, Inc. Ltd., Neptune City, N.J.
- Richardson, H. 1905. A monograph of the isopods of North America. U.S. Nat. Mus. Bull. No. 54.
- Robinson, G.R. 1982. *Lironeca vulgaris* (Cymothoidae, Isopoda): Sanddab–isopod population interactions, growth and sex change. M.S. thesis, University of California, Santa Barbara, Calif.
- Rokicki, J. 1985. Biology of adult Isopoda (Crustacea) parasitizing fishes of the North-West Africa shelf. Acta Ichthyol. Piscatoria, **15**(1): 95–118.
- Romestand, B., and Trilles, J.P. 1979. Influence of the cymothoid isopods *Meinertia oestroides*, *Meinertia parallela*, and *Anilocra physodes* (Crustacea; fish parasites) on the growth of fish hosts *Boops boops* and *Pagellus erythrinus* (Sparidae). Z. Parasitenkd. **59**: 195–202.
- Ruiz, A., and Madrid, J. 1992. Studies on the biology of the parasitic isopod *Cymothoa exigua* (Schioedte and Meinert, 1884) and its relationship with the snapper *Lutjanus peru* (Pisces: Lutjanidae, Nichols and Murphy, 1922), from commercial catch in Michoacan. Cien. Mar. **18**: 19–34.
- Sadzikowski, M.R., and Wallace, D.C. 1974. The incidence of *Lironeca ovalis* (Say) (Crustacea, Isopoda) and its effects on the growth of white perch, *Morone americana* (Gmelin), in the Delaware River near Artificial Island. Chesapeake Sci. **15**: 163–164.
- Sandifer, P.A., and Kerby, J.H. 1983. Early life history and biology of the common fish parasite, *Lironeca ovalis* (Say) (Isopoda, Cymothoidae). Estuaries, **6**: 420–425.
- Schluter, D. 1988. Estimating the form of natural selection on a quantitative trait. Evolution, **42**: 849–861.
- Segal, E. 1987. Behavior of juvenile *Nerocila acuminata* (Isopoda, Cymothoidae) during attack, attachment, and feeding on fish prey. Bull. Mar. Sci. **41**: 351–360.
- Sokal, R.R., and Rohlf, F.J. 1981. Biometry. W.H. Freeman, San Francisco.
- Thomas, D.L., Milstein, C.B., Tatham, T.R., Bieder, R.C., Margraf, F.J., Danila, D.J., Hoff, H.K., Illjes, E.A., McCullough, M.M., and Swiecicki, F.A. 1974. Ecological studies in the bays and other waterways near Little Egg Inlet and in the ocean in the vicinity of the proposed site for the Atlantic generating station. New Jersey. Vol. I. Fishes. Report prepared for Public Service Electric and Gas Co. Ichthyological Associates, Inc., Absecon, N.J. pp. 141–142.
- Van der Elst, R. 1976. Gamefish of the east coast of southern Africa. I. The biology of the elf, *Pomatomus saltatrix* (Linnaeus), in the coastal waters of Natal. S. Afr. Assoc. Mar. Biol. Res. No. 44.
- Weinstein, M.P., and Heck, K.L., Jr. 1977. Biology and host–parasite relationships of *Cymothoa excisa* (Isopoda, Cymothoidae) with three species of snappers (Lutjanidae) on the Caribbean coast of Panama. Fish. Bull. U.S. **75**: 875–877.
- Wilkinson, L. 1990. SYSTAT: the system for statistics. SYSTAT Inc., Evanston, Ill.