



REVIEW

Guests or pests? Eirenid hydroids living on the soft tissue of bivalves

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Abstract

Both wild and reared bivalves can host hydroids from the Eirenidae family which settle on the soft body parts of their host. Thousands of hydroids have been observed on a single bivalve, and often have severe detrimental effects on the host. However, this relationship has received little attention in aquaculture research, which is probably due to a lack of baseline data. An extensive review was conducted (i) to show the current level of knowledge on the association between eirenids and bivalves, providing a benchmark for future research; (ii) to detect a critical combination of biotic/abiotic factors that could switch the relationship from commensalism to infestation and (iii) to identify research priorities for future studies. Seventy scientific papers were screened to provide ecological information useful in understanding the hydroid-host-environment interactions and to show the global spatial and bathymetric distribution of the relationship. Although the main parameters influencing the hydroid abundance were identified, it was challenging to collate information from such heterogeneous data sources. A standardized method for data collection is proposed to obtain more robust and comparable data on the association. The most relevant and unstudied issue is the potential physiological and qualitative changes that could occur in infested bivalves. Monitoring the association could provide data needed to prevent or to control hyper-proliferation of the symbionts and to detect eventual synergistic effects with climate change. This could be fundamental for species living in areas particularly prone to climate regime shifts, such as semi-enclosed basins and estuarine habitats.

KEYWORDS

climate change, food security, mussel culture, parasite, pathogen hazard, shellfish farms

1 | INTRODUCTION

Wild and reared marine bivalves represent about 14% of the whole marine production.^{1,2} Bivalves can provide a source of microelements³

and natural fatty acids for human consumption⁴ that is more sustainable than wild-caught fish.⁵ However, the presence of animal pathogen hazards may affect the health or survival of bivalves⁶ and undermine food safety and quality.⁷

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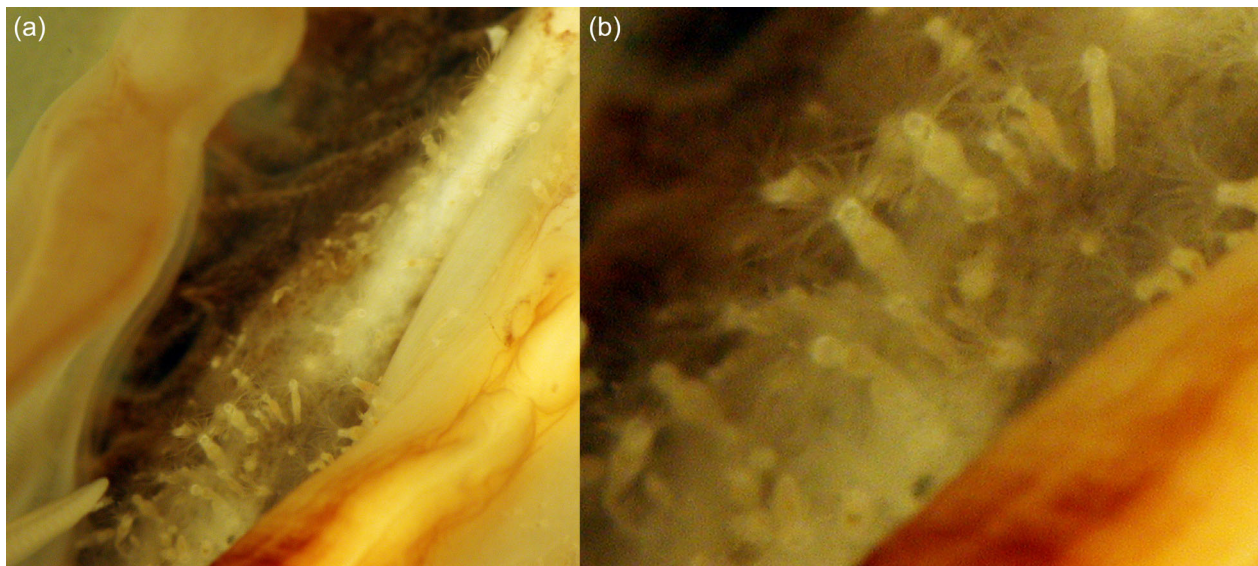


FIGURE 1 Photos at the stereomicroscope of bivalve-inhabiting hydroids: *Eugymnanthea inquilina* Palombi, 1935 infesting *Mytilus galloprovincialis* Lamarck, 1819 from Taranto, Italy.

TABLE 1 Studies reporting damages to bivalves due to the association with eirenids. Further details are in S1 (nn=unknown)

Hydroid species	Locality	Host species	Host family	Habitat	Damage description	References
<i>Eutima japonica</i> Uchida, 1925	Funka Bay, Hokkaido, Japan	<i>Mizuhopecten yessoensis</i> (Jay, 1857), juveniles	Pectinidae	cultured	Reduced shell length growth and triglyceride accumulation in the digestive glands of juvenile scallops	Baba et al. ⁸
<i>Eugymnanthea inquilina</i> Palombi, 1935	Mar Piccolo Taranto, Italy	<i>Mytilus galloprovincialis</i> Lamarck, 1819	Mytilidae	nn	Ciliary loss in <i>M. galloprovincialis</i> where hydroid basal discs were attached to the mantle epithelium; cell granules heavily stained with eosin or Orange G	Cerruti ⁹
	Mar Grande Taranto, Italy	<i>Mytilus galloprovincialis</i> Lamarck, 1819	Mytilidae	nn		
	Thermaikos Gulf, Greece	<i>Mytilus galloprovincialis</i> Lamarck, 1819	Mytilidae	cultured	Decrease in length, wet weight, flesh dry weight and condition index of the mussel	Galinou-Mitsoudi et al. ¹⁰
	Mali Ston Bay, Croatia	<i>Mytilus galloprovincialis</i> Lamarck, 1819	Mytilidae	cultured	Histopathological alterations such as disruption of mantle epithelium integrity in infested mussels, even though with milder effect in comparison to tissue reaction provoked by a turbellarian	Mladineo et al. ¹¹
	Thermaikos Gulf, Greece	<i>Mytilus galloprovincialis</i> Lamarck, 1819	Mytilidae	cultured	Mussels presented watery and soft meats with an unpleasant smell; heavily infested mussels with low condition index	Rayyan et al. ¹²
	Seča Strunjan and Debeli rtič, Slovenia	<i>Mytilus galloprovincialis</i> Lamarck, 1819	Mytilidae	cultured	Condition index lower than non-infested mussels	Žižek et al. ¹³

Different species of cultured and wild bivalves—notably *Mytilus galloprovincialis* Lamarck, 1819—can host hydrozoans of the family Eirenidae Haeckel, 1879 (Cnidaria: Leptothecata) which settle directly on

the soft body parts of the molluscs (Figure 1). This association may cause severe detrimental effects to the host (Table 1). When thousands of eirenid hydroids colonize the bivalve's gills,⁷ reduction

of filtration/feeding and inhibition of respiration can occur.¹⁰ Ciliary loss in *M. galloprovincialis* has been reported where basal discs of the hydroids were attached to the mantle epithelium.⁹ Furthermore, more than a 43% reduction in shell length growth, and a 47.4% decrease in triglyceride concentration has been observed in polyp-bearing scallops.⁸ The ultrastructure of the host cells analysed at the site of the symbiont's attachment, reported histopathological alterations, such as the disruption of the integrity of the mantle epithelium in infested individuals. Additionally, exotic bivalves unintentionally or intentionally introduced may vector alien species¹⁴—among them eirenids⁸—which could infest native molluscs.

Inhabited bivalves, especially those containing over a hundred polyps, displayed a significantly lower Condition Index (i.e. ratio of dry meat weight to dry shell in percentage¹⁵) than molluscs with no hydroids.^{12,13} Meat of colonized bivalves may be “very watery and soft and with an unpleasant smell”,¹² suggesting the need for further organoleptic testing to assess the quality of heavily infested molluscs.

Serious Eirenidae infestations in cultured bivalves may lead to a decrease in shellfish production and revenues,¹³ yet the relationship between bivalves and eirenids has received little attention from experts specialized in aquaculture science. This is likely due to the difficulty in retrieving information from heterogeneous and scattered data sources and the lack of baseline data.

The main objectives of this review, therefore were (i) to highlight the current level of knowledge on the eirenids-bivalves relationship, providing a benchmark for future research; (ii) to detect a critical combination of biotic/abiotic factors that could switch the relationship from commensalism to infestation; and (iii) to identify research priorities for future studies.

The information gathered was analysed to identify:

- biotic/abiotic factors influencing: (i) the prevalence (i.e. percentage of inhabited bivalves in a population)¹⁶ and (ii) the abundance (number of hydroids per bivalve) of eirenid hydroids;
- the most infesting eirenids' species and the most sensitive hosts;
- differences in hydroid prevalence/abundance in reared/wild bivalves;
- differences in sensory and nutritional quality of infested/non-infested bivalves;
- possible effects of climate change on the eirenids-bivalves relationship.

Results are discussed to highlight the current available knowledge and methodological gaps.

2 | METHODS

To evaluate the current level of knowledge on bivalves-inhabiting eirenids, the online scientific repository Web of Science¹⁷ (last search on 15 June 2022) was accessed and the keyword ‘Eirenidae’ was entered in the search engine. Additional papers were then selected from the references section of the retrieved articles from step one.

Each article was analysed to extract as much information as possible about the association between eirenids-bivalves, such as, occurrence/absence records, depth, prevalence, abundance of symbionts, sea temperature and salinity. The extracted data were then added to a standardized spreadsheet (Data S1, adapted from Di Camillo et al.¹⁸). The data fields are either summarized in Table 2 or provided in full in Data S1. Names of taxa mentioned in Data S1 were checked and updated according to the World Register of Marine Species.²⁰

To detect areas prone to hydroid invasions, data were used to obtain world maps of spatial distribution of hydroids and bivalve hosts (QGIS elaboration²¹), with a particular focus on hot spots of occurrence (Caribbeans, Mediterranean, Japan).

Furthermore, for the areas hosting the highest number of association records (Japan, East Sea, North Pacific Ocean), Sea Surface Temperature (SST) and salinity data were acquired from the Copernicus Marine Service dataset.²² These data presented a native resolution of 1/12°, the equivalent of around 8 km in a latitude grid-cell at a daily resolution from 1 January 1993 to 1 January 2020. Even though the data contained 50 depth levels, only surface values were considered for the analysis of both temperature and salinity, as most of the records fall within the first few metres of depth. Different descriptors (minimum, maximum, mean and standard deviation) were then calculated per decade (90s, 00s and 10s), and differences between these descriptors were estimated among decades. All maps and spatial analyses were performed in R software using raster²³ and ggplot2 packages.²⁴

The hypothesis that no correlation occurred between prevalence, hydroid abundance, and bivalves' length was tested. First, a normality test (Shapiro–Wilk test) was conducted using PAST²⁵ to verify the null hypothesis that data distribution was normal. Since the test was significant, the distribution was considered non-normal, and a non-parametric measure of correlation (Spearman's rank correlation coefficient r_s) was used considering $p < 0.05$. The same tests were performed to verify a correlation between seawater temperature (T°C) and prevalence (percentage of colonized bivalves) relative to *M. galloprovincialis* associated to *Eugymnanthea japonica* (Yamada, 1950) and *Eutima japonica* Uchida, 1925 from four Japanese localities (Tsushima, Hamada, Senzaki and Morotsu²⁶).

3 | RESULTS AND DISCUSSIONS

3.1 | Overview of the association

A total of 70 papers on bivalves-inhabiting eirenids were retrieved, spanning the period between 1935 to 2022 (Figure 2), of which many ($n = 37$, >50%) were published between 1991 and 2010. The full list of articles retrieved and retained for analysis is provided in Data S1.

The 586 records obtained (584 from the 70 papers reviewed and two from personal observation) included both occurrence ($n = 372$, 63.5%) and absence ($n = 214$, 36.5%) of hydroids in a total of over 50,000 examined bivalve specimens (Data S1).

TABLE 2 Recommended fields to consider upon collecting data on eirenids living on soft body parts of bivalves^{18,19} (Di Camillo et al. 2018 and Wiczorek et al. 2012)

Category	Fields	Category	Fields
Occurrence	OrganismID	Hyroid Taxonomy	TaxonID
	GeodeticDatum		ParentNameUsageID
	DecimalLatitude		ScientificName
	DecimalLongitude		Kingdom
	LastSamplingYear		Phylum
	EventDate		Class
	EventTime		Order
	CountryCode		Family
	Country		Genus
	Locality		SpecificEpithet
PresenceAbsence	ScientificNameAuthorship		
			TaxonRank
Article's details (Authors, sampling method...)	SamplingProtocol	Bivalve host	HostSpecies
	OccurrenceRemarks		HostFamily
	RecordedBy		Cultured_Wild
	IdentifiedBy		CultureSystem
Ecology	MinimumDepthInMeters	Infestation	HostHabitat
	MaximumDepthInMeters		SecondarySubstrate
	MedusaBuds		AssociatedTaxa
	Sheltered_Exposed		MINLentgth_mm
	DistanceFromCoastKm		MAXLentgth_mm
	DistanceFromRiversKm		PrevalenceMIN
	TemperatMIN		PrevalenceMAX
	TemperatMAX		PrevalenceAV
	TemperatAV		PrevalenceSTDV
	TemperatSTDV		MAX_NofPolypsPerBiv
	TemperatUNIT		N_BivExamined
	SamplingPeriod		Damage_Y_N
	SalinityMIN		DamageDescription
	SalinityMAX		Mantle
	SalinityAV		VisceralM
	SalinitySTDV		LabialPalp
	SalinityUNIT		Foot
	TRIX		Gills
	OxygenMIN		TOTWetWeight_gr
	OxygenMAX		TOTWetWeight_STDEV
OxygenAV	FleshWetWeight_gr		
OxygenSTDV	FleshWetWeightSTDV		
OxygenUNIT	FleshDryWeight_gr		
CurrentCmSec	FleshDryWeight_STDV		
	ConditionIndexpercentage		

Note: See Data S1 for further explanation of the fields.

Eireniidae living inside valves belong to the genera *Eugymnanthea* and *Eutima* and include seven species: *Eug. inquilina* Palombi, 1935, *Eug. japonica* (Yamada, 1950), *Eut. japonica* Uchida, 1925, *Eut.*

ostrearum (Mattox & Crowell, 1951), *Eut. sapinhoa* Narchi & Hebling, 1975, *Eut. cirrhifera* (Kakinuma, 1964), and *Eut. commensalis* (Santhakumari, 1970).

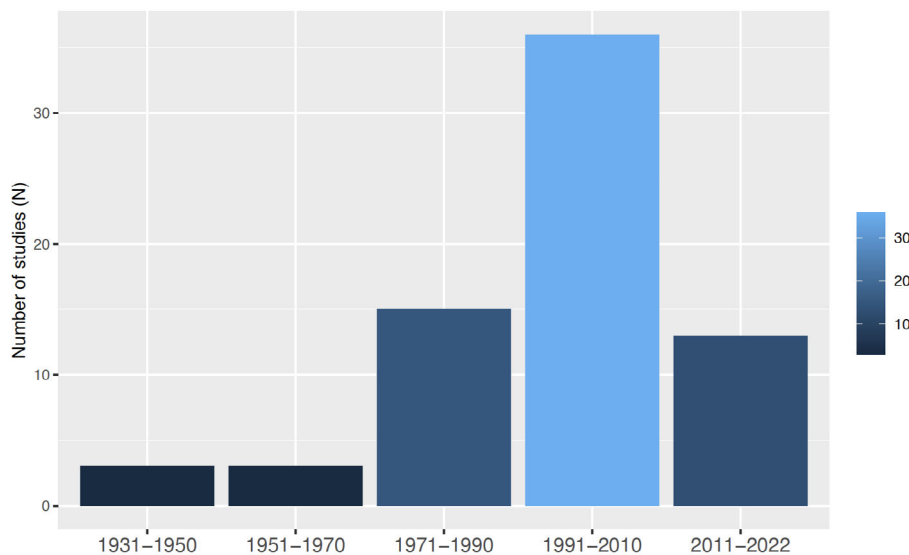


FIGURE 2 Studies conducted from 1935 to 2022 on bivalve-inhabiting hydroids.

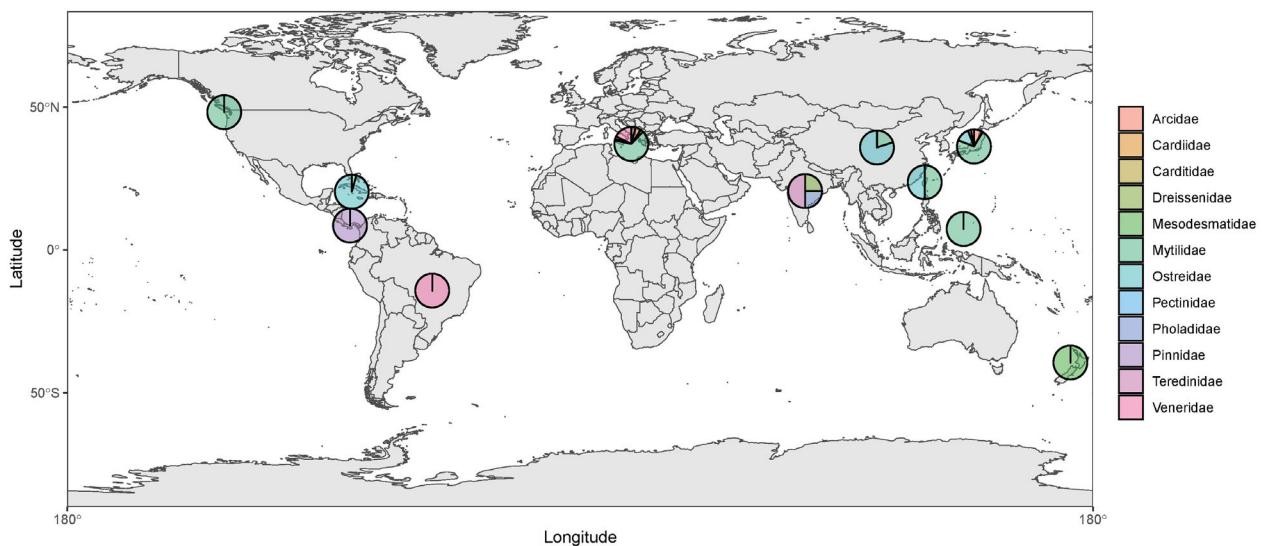


FIGURE 3 Worldwide distribution of families of bivalves hosting eirenid hydroids. Pie charts indicate the percent of occurrence record. Exact locations and coordinates are available in Data S1. (QGIS3,²¹ R²³ elaboration).

Hydroids were found in 44 bivalve species belonging to 12 families (Figures 3 and 4 and Tables 3 and 4). Sometimes, different eirenid species may coexist in the same bivalve, without any evident spatial separation of the polyps on the mollusc body parts, although their sexual reproduction is asynchronous.²⁶

Most bivalve hosts (Figure 4a and Table 4) belong to Mytilidae (occurrence records: $n = 262$, representing over 70% of the presence records), Ostreidae ($n = 51$, 13.7%), Veneridae ($n = 21$, 5.6%), and Arcidae ($n = 16$, 4.3%). Hydroids hosted by mytilids were mainly associated with *Mytilus galloprovincialis* ($n = 238$ records, ~64%). Up to 450 polyps were found in one mussel.³⁰ In studies where at least 50 bivalves of the same species were analysed, prevalence over 50% was observed only in *M. galloprovincialis* (both cultured and wild).

Regarding other bivalve hosts, several records refer to the ostreids *Crassostrea virginica* (Gmelin, 1791) ($n = 21$, 5.6%) and *Magallana gigas* (Thunberg, 1793) ($n = 16$, 4.3%), and 14 to the arcid *Barbatia virescens* (Reeve, 1844) (3.5%), while less attention was given to other species (<10 records).

Ten bivalve species were never recorded as being associated with hydroids; however, they were rarely investigated, as highlighted by the low number of studies concerning them (Table 3).

The origin of bivalves—wild (77%), cultured (19%), both (4%)—was specified for relatively few records (36%). Records of *Eugymnanthea* and *Eutima* spp. inhabiting wild bivalves were comparable, whereas, *Eugymnanthea* spp. were more common than *Eutima* spp. in farmed molluscs (Figure 4b).

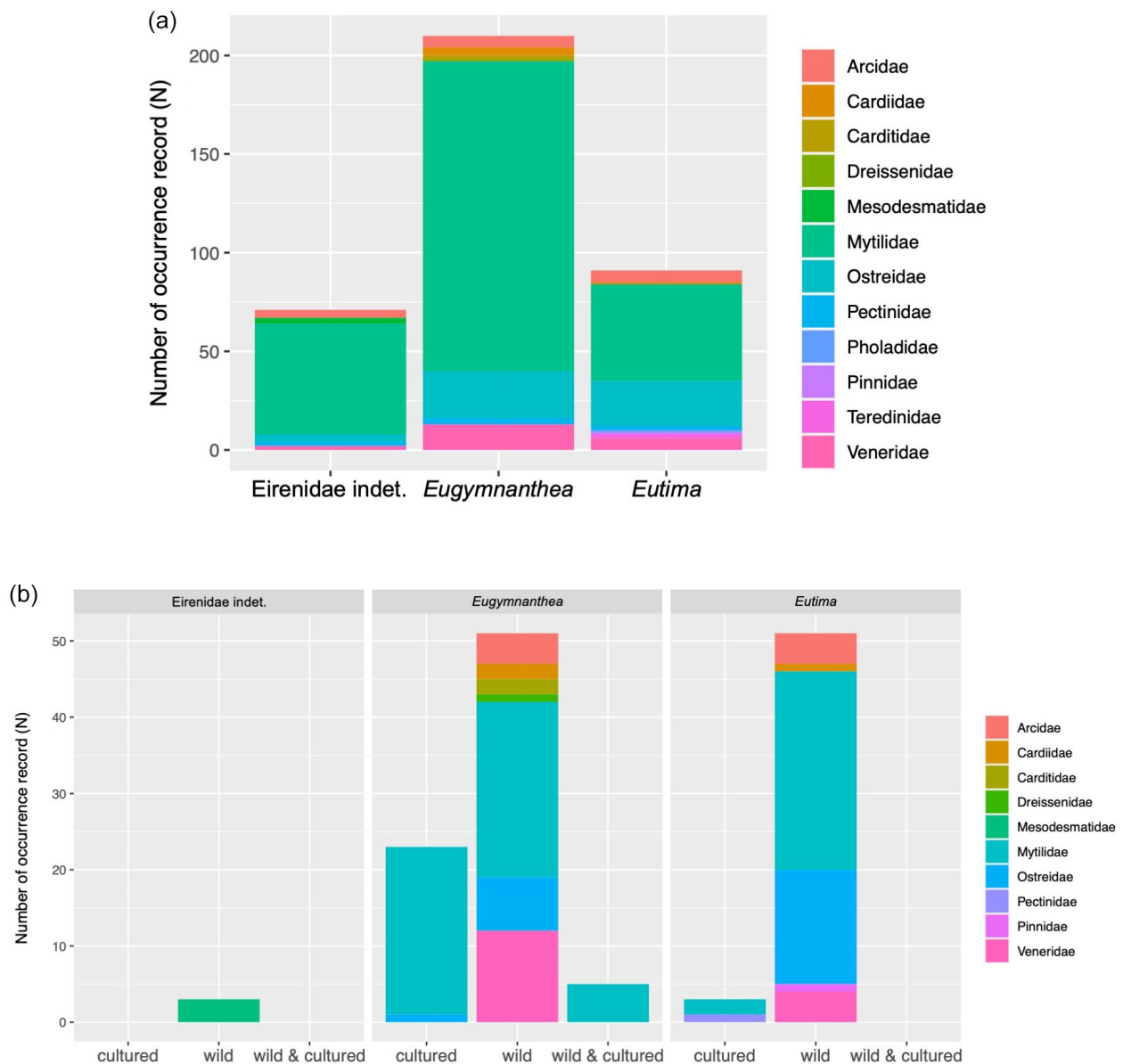


FIGURE 4 Bivalves associated with hydroids. (a) Hydroids found in 12 bivalve families. *Eugymnanthea* spp. are more frequently observed; *Eutima* spp. only were detected in Pholadidae, Pinnidae and Teredinidae. The label 'Eirenidae' indicates hydroids identified at family level. (b) Occurrence of eirenids in wild and cultured bivalves. Records of *Eugymnanthea* and *Eutima* spp. in wild bivalves are comparable, while, *Eugymnanthea* spp. were more common than *Eutima* spp. in farmed molluscs. Eirenidae are hydroids identified at family level only.

3.2 | Geographical and bathymetric distribution of hydroids

Presence and absence records were mainly collected between the surface and a depth of 5 m; the deepest occurrence recorded was around 40 m (*Eut. japonica* in the venerid *Paphies vernicosa*³¹).

The association has a circumtropical occurrence (Figure 5a); with the southernmost record being in Ripiro³² (New Zealand, unidentified eirenid in *P. ventricosa*), and the northernmost one was in Mosquito Creek³³ (USA, *Eut. japonica* in *M. galloprovincialis*). This latter finding refers to mussels settled on floating marine debris washed ashore by

a tsunami event spreading from Japan, with no actual evidence of an established population of eirenids in the USA.

Most occurrence records are from Japan, the Caribbean, and the Mediterranean seas (Figure 5b–d); *Eug. inquilina* is the sole species found in the Mediterranean basin, while *Eutima* is the only genus in the Caribbean and the Atlantic coasts of South America. Both genera are present in Japan, with *Eutima* (mainly *Eut. japonica*) being distributed from the southern part of Hokkaido to Shikoku, and *Eugymnanthea* (notably *Eug. japonica*) distributed from the central southern coasts of Honshu to Kyushu.³¹ Until the 90's, both Eirenidae species appeared absent from the northern coasts of Honshu facing the East

TABLE 3 Bivalve species not associated with Eirenidae (nn = unknown).

Bivalve species	Family	Country	Substrate	No. examined bivalves	References
<i>Tegillarca granosa</i> (Linnaeus, 1758)	Arcidae	Thailand	mud	72	Kubota et al. ²⁷
<i>Glaucanome chinensis</i> J. E. Gray, 1828	Glaucanomidae	China	nn	30	Kubota and Guo ²⁸
<i>Brachidontes mutabilis</i> (Gould, 1861)	Mytilidae	India	nn	15	Kubota and Santhakumari ²⁹
<i>Vignadula atrata</i> (Lischke, 1871)	Mytilidae	India	nn	45	Kubota and Santhakumari ²⁹
<i>Saccostrea cucullata</i> (Born, 1778)	Ostreidae	Thailand	ropes	148	Kubota et al. ²⁷
<i>Mimachlamys crassicostata</i> (G. B. Sowerby II, 1842)	Pectinidae	China	nn	20	Kubota and Guo ²⁸
<i>Irus mitis</i> (Deshayes, 1854)	Veneridae	India	nn	6	Kubota and Santhakumari ²⁹
<i>Meretrix lyrata</i> (G. B. Sowerby II, 1851)	Veneridae	Thailand	sand	39	Kubota et al. ²⁷
<i>Meretrix meretrix</i> (Linnaeus, 1758)	Veneridae	Thailand	sand	81	Kubota et al. ²⁷
<i>Paratapes undulatus</i> (Born, 1778)	Veneridae	China	nn	29	Kubota and Guo ²⁸

Sea and in the Northern region of Hokkaido, where cold waters likely limited the establishment of bivalve-inhabiting eirenids.²⁶

The distribution of *Eugymnanthea* is influenced by the Kuroshio current providing warm waters and nutrients in the North Pacific^{31,34}; moreover, a widening in the distribution range of this genus in Japan is likely due to building of new infrastructures for aquaculture and the spreading of the introduced bivalve *M. galloprovincialis*.

M. galloprovincialis was introduced in Japan, Korea and in South Africa, although it did not transport *Eug. inquilina* to these Countries.^{27,35,36}

Unlike in Japan, there are very few studies about the eirenids-bivalves association in other countries, including those in the Mediterranean Sea, despite the number of detrimental effects of the association reported for bivalves farmed in Europe (see ahead Table 5).

3.3 | The association

The “harmless” aspect of eirenid hydroids (lack of perisarc, solitary hydranths, lack of stolons, no response to mechanical and light stimuli induced in laboratory) is an adaptation evolved in relation with their endobiotic lifestyle.^{35,40} Species associated with bivalves are generally able to live isolated only under experimental conditions.^{7,41} The polyp stage is usually solitary, and it is attached to the host by a basal disc; it lacks a protective perisarc exoskeleton, generally present in thecate hydroids, most likely because protection is guaranteed by the host.⁴²

The external surface of the bivalves living on soft,⁴³ hard,⁴⁴ and artificial substrates⁴⁵ is often colonized by other organisms,⁴⁶ and it is supposed that bivalve-inhabiting eirenids fill the space between the valves to avoid spatial competition with other potential epibionts. The eirenids hosted in bivalves still bear nematocysts,^{30,47} which are probably used to catch prey that the bivalve's feeding current directs into the mantle cavity.⁹ In laboratory conditions, *Eug. inquilina* ingested offered trematode sporocysts,⁴⁸ suggesting a possible mutualistic relationship between the hydroid and its host; however, this behaviour was not demonstrated by other Authors.¹²

Regarding the localization within the host, it has been hypothesized that hydroids firstly settle on the mantle of the host.⁴⁹ It was also supposed that hydroids occurred more frequently on soft body

parts where water movement is usually intense,⁸ such as in the mantle cavity and on the gills. However, the analysed records show that the mantle is the preferential area (37%), followed by the visceral mass (18%), the labial palps (18%), and the gills (17%), while the foot is the least affected area (11%). The assessment of water flow in *M. galloprovincialis* by phase-contrast magnetic resonance imaging (MRI) demonstrated that water velocity decreases during the passage from the inhalant aperture (40–20 mm s⁻¹) to the lower mantle cavity (10–20 mm s⁻¹), and in correspondence of demibranches (5–10 mm s⁻¹); then, the speed increases again to 50 mm s⁻¹ in the exhalant siphon.⁵⁰ These findings suggest that hydroids are mainly present in the mantle cavity where they likely encounter an optimal flow to maximize their settling and feeding effectiveness.⁵¹

Polyps of *Eug. japonica* found on the gills of *M. galloprovincialis* were attached by only one end of the basal disc,⁵² confirming that at least in this species the gills are not the preferential settling area.

The hydroid's basal disc can be (i) attached to the bivalve epithelium without penetrating it⁵³ and with the polyps showing slow locomotion,⁵⁴ or (ii) deeply embedded in the host tissue.³⁹ In *Eut. commensalis* the attachment through the basal disc seems to be “further strengthened with the help of the protrusions or holdfasts that project from the basal disc into the tissue of the ctenidium”.⁵⁵ Only *Eutima* spp. were detected in bivalves occupying peculiar ecological niches, such as rock- or wood-boring bivalves (Pholadidae & Teredinidae).^{29,56} The relationship between *Eutima* and wood-boring bivalves is more intimate with respect to other bivalve-inhabiting eirenids, since the cnidarian's basal disc is implanted in the ctenidium of the host, and the hydroid is not able to detach or to glide on the mollusc's tissues.^{55,56} It has been hypothesized that a primitive bivalve-inhabiting *Eutima* gave rise to the less specialized genus *Eugymnanthea*.³⁵

3.4 | Hydroid life cycle, dispersal and infestation modality

Both *Eutima* and *Eugymnanthea* reproduce by budding within the host's valves, while the dispersal capability of the symbionts is mainly

TABLE 4 Bivalves' families and species hosting eirenid hydroids.

Family	Species	No. of occurrence record
Arcidae	<i>Arca noae</i> Linnaeus, 1758	3
	<i>Barbatia virescens</i> (Reeve, 1844)	13
Cardiidae	<i>Acanthocardia tuberculata</i> (Linnaeus, 1758)	1
	<i>Cerastoderma edule</i> (Linnaeus, 1758)	1
	<i>Cerastoderma glaucum</i> (Bruguière, 1789)	2
	<i>Keenocardium californiense</i> (Deshayes, 1839)	1
Carditidae	<i>Cardites antiquatus</i> (Linnaeus, 1758)	2
Dreissenidae	<i>Mytilopsis sallei</i> (Récluz, 1849)	1
Mesodesmatidae	<i>Paphies ventricosa</i> (Gray, 1843)	3
Mytilidae	<i>Arcuatula senhousia</i> (W. H. Benson, 1842)	3
	<i>Brachidontes</i> sp.	1
	<i>Crenomytilus grayanus</i> (Dunker, 1853)	3
	<i>Geukensia demissa</i> (Dillwyn, 1817)	1
	<i>Modiolus auriculatus</i> (Krauss, 1848)	2
	<i>Mytilaster minimus</i> (Poli, 1795)	2
	<i>Mytilisepta virgata</i> (Wiegmann, 1837)	4
	<i>Mytilus galloprovincialis</i> Lamarck, 1819	238
	<i>Mytilus trossulus</i> A. Gould, 1850	1
	<i>Mytilus unguiculatus</i> Valenciennes, 1858	6
	<i>Perna viridis</i> (Linnaeus, 1758)	1
Ostreidae	<i>Crassostrea rhizophorae</i> (Guilding, 1828)	1
	<i>Crassostrea</i> sp.	4
	<i>Crassostrea virginica</i> (Gmelin, 1791)	21
	<i>Dendostrea sandvichensis</i> (G. B. Sowerby II, 1871)	1
	<i>Magallana gigas</i> (Thunberg, 1793)	18
	<i>Ostrea</i> sp.	1
	<i>Saccostrea spathulata</i> (Lamarck, 1819)	5
Pectinidae	<i>Azumapecten farreri</i> (K. H. Jones & Preston, 1904)	3
	<i>Flexopecten glaber</i> (Linnaeus, 1758)	2
	<i>Mizuhopecten yessoensis</i> (Jay, 1857)	1
	<i>Swiftopecten swiftii</i> (Bernardi, 1858)	1
Pholadidae	<i>Martesia striata</i> (Linnaeus, 1758)	1
Pinnidae	<i>Pinna carnea</i> Gmelin, 1971	1
Teredinidae	<i>Nausitora hedleyi</i> Schepman, 1919	1
	<i>Teredo furcifera</i> E. von Martens, 1894	1
Veneridae	<i>Paphia vernicosa</i> (Gould, 1861)	2
	<i>Pitar rudis</i> (Poli, 1795)	2
	<i>Polititapes aureus</i> (Gmelin, 1791)	2
	<i>Ruditapes decussatus</i> (Linnaeus, 1758)	7
	<i>Ruditapes philippinarum</i> (A. Adams & Reeve, 1850)	3
	<i>Tivela mactroides</i> (Born, 1778)	3
	<i>Venus verrucosa</i> Linnaeus, 1758	2

related to the production of a planktonic stage: that is, a medusa in *Eutima*, and a mature and readily spawning eumedusoid in *Eugymnantheda*^{10,57} (see graphical abstract). Medusae of *Eutima* have a well-

developed manubrium and tentacles, and they can catch prey.⁵⁸ Under rearing conditions, these medusae can survive up to 53 days, and gonads were observed during the first 28 days of life.⁵⁹ The

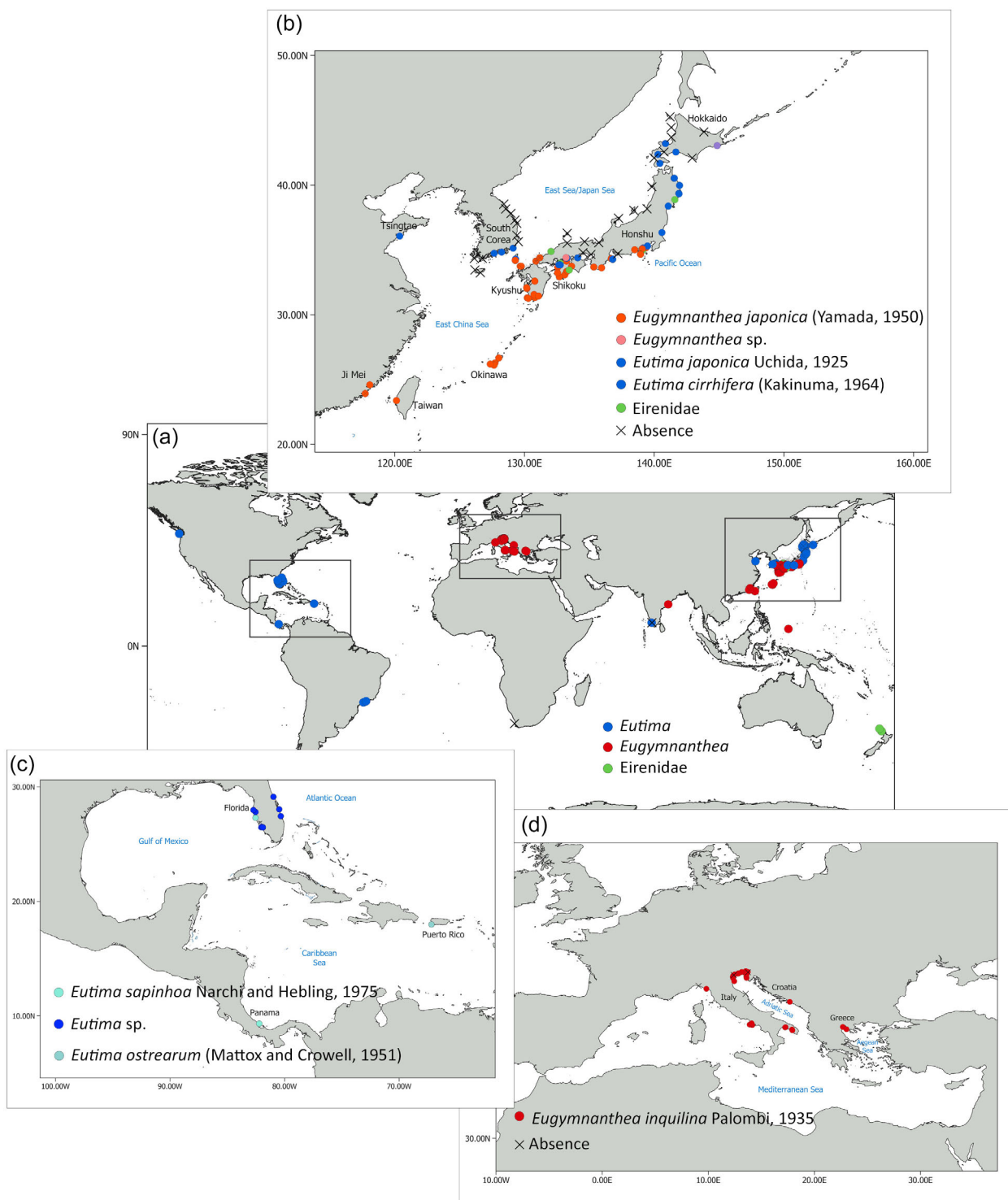


FIGURE 5 (a) World distribution of bivalve-associated eirenids. Occurrence records are represented by coloured dots (red shades = *Eugymnanthea*, blue shades = *Eutima*, green = unidentified eirenids), while crosses indicate the absence of records. Inserts focus on most studied areas with several records, that is, the Japan (b), the Caribbean (c), and the Mediterranean (d). QGIS3²¹ elaboration.

newly released medusae of *Eutima* possess immature gonads, however, when they reach maturity, they spawn repeatedly until death.²⁶

Regarding the factors triggering the medusa release, in *Eug. japonica* it occurs with diurnal periodicity irrespective of the season.^{60–62} Variations in light intensity or tidal changes apparently do not

influence timing of release,^{61,62} while the temperature influences the life span of the free-living stage. Under rearing conditions, *Eutima* medusae survived longer at 15°C than at 22°C.⁶¹ After a prolonged period in low salinity conditions,² *Eugymnanthea* medusoids were not released at all.

TABLE 5 Highest number of polyps per bivalve.

Hydroid species	Max no. of polyps per bivalve	Bivalve	Bivalve' Size (mm)	Country	References
<i>Eutima japonica</i>	376	<i>Mytilus galloprovincialis</i>	50–120	Japan	Kubota ³⁷
<i>Eugymnanthea inquilina</i>	400	<i>Mytilus galloprovincialis</i>	50–120	Italy	Crowell ³⁸
<i>Eutima cirrhifera</i>	450	<i>Mytilus galloprovincialis</i>	50–120	Japan	Kubota ³⁰
<i>Eugymnanthea</i> spp.	800	<i>Mytilopsis sallei</i>	8–25	India	Raju et al. ³⁹
<i>Eutima japonica</i>	905	<i>Mizuhopecten yessoensis</i>	100–220	Japan	Baba et al. ¹⁰
<i>Eutima</i> sp.	Thousands	<i>Crassostrea virginica</i>	70–200	Florida	Mulholland and Friedl ⁷

The planula is the infective stage,⁹ and it is likely that planulae of *Eugymnanthea* settle on the same bivalve population of the parental hydroids, while those of *Eutima* settle far from the site of origin of the medusa. The planktonic stage is usually gonochoristic, however, self-fertilizing hermaphrodite medusoids in *Eug. inquilina* were described from Taranto (Ionic Sea, Italy).⁶³

Even if the lifespan could be different in natural conditions, the available data suggest a high dispersal potential of the planktonic stage of *Eutima* spp. In contrast, eumedusoids of *Eugymnanthea*, with a vestigial (or absent) manubrium, lacking tentacles and therefore unable to capture prey, can survive only a few days.^{48,49,64,65}

It has been assumed that polyps may detach for a short time and reattach in new places within the same mollusc, probably to prevent crowding,³⁸ or leave the bivalve through the exhalant current⁶² and settle again in the nearby molluscs contributing to the species dispersal.⁶⁶ Polyps (1 to 29 per day) detaching from the mussel host⁶⁵ as well as polyps swimming freely inside the shell were reported⁶⁷; however, there is no evidence that dislodged polyps can secure a new foothold.³⁸

Planulae preferentially settle on large molluscs (40 mm in length), likely because larger bivalves inhale more efficiently creating a higher flow rate for the planulae.⁴⁸

3.5 | Biotic/abiotic factors driving abundance and prevalence

3.5.1 | Biotic factors

Hundreds, even thousands of polyps can be found inside a single bivalve (Table 5). It was reported that hydroid abundance increases with bivalve length.⁶⁸ Considering data from the reviewed papers (Data S1), a positive correlation was observed among prevalence and maximum number of polyps per bivalve ($r_s = 0.82$, $p < 0.05$), while no significant correlation occurred among bivalve length and prevalence ($r_s = 0.18$, $p > 0.05$), or among bivalve length and max number of polyps ($r_s = 0.15$, $p > 0.05$). However, several studies did not provide biometric data of colonized bivalves, and this could have influenced the analysis. It is possible that the infestation rate changed in relation to the size classes and the feeding behaviour: for example, eirenids can infest juveniles of *Mizuhopecten yessoensis* (Jay, 1857), but not larger adults feeding on zooplankton.¹⁰ It is possible that the adults can prevent an infestation by ingesting the hydroid planulae.⁶⁹

Co-occurrence of other parasites may have detrimental effects on the molluscs inhabited by eirenids,⁶⁸ even if this was not always reported.¹⁴ The severity of lesions may depend on the combination of these parasites; for example, the Condition Index of *M. galloprovincialis* was lower when *Eug. inquilina*, the turbellarian *Urastoma cyprinae* and the trematode *Proctoeces maculatus* simultaneously infested the bivalves.⁶⁸

The introduction of exotic bivalves in shell farms may facilitate the eirenids' infestation of native shellfish. *M. galloprovincialis* in Japan is a likely vector of *Eut. japonica* in juveniles of *Mizuhopecten yessoensis* in Funka Bay (Hokkaido, Japan).¹⁰ Massive mortalities of juveniles in cultured *Mizuhopecten yessoensis* were the result of simultaneous impacts of heavy infestation, low water quality in a cage rearing system, and inappropriate mollusc handling during the transfer from one cage to another.¹⁰

Regarding the intrinsic factors regulating the hydroid life cycle, the degeneration of polyps seemed to follow the production of the planktonic stage.^{49,55}

The bivalve gametogenesis may affect hydroid dynamics. Highest hydroid abundance was detected in correspondence to the beginning of the spawning period of the host.⁸ In some cases hydroids were present only in large and sexually mature mussels.⁴⁸ Mussels' gametes were found in histological sections of symbiont eirenids,⁹ while eggs and pediveligers of *M. galloprovincialis* are the main trophic sources for the hydroid *Eudendrium racemosum* (Cavolini, 1785) from the Adriatic Sea in summer.⁷⁰ This suggests that gametes/embryos/pediveligers present in waters surrounding spawners, or embryos swimming in the mantle cavity of brooding bivalves⁷¹ might provide a food source for the eirenids. To date, there are no available studies that combine bivalve-inhabiting eirenids gut contents with host life cycle. The analysis of the hydroids' gut contents would be useful to compare ingested items with food available in the surrounding environment.

3.5.2 | Abiotic factors

Among the abiotic parameters, water movement is one of the main factors driving infestation. Most records of eirenids hosted in bivalves occur in sheltered and shallow areas^{8,38,72} or in culture cages,¹⁰ since the hydroids have a greater chance to find and settle on a suitable host than in open water.³⁸ The highest percentage of infected mussels was observed in stations hosting dense mussel lines with low current

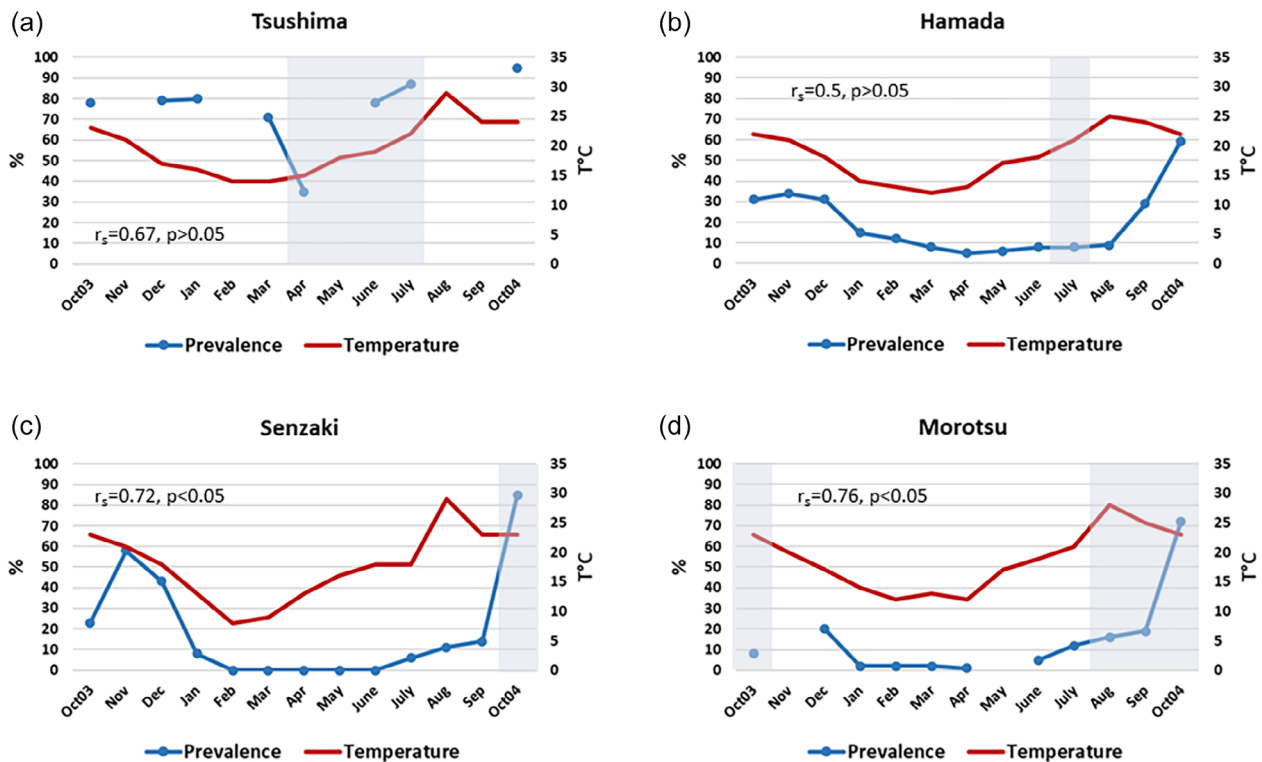


FIGURE 6 Prevalence of *Euginanthea japonica* and *Eutima japonica* (considered together²⁶) and temperature trends from four localities (a, Tsushima, b, Hamada, c, Senzaki, and d, Morotsu) in North Japan with relative Spearman's correlation coefficient. Shaded areas represent peaks in bud production. Notice that hydroids prevalence peak occurred in October in all four sites, while maximal budding anticipated the prevalence peak in Tsushima and Hamada—where hydroids are present all year round—and coincided in Senzaki and Morotsu—where the hydroids are seasonal and have a narrower temporal window of occurrence.

(2 cm s^{-1}).⁸ Since the host bivalve may alter its physiology in response to stressful conditions⁷³ and reduce the valve gape to minimize oxygen uptake,⁷⁴ we could hypothesise that a lower water flow could favour the hydroid multiplication within the valves.

Regarding the effects of temperature, the abundance of hydroids inhabiting wild *Crassostrea virginica* in the semi-enclosed Tampa Bay (Florida) dropped when the oysters remained exposed to low temperatures during the low tide.⁷ The polyp stage of Asiatic eirenids do not tolerate temperatures lower than 10°C , while the free-living stages cannot survive below 15°C .^{26,75}

The prevalence of *Eug. japonica* and *Eut. japonica* associated with *M. galloprovincialis* sharply increased about 2 months after a temperature peak²⁶ in four localities in Japan (Figure 6). On the contrary, maximal budding anticipated the prevalence peak in Tsushima and Hamada—where hydroids are present all year round—and coincided in Senzaki and Morotsu—where the hydroids are seasonal. A positive correlation (Spearman's coefficient) between prevalence and temperature trends was observed only for data from Senzaki and Morotsu, likely due to their narrower temporal window of occurrence or because of other unexplored factors (e.g. food availability). *Euginanthea inquilina* in *M. galloprovincialis* from the North Adriatic Sea peaked in late summer (prevalence 86.7%, $T = 20.3^\circ\text{C}$) and declined in winter (37%), with an average sea temperature of 9.1°C ,¹⁴ but

never entered dormancy, suggesting that this species has a wider thermal tolerance limit than other eirenids.

With respect to salinity, several authors^{53,76–78} hypothesized that low salinity caused the decline of eirenid polyps from the west coast of Florida. The drop in abundance of oyster-inhabiting polyps coincided with heavy rains and relevant freshwater inflow; the latter likely impeded or limited the production, release, and settlement of new planulae.

In the North Adriatic Sea, salinity and oxygen content have a statistically significant correlation with *E. inquilina* infection: a hydroid prevalence peak was reported in September (oxygen 6.9 mg/L and salinity of 39‰), while the lowest values occurred in March (oxygen 11.6 mg/L, salinity 32.5‰¹⁴).

Eutima commensalis occurring in wood-boring bivalves from estuarine habitats in India exhibited a narrow range of salinity tolerance (10–20‰) with an optimum at 17‰.⁵⁶ The hydroid disappeared during the heavy monsoon rains, from June (salinity around 26‰) to October (about 3‰); in contrast, maximal length and highest number of gonophores were observed in November (about 16‰). Under laboratory conditions, hydroids may extend their range of tolerance and are able to acclimate if moderate variations in salinity are gradual.⁵⁵

In the North Adriatic Sea prevalence of several endobionts (including *Eug. inquilina*) was found to be correlated with eutrophication.⁷⁹

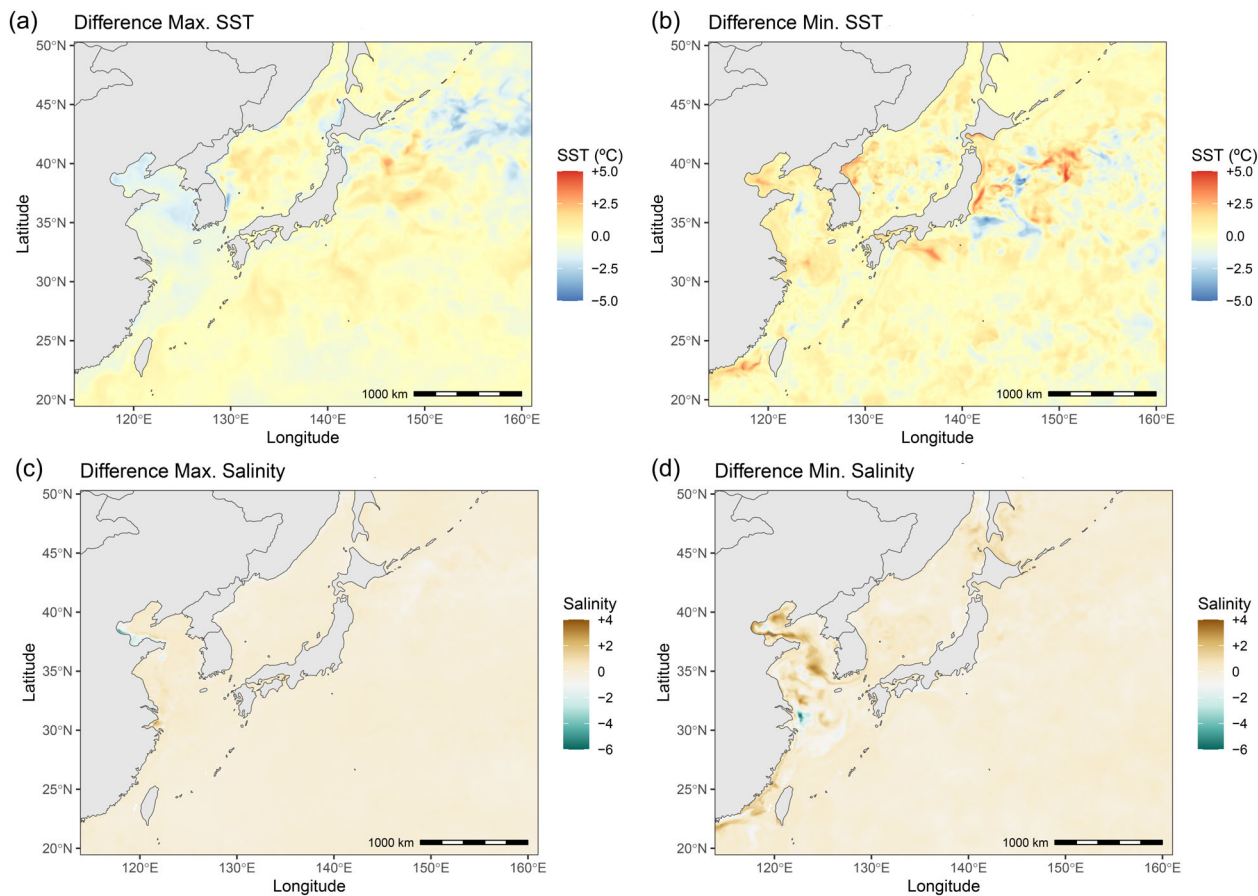


FIGURE 7 Differences observed among the periods of 1993–2010 and 2011–2022 in terms of: (a) maximum SST, (b) minimum SST, (c) maximum salinity and (d) minimum salinity in the waters surrounding Japan, Korea, East China, and Taiwan. Data acquired from the Copernicus Marine Service dataset.²²

3.5.3 | Possible effects of climate change

Anthropogenic global warming is reshaping coastal dynamics and ocean biogeochemistry due to alteration in water temperature, salinity, sea level and turbidity.⁸⁰ Particularly threatened habitats are estuaries and saltmarshes, due to sea-level rise and to the presence of anthropogenic infrastructures that limit tidal invasion and the possibility to expand landward, with profound changes to the biota.^{81,82} Fluctuations in physical parameters may select certain bivalve species⁸³ and disrupt the ecological balance in aquaculture systems.⁸⁴

Complex oceanography of the area around Japan and climate-range shifts are affecting marine fisheries resources^{85,86} as well as coral and macroalgal distribution.⁸⁷ Figure 7 shows the differences obtained between the maximum and minimum values of salinity and SST, between 1993–2010 and 2011–2020 around Japan, Korea, East China, and Taiwan. Sharper differences occurred for both minimal values of SST and salinity between 1993–2010 and 2011–2020, which increased up to 5°C and 4°C, respectively. A new study on bivalve-inhabiting eirenids found in these basins could be useful to verify eventual changes in the distribution of the association and to detect areas that are more vulnerable to infestations.

Even if long-term environmental data series are needed to demonstrate that climate change could interfere with the eirenids-bivalves relationship, we should increase our attention towards this association, above all in habitats prone to climate regime shifts, such as semi-enclosed basins and estuarine habitats.⁸⁸ Monitoring activities will allow for prevention or control of eventual hydroid hyperproliferation.

4 | CONCLUSIONS

Regarding biotic/abiotic factors influencing the eirenids' prevalence and abundance, the proliferation of the polyp stage and the production of the free-living medusae/eumedusoids occur with high values of salinity; infestation occurs in sheltered and likely eutrophic areas with low water movement and low oxygen concentration. As such, the association could be considered as an indicator of water quality.

Low temperatures (lower than 10°C in Japan, but likely lower for *Eug. inquilina* from the Mediterranean Sea) causes the disappearance of the polyp stage.

Most of the recorded detrimental effects are caused by *Eug. inquilina*, which is particularly resistant to both low and high temperatures,

oxygen-depleted water and reduced current speed. Moreover, *Eugymnanthea* spp. are more common than *Eutima* spp. in farmed molluscs, likely due to their higher tolerance to fluctuations of physical parameters and culture practices.

Mytilus galloprovincialis is the host showing the highest prevalence. Both wild and cultured bivalves may be infested. High mollusc densities in culture systems may reduce water movement and shorten distance between bivalves thus favouring the spread of species with a lower dispersal potential, such as *Eugymnanthea* spp. Handling may worsen conditions of reared bivalves and favour the eirenid infestation. Allochthonous bivalve species may be vectors of associated hydroids in shellfish farms.

Increase in salinity may favour hydroids' proliferation. Furthermore, hydroids that usually disappear in colder months may overwinter due to a rise in minimal temperature values. Anthropogenic disturbance (i.e. deployment of artificial substrates, input of floating debris) could couple with environmental changes and favour the proliferation of the association.

The association between eirenids and bivalves can shift from commensalism to pest,⁸⁹ but our understanding of the relationship should be improved. Most hypotheses summarized in this review are based on observations conducted in laboratories and should be confirmed by further research carried out in the field. An extensive—at least annual study—of the eirenid benthic and pelagic phases, coupled with the population dynamics of the host are crucial to improve our understanding of how the hydroid and bivalve life cycles are synchronized.

The assessment of the impact of infestation on bivalves' health and physiology requires urgent attention. It is also necessary to implement a sensory test to evaluate the organoleptic properties of commercial species subjected to heavy infestation. Except for one report of unpleasant smell¹³ of inhabited bivalves, no studies exist that compare sensory and nutritional quality of infested and non-infested molluscs.

The baseline data obtained through this review could be improved by future research that investigates and performs further spatial and temporal analyses. Of the 372 occurrence records, only 19 (about 5%, Data S1) included data on prevalence, bivalves' morphology/health status and environmental parameters. We reiterate the need for more standardized and exhaustive data collection as suggested in Table 2 and Data S1 that will allow reliable comparisons to be made between study cases and to improve the understanding of the factors influencing the relationship.

AUTHOR CONTRIBUTIONS

Cristina Gioia Di Camillo: Conceptualization; data curation; formal analysis; writing – original draft; methodology; supervision; writing – review and editing; software; funding acquisition; visualization. **Camilla Roveta:** Formal analysis; writing – original draft; writing – review and editing; software; data curation. **Torcuato Pulido Mantas:** Data curation; formal analysis; writing – original draft; writing – review and editing; software. **Cinzia Gravili:** Writing – original draft; data curation; writing – review and editing; investigation. **Carlo Cerrano:** Writing – original draft; writing – review and editing; supervision. **Barbara Calcinaï:**

Writing – original draft; writing – review and editing. **Martina Coppari:** Writing – original draft; writing – review and editing. **Chiara Gregorin:** Writing – original draft; writing – review and editing. **Teo Marrocco:** Writing – original draft; writing – review and editing. **Agnese Riccardi:** Writing – original draft; writing – review and editing. **Stefania Puce:** Writing – original draft; writing – review and editing; supervision.

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CONFLICT OF INTEREST

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available in the supplementary material of this article

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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