

Bering Sea Marine Invasive Species Assessment

Alaska Center for Conservation Science

Scientific Name: *Mytilicola orientalis*

Common Name *a bivalve-parasitic copepod*

Phylum Arthropoda

Class Maxillopoda

Order Cyclopoida

Family Mytilicolidae

Species Occurrence by Ecoregion

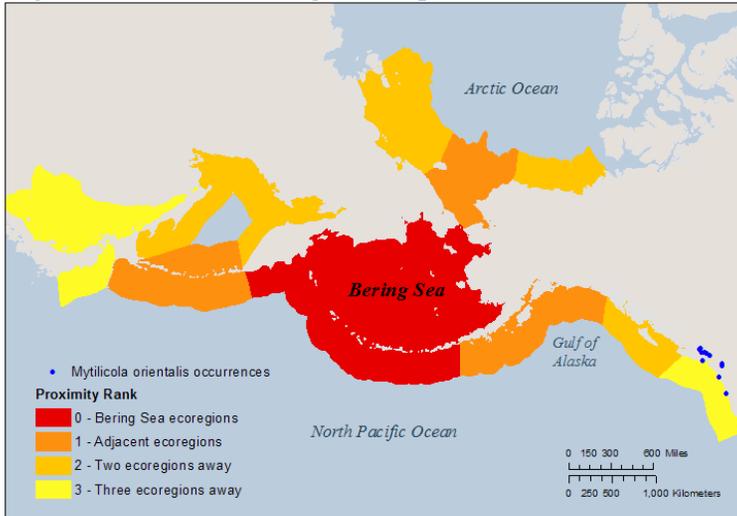


Figure 1. Occurrence records for non-native species, and their geographic proximity to the Bering Sea. Ecoregions are based on the classification system by Spalding et al. (2007). Occurrence record data source(s): NEMESIS and NAS databases.

Final Rank 36.12
Data Deficiency: 16.25

Category Scores and Data Deficiencies			
Category	Score	Total Possible	Data Deficient Points
Distribution and Habitat:	10	19	11.25
Anthropogenic Influence:	3.25	10	0
Biological Characteristics:	13.25	25	5.00
Impacts:	3.75	30	0
Totals:	30.25	83.75	16.25

General Biological Information

Tolerances and Thresholds

Minimum Temperature (°C)	NA	Minimum Salinity (ppt)	31*
Maximum Temperature (°C)	NA	Maximum Salinity (ppt)	35*
Minimum Reproductive Temperature (°C)	NA	Minimum Reproductive Salinity (ppt)	NA
Maximum Reproductive Temperature (°C)	NA	Maximum Reproductive Salinity (ppt)	NA

Additional Notes

A parasitic copepod that infects the Pacific oyster, *Crassostrea gigas*, the blue mussel *Mytilus edulis*, the Mediterranean mussel *M. galloprovincialis*, and other bivalves (Torchin et al. 2002; Bower 2010). Infestations rate as high as 73.6% have been recorded (Bower 2010). Can also be transported on ships' hulls through infected bivalves.

1. Distribution and Habitat

1.1 Survival requirements - Water temperature

Choice: Unknown/Data Deficient

U

Score:

of

Ranking Rationale:

Temperatures required for survival are unknown.

Background Information:

Current distribution is largely restricted to cold temperate and warm temperate waters. *Crassostrea gigas*, one of its native hosts, has recently been found as far north as 60°N, likely as a result of recent warming events, but it is still unknown whether *C. gigas* can establish populations in Alaska. The blue mussel *Mytilus edulis* has recently expanded its northern distribution in the Arctic, and is now found north up to 77°N, in water temperatures as cold as -1°C (Thyrring et al. 2015). Not known whether *Mytilicola orientalis* can survive in these more northern populations.

Sources:

Thyrring et al. 2015 NEMESIS; Fofonoff et al. 2003

1.2 Survival requirements - Water salinity

Choice: Considerable overlap – A large area (>75%) of the Bering Sea has salinities suitable for year-round survival

A

Score:

3.75 of

High uncertainty?

3.75

Ranking Rationale:

Although salinity thresholds are unknown, this species is a marine organism. We therefore assume that it can survive in saltwater (31 to 35 ppt); these salinities occur in a large (>75%) portion of the Bering Sea.

Background Information:

No species-specific thresholds listed in literature. Fofonoff et al. (2003) lists *M. orientalis* as a polyhaline-euhaline species with a salinity range somewhere between 18 PSU and 40 PSU.

Sources:

NEMESIS; Fofonoff et al. 2003

1.3 Establishment requirements - Water temperature

Choice: Unknown/Data Deficient

U

Score:

of

Ranking Rationale:

Background Information:

No information available in the literature.

Sources:

None listed

1.4 Establishment requirements - Water salinity

Choice: Unknown/Data Deficient

U

Score:
[] of
[]

Ranking Rationale:

Background Information:

No information available in the literature.

Sources:

None listed

1.5 Local ecoregional distribution

Choice: Present in an ecoregion greater than two regions away from the Bering Sea

D

Score:
1.25 of
5

Ranking Rationale:

Present in British Columbia.

Background Information:

Found along the North American West Coast from California to Vancouver Island, British Columbia (Fofonoff et al. 2003).

Sources:

NEMESIS; Fofonoff et al. 2003

Choice: In a moderate number of ecoregions globally

B

Score:
3.25 of
5

Ranking Rationale:

Found in Japan, Korea, the West Coast of North America, and Europe.

Background Information:

Distribution is largely restricted to cold temperate and warm temperate waters. Native to Japan and Korea. Has been accidentally introduced to the Pacific Coast of North America, from California to British Columbia. In Europe, introduced to France, Ireland, the Netherlands, and the French Mediterranean Coast. Northernmost European record is the Island of Sylt in Germany's North Sea (55°N). In NA, north to ~50°N.

Many bivalves cannot establish self-sustaining populations in areas where they are cultivated, and the aquaculture industry relies on spat supplied from elsewhere (Steele and Mulcahy 2001). Distribution of *M. orientalis* is limited to the immediate vicinity where infested oysters have been introduced (Bernard 1969). Nearby areas are free of *Mytilicola*, even where the oyster population is contiguous due to natural spawning (Bernard 1969)

Sources:

Steele and Mulcahy 2001 Bernard 1969 Bower 2010 NEMESIS; Fofonoff et al. 2003 Torchin et al. 2002

1.7 Current distribution trends

Choice: Established outside of native range, but no evidence of rapid expansion or long-distance dispersal
C

Score:
1.75 of
5

Ranking Rationale:

Limited to wherever infected bivalves have been introduced.

Background Information:

Larvae are limited to short distance dispersals, and distribution is limited to areas where infected bivalves have been introduced. Distribution of *M. orientalis* is limited to the immediate vicinity where infested oysters have been introduced (Bernard 1969). Nearby areas are free of *Mytilicola*, even where the oyster population is contiguous due to natural spawning (Bernard 1969).

Sources:

Bernard 1969

Section Total - Scored Points:	10
Section Total - Possible Points:	18.75
Section Total -Data Deficient Points:	11.25

2. Anthropogenic Transportation and Establishment

2.2 Establishment requirements: relies on marine infrastructure, (e.g. harbors, ports) to establish

Choice: C Uses anthropogenic disturbance/infrastructure to establish; never observed establishing in undisturbed areas

Score:
1.25 of
4

Ranking Rationale:

Has only been observed establishing in areas of anthropogenic disturbance, usually areas associated with the Pacific Oyster culture.

Background Information:

Distribution is sporadic and limited to the immediate vicinity where infected oysters have been introduced. Nearby areas are free of *Mytilicola*, even where the oyster population is contiguous due to natural spawning (Bernard 1969).

Sources:

Bernard 1969 NEMESIS; Fofonoff et al. 2003

2.3 Is this species currently or potentially farmed or otherwise intentionally cultivated?

Choice: B No

Score:
0 of
2

Ranking Rationale:

This species is not currently farmed or intentionally cultivated.

Background Information:

While this species is not farmed, it is associated with the Pacific Oyster that is intentionally farmed.

Sources:

NEMESIS; Fofonoff et al. 2003

2.1 Transport requirements: relies on use of shipping lanes (hull fouling, ballast water), fisheries, recreation, mariculture, etc. for transport

Choice: B Has been observed using anthropogenic vectors for transport but has rarely or never been observed moving independent of anthropogenic vectors once introduced

Score:
2 of
4

Ranking Rationale:

Readily transported by hull fouling and the stocking of infected oysters. However, *M. orientalis* has a limited natural dispersal ability.

Background Information:

Can be transported in oysters on ships' hulls; however, the main introduction pathway is the stocking of infected oysters for the aquaculture industry.

Sources:

NEMESIS; Fofonoff et al. 2003

Section Total - Scored Points: 3.25

Section Total - Possible Points: 10

Section Total -Data Deficient Points: 0

3. Biological Characteristics

3.2 *Habitat specialization and water tolerances*

Does the species use a variety of habitats or tolerate a wide range of temperatures, salinity regimes, dissolved oxygen levels, calcium concentrations, hydrodynamics, pollution, etc?

Choice: Specialist; dependent on a narrow range of habitats for all life stages

C

Score:
1.75 of
5

Ranking Rationale:

Has a short free-swimming stage as a nauplii, followed by a parasitic relationship within a bivalve.

Background Information:

Restricted regional distribution of this copepod in Barkley Sound (and throughout the Pacific Northwest) may be limited by factors that confine transmission to sheltered, muddy estuaries (Goater and Weber 1996). Within such sites, copepod abundance is highest in large mussels collected near the low-tide mark. Factors such as wave action, tidal currents, salinity and/or substratum may restrict colonization by free-swimming larvae.

Natural distribution of *M. orientalis* is limited by the bivalve species it parasitizes. Many bivalves in which it occurs, including the Mediterranean mussel and the Pacific oyster, cannot live in cold waters. There are several bivalve species that occur in Alaska and that are potential hosts of *M. orientalis*: *Mytilus californianus*, *Mytilus edulis*, *Protothaca staminea*, and *Saxidomus giganteus* (Foster 1991; Fofonoff et al. 2003). Enclosed inlets with poor to moderate tidal flushing are more likely to develop local populations (Holmes and Minchin 1995, qtd. in Bower 2010). Obligate parasitic life stage severely limits distribution.

Sources:

Goater and Weber 1996 Foster 1991 NEMESIS; Fofonoff et al. 2003

3.3 *Desiccation tolerance*

Choice: Unknown

U

Score:
of

Ranking Rationale:

Background Information:

No information available in the literature.

Sources:

None listed

3.1 Dietary specialization

Choice: Specialist; dependent on a narrow range of foods for all life stages and/or foods are not commonly available in the study area

C

Score:
1.75 of

5

Ranking Rationale:

Relies on bivalves for food.

Background Information:

Larval stages are non-feeding. Adults are parasitic, and found inside the gut of bivalves. Flexible in its host choices (Pogoda et al. 2012).

Sources:

NEMESIS; Fofonoff et al. 2003 Pogoda et al. 2012

Choice: Moderate – Exhibits one or two of the above characteristics

B

Score:
3.25 of

5

Ranking Rationale:

Sexual reproduction, high fecundity, low parental investment, generation time unknown.

Background Information:

Sexual reproduction. In California, *M. orientalis* showed continuous reproductive activity (Bradley and Siebert 1978). In British Columbia, there was a single reproductive period from June to late August (Bernard 1969). The wormlike adult female and male mate inside the host's intestine. The female produces paired egg sacs containing approximately 200 eggs.

Sources:

Bradley and Siebert 1978 Bernard 1969 Bower 2010 NEMESIS; Fofonoff et al. 2003

3.5 Likelihood of long-distance dispersal or movements

Consider dispersal by more than one method and/or numerous opportunities for long or short distance dispersal e.g. broadcast, float, swim, carried in currents; vs. sessile or sink.

Choice: Disperses short (< 1 km) distances

C

Score:
0.75 of

2.5

Ranking Rationale:

Background Information:

Experiments in Ladysmith Harbour, British Columbia, indicate that larval stages are short and do not travel far (Bernard 1969). Adult is parasitic on sessile bivalves.

Sources:

Bernard 1969

3.6 Likelihood of dispersal or movement events during multiple life stages

i. Can disperse at more than one life stage and/or highly mobile ii. Larval viability window is long (days v. hours) iii. Different modes of dispersal are achieved at different life stages (e.g. unintentional spread of eggs, migration of adults)

Choice: Low – Exhibits none of the above characteristics

C

Score:
0.75 of

2.5

Ranking Rationale:

Not highly mobile, larval viability window is short, adults are restricted to parasitic host.

Background Information:

Larval stages are free-swimming but short-lived, and do not disperse great distances. Adults are parasites within the intestine of a bivalve.

Sources:

Bernard 1969 NEMESIS; Fofonoff et al. 2003

3.7 *Vulnerability to predators*

Choice: Lacks natural predators
A

Score: 5 of 5

Ranking Rationale:

Background Information:

No known natural predators.

Sources:

None listed

Section Total - Scored Points:	13.25
Section Total - Possible Points:	25
Section Total -Data Deficient Points:	5

4. Ecological and Socioeconomic Impacts

4.101 Recreation

Choice: Limited – Has limited potential to cause degradation to recreation opportunities, with limited impact and/or within a very limited region
C

Score:
0.75 of
3

Ranking Rationale:

Has an adverse effect on bivalves harvested for recreation.

Background Information:

M. orientalis is a parasite that resides in the intestinal tract of bivalves. This can alter the epithelial lining in the gut. Otherwise, effects appear to be minor beyond minimal tissue damage and decreased condition factors (Odling 1946; Bernard 1969; Grizel 1985; Steele and Mulcahy 2001; Bower 2010). In Ireland, infected oysters were associated with increased attacks by shell-boring *Polydora* spp. (Steele and Mulcahy 2001).

Sources:

Odling 1946 Bernard 1969 Grizel 1985 Steele and Mulcahy 2001 Bower 2010 NEMESIS; Fofonoff et al. 2003

4.3 Impact on ecosystem function and processes

Choice: No impact
D

Score:
0 of
2.5

Ranking Rationale:

To date, no impacts on ecosystem functions and processes have been reported for *M. orientalis*, and given its ecology, none would be expected.

Background Information:

No information available in the literature.

Sources:

None listed

4.4 Impact on high-value, rare, or sensitive species and/or communities

Choice: Limited – Has limited potential to cause degradation of one more species or communities, with limited impact and/or within a very limited region
C

Score:
0.75 of
2.5

Ranking Rationale:

Species parasitized by *M. orientalis* are economically and culturally important.

Background Information:

Causes a decrease in the condition factors (increased water, decreased fat content) of the host without directly killing it (Odling 1946; Bernard 1969; Grizel 1985; Steele and Mulcahy 2001; Bower 2010). Infected bivalves are also correlated with higher rates of polydora infections, that when sufficiently high, will kill the host (Steele and Mulcahy 2001). Furthermore, the distribution of *M. orientalis* is associated with the Pacific Oyster culture (Fofonoff et al. 2003).

Sources:

Odling 1946 Bernard 1969 Grizel 1985 Steele and Mulcahy 2001 Bower 2010 NEMESIS; Fofonoff et al. 2003

4.5 Introduction of diseases, parasites, or travelers

What level of impact could the species' associated diseases, parasites, or travelers have on other species in the assessment area? Is it a host and/or vector for recognized pests or pathogens, particularly other nonnative organisms?)

Choice: No impact
D

Score:
0 of
2.5

Ranking Rationale:

Background Information:

M. orientalis itself is a parasite of bivalves.

Sources:

NEMESIS; Fofonoff et al. 2003

4.6 Level of genetic impact on native species

Can this invasive species hybridize with native species?

Choice: No impact
D

Score:
0 of
2.5

Ranking Rationale:

To date, hybridization has not been reported for M. orientalis, and given its biology, hybridization would not be expected.

Background Information:

No information available in the literature.

Sources:

None listed

4.7 Infrastructure

Choice: No impact
D

Score:
0 of
3

Ranking Rationale:

To date, no impacts on infrastructure have been reported for M. orientalis, and given its ecology, none would be expected.

Background Information:

No information available in the literature.

Sources:

None listed

4.1 Impact on community composition

Choice: Limited – Single trophic level; may cause decline but not extirpation

C

Score:
0.75 of

2.5

Ranking Rationale:

M. orientalis has been linked to decreased condition factors of oysters and mussels, but does not directly cause death.

Background Information:

Low condition indices of mussels and oysters has been linked to high infestation rates of *M. orientalis* (Katkansky et al. 1967; Korringa 1968; Paul 1983 as qtd. In NOBANIS 2016). However, long-term studies suggest that *M. orientalis* live as commensals and are not harmful parasites (Gee and Davey 1986 as qtd. In NOBANIS 2016; Davey and Gee 1988 as qtd. In NOBANIS 2016; Davey 1989 as qtd. In NOBANIS 2016; Steele and Mulcahy 2001). A recent study by Pogoda et al. (2012) supports this assertion – they found no correlation between infestation rate and condition index of bivalves.

Sources:

Katkansky et al. 1967 Korringa 1968 NOBANIS 2016 Steele and Mulcahy 2001 Pogoda et al. 2012

Choice: Limited – Has limited potential to cause degradation to fisheries and aquaculture, and/or is restricted to a limited region

C

Score:
0.75 of

3

Ranking Rationale:

May have an adverse affect on quality and appearance (and thus price) of species important for fisheries and aquaculture.

Background Information:

M. orientalis is a parasite that resides in the intestinal tract of bivalves. This can alter the epithelial lining in the gut. Otherwise, effects appear to be minor beyond minimal tissue damage and decreased condition factors (Odlaug 1946; Bernard 1969; Grizel 1985; Steele and Mulcahy 2001; Bower 2010). In Ireland, infected oysters were associated with increased attacks by shell-boring *Polydora* spp. (Steele and Mulcahy 2001). From a consumer standpoint, macro-parasites are undesirable. Copepod parasites are easy to spot when oysters are eaten raw. This is due to the parasites bright red color and their large size (Pogoda et al. 2012).

Sources:

Odlaug 1946 Bernard 1969 Grizel 1985 Steele and Mulcahy 2001 Bower 2010 Pogoda et al. 2012 NEMESIS; Fofonoff et al. 2003

4.9 Subsistence

Choice: Limited – Has limited potential to cause degradation to subsistence resources, with limited impact and/or within a very limited region

C

Score:
0.75 of

3

Ranking Rationale:

Has an adverse effect on bivalves important for subsistence.

Background Information:

M. orientalis is a parasite that resides in the intestinal tract of bivalves. This can alter the epithelial lining in the gut. Otherwise, effects appear to be minor beyond minimal tissue damage and decreased condition factors (Odlaug 1946; Bernard 1969; Grizel 1985; Steele and Mulcahy 2001; Bower 2010). In Ireland, infected oysters were associated with increased attacks by shell-boring *Polydora* spp. (Steele and Mulcahy 2001).

Sources:

Odlaug 1946 Bernard 1969 Grizel 1985 Steele and Mulcahy 2001 Bower 2010 NEMESIS; Fofonoff et al. 2003

4.11 Human health and water quality

Choice: No impact

D

Score:
0 of

3

Ranking Rationale:

To date, no impacts on human health or water quality have been reported for *Mytilicola orientalis*.

Background Information:

Macroparasites such as *M. orientalis* reduce monetary value of oysters because they cause discolouration in the flesh, however, they do not cite any human health concerns (Pogoda et al. 2012; Bower 2010).

Sources:

Pogoda et al. 2012 Bower 2010

4.2 Impact on habitat for other species

Choice: No impact

D

Score:
0 of

2.5

Ranking Rationale:

Background Information:

M. orientalis lives inside of other bivalves and have no impact on habitat for other species.

Sources:

NEMESIS; Fofonoff et al. 2003

Section Total - Scored Points:	3.75
Section Total - Possible Points:	30
Section Total -Data Deficient Points:	0

5. Feasibility of prevention, detection and control

5.2 Cost and methods of management, containment, and eradication

Choice: Major long-term investment, or is not feasible at this time
A

Score: of

Ranking Rationale:

Currently, the only effective method of control is to avoid the transfer of live mussels from infected areas.

Background Information:

Pesticides have been tested, but are highly toxic to other organisms as well (Blateau et al. 1992 as qtd. in NOBANIS 2016). Chlorine can kill the free-swimming stages (Korringa 1968). Currently, the most effective measure is to control the transfer of live mussels from infected areas.

Sources:

NOBANIS 2016 Korringa 1968 Bower 2010

5.3 Regulatory barriers to prevent introductions and transport

Choice: Regulatory oversight and/or trade restrictions
C

Score: of

Ranking Rationale:

There are no species specific regulations but *Mytilicola* spp. are regulated by the State of Alaska. The U.K. also has regulations regarding a closely related species.

Background Information:

A closely related species, *Mytilicola instestinalis*, is regulated. The UK considers it a "controlled pest" and carefully monitors the transport of mussels from infected areas (Gresty 1992). To control outbreaks, it will help to decrease the stocking density of mussel farms (Blateau et al. 2002 as qtd. in NOBANIS 2016). As such, mussel farmers in France have created a union to voluntarily decrease stocking density of mussels (Mongruel and Thebaud 2006).

In Alaska, *Mytilicola* spp. (including *M. orientalis*) are listed as critical concern, and the presence of this disease must be immediately reported and subsequently treated (Alaska Administrative Code 2016).

Sources:

Gresty 1992 Mongruel and Thebaud 2006 NOBANIS 2016 AAC 2016

5.4 Presence and frequency of monitoring programs

Choice: No surveillance takes place
A

Score: of

Ranking Rationale:

Background Information:

No organized monitoring programs currently exist for *M. orientalis*.

Sources:

None listed

5.5 *Current efforts for outreach and education*

Choice: No education or outreach takes place

A

Score: of

Ranking Rationale:

Background Information:

No outreach or education efforts currently take place for *M. orientalis*.

Sources:

None listed

5.1 *History of management, containment, and eradication*

Choice: Not attempted

B

Score: of

Ranking Rationale:

Background Information:

No information was found in the literature regarding species-specific management efforts.

Sources:

None listed

Section Total - Scored Points:

Section Total - Possible Points:

Section Total -Data Deficient Points:

Bering Sea Marine Invasive Species Assessment

Alaska Center for Conservation Science

Literature Cited for *Mytilicola orientalis*

- Fofonoff, P. W., G. M. Ruiz, B. Steves, C. Simkanin, and J. T. Carlton. 2017. National Exotic Marine and Estuarine Species Information System. <http://invasions.si.edu/nemesis/>. Accessed: 15-Sep-2017.
- Thyrring, J., Rysgaard, S., Blicher, M. E., and M. K. Sejr. 2015. Metabolic cold adaptation and aerobic performance of blue mussels (*Mytilus edulis*) along a temperature gradient into the High Arctic region. *Marine Biology* 162:235-243.
- Bernard, F. R. 1969. The parasitic copepod *Mytilicola orientalis* in British Columbia bivalves. *Journal of the Fisheries Research Board of Canada*. 26(1): 190-191. doi:10.1139/f69-022
- Bower, S. M. 2010. Synopsis of infectious diseases and parasites of commercially exploited shellfish: *Mytilicola orientalis* (Red Worm) of mussels. Fisheries and Ocean Canada. Available from: <http://www.dfo-mpo.gc.ca/science/aah-saa/diseases-maladies/morwm>
- Steele, S., and M. F. Mulcahy. 2001. Impact of the copepod *Mytilicola orientalis* on the Pacific oyster *Crassostrea gigas* in Ireland. *Diseases of Aquatic Organisms* 47:145-149.
- Torchin, M. E., Lafferty, K. D., and A. M. Kuris. 2002. Parasites and marine invasions. *Parasitology* 124:S137-S151.
- Foster, N. R. 1991. Intertidal bivalves: A guide to the common marine bivalves of Alaska. University of Alaska Press, Fairbanks, AK, U.S.A.
- Pogoda, B., Jungblut, S., Buck, B. H., and W. Hagen. 2012. Infestation of oysters and mussels by mytilicolid copepods: differences between natural coastal habitats and two offshore cultivation sites in the German Bight. *Journal of Applied Ichthyology*. 28:
- NOBANIS. *Mytilicola intestinalis*. European Network on Invasive Alien Species. Available from: <https://www.nobanis.org/marine-identification-key/small-crustaceans/mytilicola-intestinalis/> Accessed 16-Nov-2016.
- Alaska Administrative Code. 2016. 5 AAC 41.080 Reporting and control of fish diseases at egg-take sites, hatcheries, and rearing facilities.
- Goater, C. P., and A. E. Weber. 1996. Factors affecting the distribution and abundance of *Mytilicola orientalis* (Copepoda) in the mussel, *Mytilus trossulus*, in Barkley Sound. *B.C. Journal of Shellfish Research* 15:681-684.
- Bradley, W., and A. E. Siebert. 1978. Infection of *Ostrea lurida* and *Mytilus edulis* by the parasitic copepod *Mytilicola orientalis* in San Francisco Bay, California. *The Veliger* 21: 131-134.
- Katkansky, S. C., Sparks, A. K., and K. K. Chew. 1967. Distribution and effects of the endoparasitic copepod, *Mytilicola orientalis*, on the Pacific Oyster, *Crassostrea gigas*, on the Pacific Coast. *Proceedings of the National Shellfisheries Association* 57:5
- Korrynga, P. 1968. On the ecology and distribution of the parasitic copepod *Mytilicola intestinalis* Steuer. *Bijdragen tot de Dierkunde* 38:47-57.
- Odlaug, T. O. 1946. The effect of the copepod, *Mytilicola orientalis* upon the Olympia oyster, *Ostrea lurida*. *Transactions of the American Microscopical Society* 65:311-317.
- Grizel, H. 1985. *Mytilicola orientalis* mori, parasitism. *ICES Identification Sheets for Diseases and Parasites* 20:1-4.
- Gresty, K. A. 1992. Ultrastructure of the midgut of the copepod *Mytilicola intestinalis* Steuer, an endoparasite of the mussel *Mytilus edulis* L. *Journal of Crustacean Biology* 12(2):169-177.

- Mongruel, R., and O. Thebaud. 2006. Externalities, institutions and the location choices of shellfish producers: The case of blue mussel farming in the Mont-Saint-Michel Bay (France). *Aquaculture Economics & Management* 10(3):163-181.