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***FICOPOMATUS ENIGMATICUS* FAUVEL, 1923:  
A REVIEW OF GLOBAL DISTRIBUTION, BIOLOGY  
AND POPULATION MANAGEMENT ATTEMPTS**

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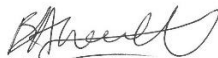
# ***FICOPOMATUS ENIGMATICUS* FAUVEL, 1923: A REVIEW OF GLOBAL DISTRIBUTION, BIOLOGY AND POPULATION MANAGEMENT ATTEMPTS**

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## EXECUTIVE SUMMARY

*Ficopomatus enigmaticus* Fauvel, 1923 is a marine polychaete in the family Serpulidae. The species is characterised by its formation of extensive biogenic reefs in hard- and soft-substrate habitats. Non-indigenous and highly isolated populations of *F. enigmaticus* have been observed in New Zealand since the 1960s. Hawke's Bay Regional Council (HBRC) is concerned about the development and progressive expansion of substantial *F. enigmaticus* reefs around local waterbodies, as they pose risks to the integrity of native ecosystems and critical flood prevention infrastructure.

Hawke's Bay Regional Council engaged the Cawthron Institute (Cawthron) to provide advice on the feasibility of potential management interventions. One of the objectives of this project, addressed in this report, is the development of a review that captures current knowledge of the distribution, ecology and reproductive seasonality of *F. enigmaticus*, the scale and impacts of its invasion or population explosion events worldwide, and the outcomes of attempts undertaken to eradicate or manage *F. enigmaticus* populations.

We conducted a review of the published international literature and engaged in direct communication with seven recognised experts on *F. enigmaticus* invasions in different global regions. In this report, we describe the discovery, extent, densities, growth rates, reproduction and recruitment characteristics, impacts, and attempts at management of invasive or nuisance *F. enigmaticus* populations in Europe, Africa, North and South America and Australia. Our review indicates that introduced *F. enigmaticus* populations can grow at very high rates – up to 9 ha per year – with worm reefs attaining a biomass of up to 550 kg/m<sup>3</sup> (observed in Italy). Multiple spawning events may occur in a single year; however, reproductive seasonality, growth rates, reef morphology and size appear to vary geographically; moreover, the studies are too limited to allow generalised conclusions.

Disappointingly, only a small number of studies have examined the impact of invasions or population expansions of *F. enigmaticus*, and communication with global experts suggests that very few attempts have been made to eradicate or remove *F. enigmaticus* from natural or artificial environments. Global case studies can therefore contribute only limited information towards considerations for *F. enigmaticus* control in New Zealand. However, our review presents some important conclusions. First, it appears that the extent of *F. enigmaticus* infestations in the Hawke's Bay region in New Zealand is relatively small compared to invasive populations in other parts of the world. This is important for the consideration of potential population control measures, as it may provide a (temporary) advantage for interventions. This view was shared by several of the international experts we consulted. Second, control attempts for global *F. enigmaticus* populations seem to have been sporadic; furthermore, they have been conducted at a relatively small scale over a short period of time rather than in a sustained manner following a medium- to long-term strategy. We consider that the lack of success reported from overseas is not a reason to assume that population control in the Hawke's Bay region is not possible. In addition, there are several helpful findings reported in the information gathered for this review. For example,

control measures (i) should not be undertaken when worms may release gametes or larvae, and (ii) there is a need to ensure that no reef material / fragments are generated or, if unavoidable, left behind, as these can act as nuclei for the formation of new reefs. There are also indications (although not based on rigorous data) that variations in eutrophication and salinity levels may influence population dynamics of this species. The incorporation of these (and other) conclusions into HBRC's approach will likely strengthen the chances of successful reef management.

Despite the apparent lack of success of previous management efforts, *F. enigmaticus* population control attempts in the Hawke's Bay region should not be ruled out. Instead, we recommend that HBRC continue to evaluate the feasibility of population control or attempted local eradication. The next step is the preparation of a feasibility assessment that examines potential management approaches against a range of criteria to provide recommendations on appropriate methods for controlling the invasive worm reefs in the Ahuriri estuary and the Clive River.

## TABLE OF CONTENTS

1. BACKGROUND AND OBJECTIVES .....	1
2. OVERVIEW OF <i>FICOPOMATUS ENIGMATICUS</i> .....	2
2.1. Taxonomy and distribution .....	2
2.2. Ecology .....	5
2.3. Reproductive biology .....	7
2.3.1. <i>Reproduction</i> .....	9
2.3.2. <i>Development</i> .....	10
2.3.3. <i>Larval dispersal</i> .....	10
2.3.4. <i>Settlement, recruitment and maturation</i> .....	10
3. RESEARCH ON INTRODUCED POPULATIONS OF <i>FICOPOMATUS ENIGMATICUS</i> .....	13
3.1. Europe .....	13
3.2. Africa .....	14
3.3. North America .....	15
3.3.1. <i>Pacific Coast</i> .....	15
3.3.2. <i>Atlantic Coast</i> .....	17
3.4. South America .....	17
3.5. Australia .....	20
3.6. Summary of insights from global locations subject to <i>Ficopomatus enigmaticus</i> invasion .....	22
3.7. Recommendations for HBRC .....	22
4. ACKNOWLEDGEMENTS .....	24
5. APPENDICES .....	25
6. REFERENCES .....	30

## LIST OF FIGURES

Figure 1. Global distribution of <i>Ficopomatus enigmaticus</i> as identified in this review .....	4
Figure 2. <i>Ficopomatus enigmaticus</i> reefs at the Mar Chiquita lagoon, Buenos Aires, Argentina at low tide .....	6
Figure 3. <i>Ficopomatus enigmaticus</i> individual removed from its tube; seen from dorsal (left) and ventral (right); found in a stromatolite pool on the south coast of South Africa. ....	7
Figure 4. <i>Galeolaria gemino</i> a Halt, Kupriyanova, Cooper & Rouse, 2009; removed from its tube and releasing oocytes. ....	8
Figure 5. Larvae of <i>Spirobranchus cariniferus</i> 25 days after hatching .....	12
Figure 6. <i>Arcuatula senhousia</i> (Asian date mussel) found in Izmir Bay, Turkey. ....	14
Figure 7. <i>Ficopomatus enigmaticus</i> aggregation on old wooden pillars in the Elkhorn Slough marine reserve, USA .....	16
Figure 8. <i>Ficopomatus enigmaticus</i> reefs at the Mar Chiquita lagoon, Argentina .....	18
Figure 9. Aerial view of <i>Ficopomatus enigmaticus</i> reefs at the Mar Chiquita lagoon, Argentina. ....	19
Figure 10. <i>Ficopomatus enigmaticus</i> recruits on the shell of a turtle at the Lower Lakes, Australia. ....	21
Figure 11. <i>Ficopomatus enigmaticus</i> settled on a shell of <i>Velesunio ambiguus</i> at the Lower Lakes, Australia .....	21

## LIST OF APPENDICES

A.1 Global distribution of *Ficopomatus enigmaticus* ..... 25  
A.2 Questions for international experts ..... 27  
A.3 Studied populations ..... 28



## 1. BACKGROUND AND OBJECTIVES

*Ficopomatus enigmaticus* Fauvel, 1923 is a sessile serpulid worm that is non-indigenous to New Zealand. It was first discovered in Whangārei Harbour, New Zealand in 1967 (Read & Gordon 1991) and is now established in Tāmaki estuary (Gulf Harbour), Whangārei Harbour, Ahuriri estuary and Clive River near Napier (Probert 1993; Cranfield et al. 1998; Hayward & Morley 2005; Inglis et al. 2006a, 2006b; Kelly 2008; pers. comm. A. Madarasz-Smith). *Ficopomatus enigmaticus* is regarded as a pest species in several global regions and is infamous for its high rates of recruitment and fast-growing biogenic reefs (Cranfield et al. 1998; Bianchi & Morri 2001; Schwindt et al. 2004b; Dittmann et al. 2009). In Europe, *F. enigmaticus* is regarded as one of the 100 ‘worst’ marine non-indigenous species in terms of ecological and economic impacts (Streftaris & Zenetos 2006; CABI 2013). It is invasive in locations in Europe, Africa, North and South America, New Zealand and Japan (reviewed in Dittmann et al. 2009). *Ficopomatus enigmaticus* also occurs extensively in some Australian coastal locations; however, there is some debate regarding its status as a native versus non-indigenous species (Dittmann et al. 2009).

In recent years, Hawke’s Bay Regional Council (HBRC) have observed a steep increase in regional populations of *F. enigmaticus*. In particular, the development of substantial worm ‘reefs’ around some local waterbodies has raised concerns about the integrity of native ecosystems and civic infrastructure required for flood protection. HBRC has therefore engaged the Cawthron Institute (Cawthron) to provide advice on the feasibility of potential management interventions.

The objectives of this project were to:

1. develop a manual to guide HBRC in conducting recruitment monitoring of *F. enigmaticus* to ascertain its current distribution and reproductive seasonality.
2. undertake a review of global case study literature and communication with relevant international experts to capture current knowledge of *F. enigmaticus* ecology, regional seasonality, reproduction and recruitment, as well as the scale, timeframes and impacts of invasion or population explosion events, and the methods and outcomes of previous control attempts.

This report addresses item (ii) above and follows the delivery of item (i) in August 2022 (Wolf 2022).

## 2. OVERVIEW OF *FICOPOMATUS ENIGMATICUS*

### 2.1. Taxonomy and distribution

*Ficopomatus enigmaticus* is a species in the polychaete worm family Serpulidae Rafinesque, 1815. All species in this family are sessile and live in a mineral tube (Watabe 1990; Riedi 2012). *Ficopomatus enigmaticus* belongs to the sub-family Serpulinae Rafinesque, 1815, which can be differentiated from other sub-families of the serpulids by their reproductive biology (Kupriyanova et al. 2001, 2006; Kupriyanova 2003). Serpulins inhabit fresh, brackish and marine waters (Kupriyanova et al. 2009).

*Ficopomatus enigmaticus* was first observed in 1921 in the Caen Channel on the north-west coast of France, and it was initially described as the non-indigenous species *Mercierella enigmatica* by Fauvel, 1923 (Dixon 1977; Charles et al. 2018). Since its first description, the species has been recorded in nearly every continent in brackish temperate habitats (see Figure 1). *Ficopomatus enigmaticus* is an invasive species in areas in Europe, Africa, North and South America, New Zealand, Japan and, likely, Australia (Dittmann et al. 2009). Following the identification of morphological similarities, early Australian research suggested that the serpulid *Neopomatus uschakovi* Pillai, 1960 (occurring in northern Australia) was synonymous with *M. enigmatica* from south Australia (Straughan 1966). This led to the attribution of *N. uschakovi*'s ecological and reproductive characteristics to the northern *M. enigmatica* (Straughan 1972a, 1972b). However, within the same decade, a systematic review of brackish water polychaetes separated the two species and placed them into the genus *Ficopomatus* Southern, 1921 as *F. enigmaticus* and *F. ushakovi* (ten Hove & Weerdenburg 1978; Dittmann et al. 2009). Despite this separation, aspects of the reproductive biology of the two species of *Ficopomatus* are still confused, a 'hangover' of Straughan's earlier synonymisation (Dittmann et al. 2009; Bengert et al. 2010).

The genus *Ficopomatus* includes four additional brackish water species: *F. macrodon* Southern, 1921; *F. talehsapensis* Pillai, 2008; *F. shenzhensis* Li, Wang & Deng, 2012; and *F. miamiensis* Treadwell, 1934. *Ficopomatus ushakovi* and *F. miamiensis* are also invasive non-indigenous species in some tropical brackish water habitats, with potentially comparable impacts on local environments (Tovar-Hernández et al. 2009; Liñero-Arana & Díaz-Díaz 2012; Tovar-Hernández & Yáñez-Rivera 2012; Arteaga-Florez et al. 2014).

The type locality for *F. enigmaticus* is in France (the location of its first description), but the geographic origin of the species is unclear (Styan et al. 2017). Publications from the late 19th century suggested that *F. enigmaticus* may have originated from Australia (Dixon 1981; Bianchi & Morri 1996; Luppi & Bas 2002). More recent theories suggest that the genus *Ficopomatus* originated from the Indian subcontinent or

adjacent Indo-Pacific coastline, where *F. enigmaticus* and con-generic species are thought to be native or cryptogenic (of uncertain origin) (Fauvel 1932; Pollard & Hutchings 1990; Hewitt et al. 2004; Dittmann et al. 2009; Tovar-Hernández et al. 2009; Tovar-Hernández & Yáñez-Rivera 2012; Bastida-Zavala et al. 2017; Styan et al. 2017).



Figure 1. Global distribution of *Ficopomatus enigmaticus* as identified in this review. Red dots indicate records of population based on communications and literature.

## 2.2. Ecology

*Ficopomatus enigmaticus* populations occur in soft- and hard-substrate habitats associated with estuaries, lagoons and coastal embayments. Adult populations are generally found at salinities ranging from ~10 to ~30 psu (Dittmann et al. 2009). All Serpulinae are non-selective suspension feeders that remove food particles of a certain size range from the water column (Fauchald & Jumars 1979; Jumars et al. 2015). Adult individuals of *F. enigmaticus* (of ~5 g dry weight) remove ~0.2 g of organic material from the water per hour, primarily within a size range of 2–16 µm but including smaller and larger particles (Davies et al. 1989). This results in an estimated hourly clearance rate of 8 L/g of worm dry weight (Davies et al. 1989; Jumars et al. 2015).

*Ficopomatus enigmaticus* is considered an ecosystem engineer, whose reefs can provide a structurally complex habitat (Figure 2) in an otherwise muddy or sandy environment (Jones et al. 1994, 1997; Schwindt et al. 2001; Vanaverbeke et al. 2009). The dry mass of *F. enigmaticus* (worms only) can reach up to 10 kg/m<sup>3</sup>, whereas the hard structure of the reef (made of worm tubes) can average 500 kg/m<sup>3</sup> of which 80% is calcium carbonate (Bianchi & Morri 1996). A single cubic metre of *F. enigmaticus* reef can filter up to 80 L of water and remove up to 400 g of plankton per hour (Davies et al. 1989; Bianchi & Morri 1996; Jumars et al. 2015). Each year, each cubic metre of reef (at the Po River estuary, Italy) removes ~13 kg of calcium carbonate from the water column and secretes this as tube material for reef expansion (Bianchi & Morri 1996). The total reef mass in the Po River estuary increased by ~9 ha (from 15 to 200 ha) per year between 1979 and 2000 (Bianchi & Morri 1996, 2001). Studies in Argentina, Italy and Spain indicated that the shape of reefs, as well as the direction of their growth, is influenced by environmental factors such as salinity and currents (Fornós et al. 1997; Bianchi & Morri 2001; Schwindt et al. 2004a). For example, in areas with multidirectional currents, the reefs seem to be circular and flat and grow in all directions. In contrast, in areas of unidirectional water flow, reefs are bulkier and seem to attain a more linear shape (Fornós et al. 1997; Schwindt et al. 2004a). Variation in reef density across a lagoon is also likely to be related to salinity and other environmental factors (Schwindt et al. 2004b). As reefs increase in size and abundance, they can affect local hydrodynamics and water turbidity, and separate smaller reefs can amalgamate into bigger reefs (Schwindt et al. 2004b; Bengner et al. 2010). *Ficopomatus enigmaticus*' high filtration rate is also likely to make it an efficient resource competitor for native suspension feeders (Bruschetti et al. 2008, 2015; Konrad 2014; Sánchez et al. 2016; Galimany et al. 2017; Zwerschke et al. 2018; Montefalcone et al. 2022).



Figure 2 *Ficopomatus enigmaticus* reefs at the Mar Chiquita lagoon, Buenos Aires, Argentina at low tide. Source: Bruschetti (2019), figure 2, p. 5. Photo credit: MI Jaubet.

Individual worms of *F. enigmaticus* (Figure 3) usually attain lengths of 2–4.4 cm (ten Hove and Weerdenburg 1978; Shumka et al. 2014). However, worms found in a wetland on the Azores were up to 8 cm in length (Costa et al. 2019). Studies of other serpulins indicate that the tube grows up to four times the length of the adult worm (pers. obs. Wolf). Tube growth is dependent on various factors, including population density and competition. At high densities, many sessile invertebrates grow longer shells or tubes to maximise access to resources, leading to the formation of ‘hummocks’ in which individuals at the centre of the aggregation have longer tubes (Straughan 1968; Menge 1976; Bertness et al. 1998; Schwindt et al. 2001). *Ficopomatus enigmaticus* populations may also be affected by ambient pollution levels. Research from Australia showed that the presence of copper (a common heavy metal pollutant in urbanised coastal environments) can suppress sensitive species, which provides a competitive advantage to more tolerant species, including *F. enigmaticus* (Johnston & Keough 2003).

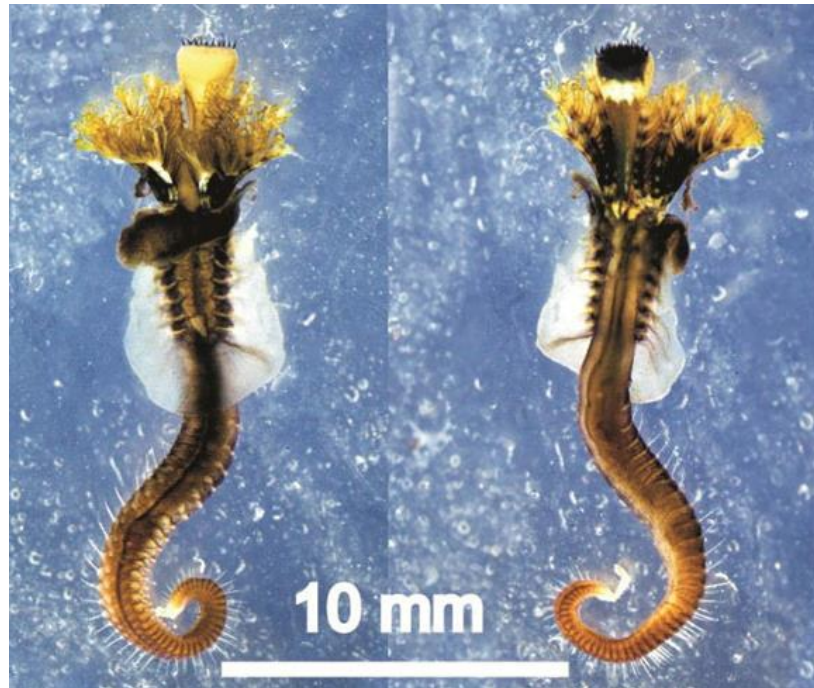


Figure 3 *Ficopomatus enigmaticus* individual removed from its tube; seen from dorsal (left) and ventral (right); found in a stromatolite pool on the south coast of South Africa. Source: Miranda et al. (2016), figure 2b & 2c, p. 260. Photo credit: NAF Miranda.

The holistic communal impacts of *F. enigmaticus* are yet to be fully examined (Brundu & Magni 2021). Some studies have reported that reefs of *F. enigmaticus* can affect the composition of native biota; other research has documented that *F. enigmaticus* reefs support other non-indigenous species (Schwindt et al. 2001; Heiman et al. 2008; Bazterrica et al. 2011; Despalatović et al. 2013). Several studies concluded that local sedimentation rates double as a result of the development of *F. enigmaticus* reefs (Fornós et al. 1997; Katsanevakis et al. 2014; Shumka et al. 2014), which may affect nutrient availability and oxygen levels near and within the benthos (Burfeind et al. 2013). Non-indigenous species can also enhance the transmission of parasites and viruses by either functioning as a vector or facilitating accumulation of vector species (Dinamani 1986; Huchette et al. 2006; Callaway et al. 2012; Etchegoin et al. 2012; Brenner et al. 2014; Pernet et al. 2016; Hernroth & Baden 2018; Costello et al. 2021).

### 2.3. Reproductive biology

To date, the reproductive biology of only a small number of the Serpulinae (a subfamily of the Serpulidae) has been described (Giangrande 1997). Of the species examined, the majority are broadcast spawners (Kupriyanova et al. 2001). Broadcast spawners release their gametes into the water (Figure 4), where sperm cells fertilise the egg cells. The release of gametes is synchronised, and although it is thought to be regulated via external factors such as temperature, moon phase and water

movement, the relative importance of these factors is not understood (Kupriyanova et al. 2001; Counihan et al. 2001; Onitsuka et al. 2007).

It has been suggested that individuals of *F. enigmaticus* are protandric hermaphrodites (a form of sequential hermaphroditism). Protandric hermaphroditism – where an individual is initially male but becomes female during its lifetime – is thought to be common in serpulins (Ghiselin 1969, 1974; Hoagland 1984; Kupriyanova et al. 2001; Cotter et al. 2003). However, some authors have suggested that *F. enigmaticus* may instead display alternating sexuality (a secondary form of sequential hermaphroditism), similar to some species of bivalve (Ghiselin 1974; Strathmann 1978; Runham 1992; Giangrande et al. 1994; Rouse & Fitzhugh 1994; Bhaud et al. 1995; Premoli & Sella 1995; Ghazala & Muzammil 2002; Wolf 2020). In this form of hermaphroditism, individuals can change their sex in response to population structure or energy levels (Coe 1932a; Heller 1993; Sella and Ramella, 1999; Juchault 2002; Prevedelli et al. 2006). Thus, this form of hermaphroditism could enhance overall reproductive output and allow for elevated dispersal and recruitment through the occurrence of multiple spawning events per season (Wolf 2020).



Figure 4 *Galeolaria gemino*a Halt, Kupriyanova, Cooper & Rouse, 2009; removed from its tube and releasing oocytes. Source: Olito et al. (2017), p. 17. Photo credit: L McLeod (Marshall lab, Monash University).



### 2.3.1. Reproduction

The timing and environmental conditions associated with the reproduction of *F. enigmaticus* are not fully understood. The reproduction of this species in the UK is reported to occur once the water temperature exceeds 10 °C (Thorp 1994); however, *F. enigmaticus* in Italy appear to reproduce only between 18 °C and 24 °C (Bianchi & Morri 1996). Notably, the reproductive season cannot be accurately deduced from observing recruitment (Manahan 1983, 1990; Havenhand & Svane 1991; Boidron-Métairon 1995; Havenhand 1995; Grubert & Ritar 2004a). For example, reproduction and gamete release in marine polychaetes can occur at temperatures in which larvae are less likely to survive (Costlow & Bookhout 1971; Hoegh-Guldberg & Pearse 1995; Peria & Pernet 2019).<sup>1</sup> Along the coastline of California, USA, *F. enigmaticus* appears to reproduce throughout the year, as recruitment is being observed at the full seasonal range of water temperatures between 13 °C and 22 °C (pers. comm. B. Pernet). *Ficopomatus enigmaticus* populations in the Po River estuary, Italy have two spawning periods, resulting in recruitment from May to July (water temperature increases between spring and early summer) and again during September (water temperature decreases in autumn) (Bianchi & Morri 1996). The existence of two spawning periods has also been reported in Argentina, but this observation was based on a very different approach – the examination of gametogenesis. The first developing oocytes within adult worms were observed during August and September (late winter to early spring), resulting in spawning around November (late spring). Oocyte development was again observed in January, with worms reaching sexual maturity around April (autumn) (Obenat & Pezzani 1994; Obenat et al. 2006). The possibility of multiple spawning periods has been also reported for other serpulid species (Zuraw & Leone 1968; O'Donnell 1986). The combination of alternating sexuality and multiple spawning periods could provide potential benefits to worm population growth: individuals that released oocytes during the first event could spawn the energetically cheaper spermatocytes during the second event, and vice versa (Coe 1932a, 1932b, 1934; Hoagland 1984; Runham 1992; Premoli & Sella 1995).

Research from the UK suggested that female individuals (younger than 1 year) produce  $1.5 \times 10^3$  oocytes per reproductive season (Gabilondo et al. 2013). An earlier study (reviewed in Kupriyanova et al. 2001) estimated the fecundity of a female *F. enigmaticus* to be between  $1 \times 10^3$  and  $1 \times 10^4$  oocytes, but the age of these individuals was not clear. Females of a similar sized worm endemic to New Zealand – *Spirobranchus cariniferus* Gray, 1843 – can produce up to  $2.3 \times 10^5$  oocytes, which are up to one-third larger in size than the oocytes of *F. enigmaticus* (Kupriyanova et

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<sup>1</sup> To avoid confounding reproduction with recruitment, the use of the reproductive biological zero point (rBZP – the temperature above which an organism invests energy into the production of gametes) is a suitable alternative. Once the rBZP is known, the estimated accumulative temperature (EAT) can be calculated as the sum of the average daily degrees above the rBZP until an individual is mature. If rBZP and EAT are known, the expected time to maturation can be estimated provided that sufficient food is available (Shoukry & Hafez 1979; Bulter et al. 1989; Ritar & Elliott 2004; Grubert & Ritar 2004b, 2005; Grubert 2005; Viana 2005; Leighton 2008; McCormick et al. 2016; Wolf & Ruawai 2020).

al. 2001; Obenat et al. 2006; Wolf 2020). Older individuals of *F. enigmaticus* may therefore produce substantially more oocytes than what has previously been reported.

### 2.3.2. Development

The larval development of *F. enigmaticus* is not fully understood, and the information presented is based on the generic larval development of the sub-family Serpulinae. One to two days following fertilisation of the female gametes, the trochophore larvae 'hatch' (Figure 5a) and swim near the water surface, exhibiting positive phototaxis (Dixon 1981; Fernald et al. 1987; Marsden 1988; Gabilondo et al. 2013). Within four days, these larvae grow into a metatrochophora (Figure 5b), which enables the shift from a pelagic to a benthic life (Fernald et al. 1987; Gabilondo et al. 2013). The benthic larvae explore the substrate for suitable settlement sites and the individuals then attach to the substrate. Generally, this occurs 5–10 days after hatching (see following section). During attachment, larvae form their primary and (later) secondary tubes and then metamorphose from larvae to juveniles of *F. enigmaticus* (Figure 5c).

Based on observations from Nigeria, recruits of *F. enigmaticus* can reach maturity within four weeks (Hill 1967), which is consistent with observations of other serpulins (Qui & Qian 1998; Kupriyanova 2001). However, given the tropical climate of Nigeria, there are doubts whether the *Ficopomatus* species examined by Hill (1967) were indeed *F. enigmaticus* or whether they belonged to the *F. cf. ushakovi* species complex that is known from global areas with warmer sea temperatures (Dittman 2009; pers comm. E. Kupriyanova). Similar to larval development, maturation is dependant on external factors such as temperature, salinity and food (Gee 1967; Leone 1970; Qiu & Qian 1998; Kupriyanova et al. 2001).

### 2.3.3. Larval dispersal

Pelagic larvae of marine invertebrates often have cilia (Figure 5a & b) that enable the larvae to undertake restricted movements within the water column to avoid predation, reach food sources, achieve dispersal and find settlement substrates (Mileikovsky 1973; Boicourt 1982; Shanks 1983; Hannan 1984; Banse 1986; Cronin & Forward 1986; Marsden 1994). Orientation can be achieved using phototactic and geotactic senses (Bayne 1964; Marsden 1988). The planktotrophic larvae of serpulins are thought to be able to extend their pelagic period and potential distance via movements within the water column (reviewed by Kupriyanova et al. 2001; Toonen & Pawlik 2001; Wolf 2020). The larvae of *F. enigmaticus* can potentially remain pelagic for up to three months (Dixon 1981).

### 2.3.4. Settlement, recruitment and maturation

Recruitment of *F. enigmaticus* generally occurs between zero and four metres depth (Thorpe 1994; Fornós et al. 1997; Weitzel 2021). The lower vertical recruitment limit is often defined by the presence of suitable settlement substrates, competitors,

predators and overall depth (Stephenson & Stephenson 1949; Paine 1974; Weitzel 2021), whereas the upper limit is usually determined by abiotic factors such as UV radiation, air exposure or tidal movement (Connell 1961; Moyle & Knight-Jones 1965; Bayne et al. 1988; Raimondi 1988a, 1988b; Bertness et al. 1999; Shafer et al. 2007). Most serpulins recruit to substrates covered in biofilms. Since biofilms are affected by UV radiation (Hung et al. 2005), recruitment to higher tidal levels generally occurs in shaded places (O'Donnell 1986; Wolf 2020). Both *F. enigmaticus* and *F. ushakovi* have been observed to settle up to 1 metre above the vertical limit of established adult populations (Thorp 1994), particularly after rainfall (Straughan 1972a). According to observations from California, USA and South Africa, recruitment appears limited in dry years relative to wetter years (pers. comm. B. Pernet & T. Robinson-Smythe).

Most serpulins – including *F. enigmaticus* – live in aggregations, but it is not understood how these aggregations are formed. Propagules of *F. enigmaticus* appear less substrate specific compared to recruits of other serpulins (Chapman et al. 2007; Wolf 2020). A wide range of materials, including glass bottles, concrete, mollusc and turtle shells, can act as nuclei for new aggregations that grow into larger reefs (Fornós et al. 1997; Schwindt & Iribarne 2000; Bengner et al. 2010). Studies of other serpulid species have reported that algal blades can act as nuclei for new reefs (Riedi 2012). Where *F. enigmaticus* settle on living shells, the subsequent development of reefs can cause the death of the base organism (Wahl 1996; Donovan et al. 2003; Dittmann et al. 2009; Bengner et al. 2010). Occasionally, fragile parts of a reef may break off and be carried downstream by tides and currents; they can then form a new reef some distance away (Thomas & Thorp 1994; Fornós et al. 1997; pers. comm. B. Pernet).



Figure 5 Larvae of *Spirobranchus cariniferus* 25 days after hatching; Figure a & b: metatrochophora larvae at different point of their development; Figure c: settled and attached larvae in its secondary tube developing to a juvenile individual; **ci**: cilia; **oc**: ocellus (eyes); **st**: secondary tube; Individuals in Figure a & c are stained with Nile blue; Scale bar: a: 50  $\mu\text{m}$ ; b & c: 100  $\mu\text{m}$ . Source: Wolf (2020).

### 3. RESEARCH ON INTRODUCED POPULATIONS OF *FICOPOMATUS ENIGMATICUS*

The introduction of *F. enigmaticus* to global coastal regions has likely occurred via ballast water transport, biofouling of submerged hull surfaces and potentially airborne transport by birds (Davidson et al. 2010; Patti & Gambi 2001; Costa et al. 2019; Giangrande et al. 2020). A comprehensive account of the global distribution of *F. enigmaticus* is provided in Dittmann et al. (2009), table 1, p. 13, which has been updated and included as Appendix A.1 of this report. In the sections below, we summarise available information<sup>2</sup> on *F. enigmaticus*' impacts on invaded locations, and the nature and outcomes of the management and control efforts undertaken.

#### 3.1. Europe

Since the first description of *F. enigmaticus* in the early 20th century, the majority of work on the reproductive biology and recruitment of this worm has been undertaken in the UK (Dixon 1977, 1981; Thomas & Thorp 1994). With regard to studies on the introduction, expansion and impacts of *F. enigmaticus*, the work by Bianchi & Morri (1996, 2001) is particularly significant. They recorded the worm's initial establishment in Italy's Po River estuary and subsequently documented the increase in local population (reef) size from 15 ha in 1979 to 200 ha in 2000, an average increase of 9 ha per year.

*Ficopomatus enigmaticus* is seen as a nuisance to tourism in Menorca, Spain, as its extensive reefs can cause injuries, degrade the aesthetics of beaches and double sedimentation rates (Fornós et al. 1997). Its excessive fouling aggregations and rapid growth also impact boat and marina operators in the UK (pers. comm. G. Watson). In areas of the eastern Adriatic Sea, *F. enigmaticus* reefs increase local sedimentation rates and support recruitment of the non-indigenous bivalve *Arcuatula senhousia* (Asian date mussel) Benson, 1842 (Figure 6) (Despalatović et al. 2013; Shumka et al. 2014), which is also a non-indigenous species to New Zealand (Hayward et al. 2008).

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<sup>2</sup> Obtained from the published literature and via recent dialogue with experts involved in *F. enigmaticus* research or management. See Appendix Table A.2: Questionnaire sent to international experts. These experts are identified in the Acknowledgements section.

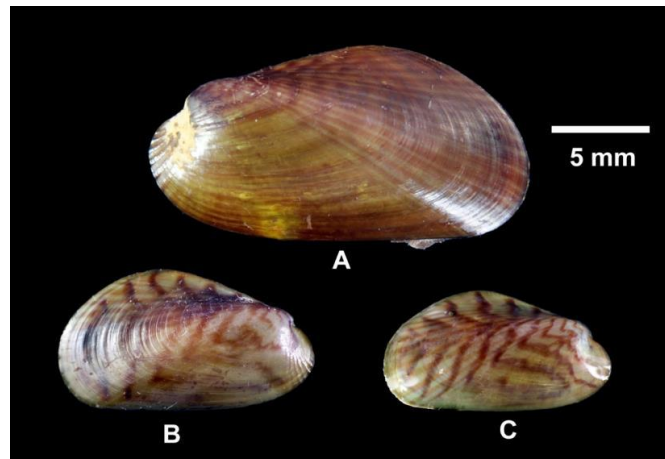


Figure 6 *Arcuatula senhousia* (Asian date mussel) found in Izmir Bay, Turkey. Source: Doğan et al. (2014).

Despite the extensive population growth and associated impacts of *F. enigmaticus* documented for the areas listed above, it appears that no substantial efforts have been made to control or eradicate *F. enigmaticus* in Europe. A case of attempted management was reported in a PhD thesis from the 1970s, in which chlorine was applied to a small population observed at a power station in Tilbury, UK (Dixon 1977). While daily application of the treatment was reported to have no effect on the worms, details regarding the treatment concentration and the conditions under which it was applied were sparse, precluding meaningful conclusions regarding potential efficacy of chlorine exposure. Notably, in some areas (e.g. the Black Sea and Italy), *F. enigmaticus* is considered potentially beneficial to the environment, as it can increase biodiversity (via the development of complex reef habitats) and filter organic pollutants from contaminated waterbodies (Bianchi & Morri 1996, 2001; Gubbay et al. 2016; Micu et al. 2016; pers. comm. A. Giangrande).

### 3.2. Africa

*Ficopomatus enigmaticus* was first identified in South Africa by J.H. Day in 1951 (pers. comm. T. Robinson-Smythe). Today, the species is found along the entire coastline of South Africa. As this distribution includes tropical as well as temperate waters, it may be that other species of the genus *Ficopomatus* also occur in South Africa but have been misidentified as *F. enigmaticus*. This may also be the case for *F. enigmaticus* populations reported from Lagos, Nigeria in 1953 (Hill 1967).

In South Africa, views on *F. enigmaticus* are somewhat controversial. In the Zandvlei estuary, its water filtering capacity is regarded as beneficial to the environment (Davies et al. 1989; pers. comm. T. Robinson-Smythe). However, more recent reports about the Zandvlei location and other South African estuaries describe the growing

worm populations as a nuisance to recreational activities such as canoeing and fishing (McQuaid & Griffiths 2014; pers. comm. T. Robinson-Smythe). To date, only the population at the Zandvlei estuary and adjacent marina have been monitored. In 2012, a total reef area of 6843 m<sup>2</sup> was reported (McQuaid & Griffiths 2014).

The only attempts at population control have been in Cape Town at the Zandvlei estuary. In 2015, recreational canoers used handheld spades to remove ~30 m<sup>2</sup> of *F. enigmaticus* aggregations. This was repeated after two years, presumably following recovery and regrowth of worms within the target area. A sustained decrease in population size and density was observed in the years following this removal attempt, but this may have been a consequence of sustained droughts in the region and associated changes to water levels and temperatures that occurred during the same period (pers. comm. T. Robinson-Smythe). Limited rainfall can cause an increase in temperature and salinity, the latter via a reduction in the supply of fresh water from rivers to estuaries. The topographic profile of the estuary affects the local population structure of *F. enigmaticus*. If the estuary is below sea level, the salinity will increase further upstream in the river through elevated saltwater influx. In such instances (see section 3.5 Australia), recruitment of *F. enigmatius* is likely to occur upstream of the parent populations. If an estuary is at sea level, populations of *F. enigmaticus* will likely proliferate in limited regions where salt and freshwater mix and the salinity is between 5 and 30 psu (see section 3.4 South America).

Interesting observations were made at Lake Tunis, Tunisia, an area where *F. enigmaticus* has been observed since the 1950s (Diawara et al. 2008). The northern lagoon near the city of Tunis was known as one of the most polluted and eutrophic waterbodies in the Mediterranean Sea. It was initially suggested that because of *F. enigmaticus*' large local population size and high filtration rate, the presence of the worms would further reduce oxygen levels and increase eutrophication (Keene 1980). However, recent attempts at restoration of this ecosystem via curbing pollution have achieved a significant reduction in eutrophication. Notably, this appeared to result in a concomitant decline (and in some areas disappearance) of *F. enigmaticus* populations, suggesting a possible connection between eutrophication and reef growth (Diawara et al. 2008). To date, there have been no deliberate attempts to control or eradicate *F. enigmaticus* in Tunisia.

### 3.3. North America

#### 3.3.1. Pacific Coast

*Ficopomatus enigmaticus* was first observed in North America in San Francisco Bay in the 1920s (Pernet et al. 2016; Yee et al. 2019). For around 70 years, it appeared to remain within this location before a new population was discovered in the late 1990s in the Elkhorn Slough marine reserve (Wasson et al. 2001). Since then,

*F. enigmaticus* has also been reported in other locations in California, including the port of Los Angeles (Cohen et al. 2000; Pernet et al. 2016) and estuaries in Santa Barbara (Yee et al. 2019). However, in the absence of targeted surveys, many observations were opportunistic and the species may have spread further than currently reported (Yee et al. 2019).

Research at the Elkhorn Slough marine reserve shows that in terms of space, *F. enigmaticus* outcompetes the native oyster *Ostrea conchaphila* Carpenter, 1857 (Figure 7). In addition, reefs of *F. enigmaticus* have also been shown to support up to three times more non-indigenous species than native oyster reefs (Heiman et al. 2008). The association between *F. enigmaticus* and other non-indigenous species has also been reported from other locations along the US Pacific coast (pers. comm. B. Pernet). Reefs of *F. enigmaticus* likely create complex habitats that enable the establishment of non-indigenous species that would not be able to colonise the original, pre-*Ficopomatus* soft-sediment environments (Heiman et al. 2008).



Figure 7 *Ficopomatus enigmaticus* aggregation on old wooden pillars in the Elkhorn Slough marine reserve, USA. Source: Noble & Zabin (2014); Photo credit: C Zablín (Smithsonian).

Recent genetic studies established the presence of two genotypes of *F. enigmaticus* along the Californian coastline (Yee et al. 2019). This could have two possible causes: first, one genotype may be more adapted to certain environmental conditions, resulting in geographic separation of the two genotypes without a separation in phenotypes or speciation (pers. comm. B. Pernet); second, *F. enigmaticus* was introduced to the US Pacific coast multiple times from different donor regions, which



increases the potential gene pool and therefore could stabilise the populations (Roman & Darling 2007). A population with a more diverse gene pool presents a larger challenge for mitigation and eradication, as it may have a higher tolerance to stressors. In addition, the risk of reintroduction following eradication may be elevated when there are multiple donor regions. To date, no efforts appear to have been made to manage or eliminate *F. enigmaticus* from areas along the US Pacific coast.

### 3.3.2. Atlantic Coast

*Ficopomatus enigmaticus* was first discovered on the US Atlantic coast in 1951 at Rockport, Texas. Further discoveries followed in Barnegat Bay, New Jersey in the 1980s (ten Hove & Weerdenburg 1978; Hoagland & Turner 1980); more recently, *F. enigmaticus* has been found in estuaries in Florida and South Carolina (Bastida-Zavala et al. 2017). Despite being widespread and attaining high levels of abundance in some of these locations, no formal research has been undertaken on its impacts on Atlantic coastal ecosystems (Bastida-Zavala et al. 2017), and there have been no reports of eradication or control attempts.

## 3.4. South America

*Ficopomatus enigmaticus* has established populations in coastal areas in southern Uruguay and northern Argentina (Orensanz et al. 2002; Muniz et al. 2005; Borthagaray et al. 2006; pers. comm. Schwindt). The species was first detected in the Quequén estuary, Argentina in the 1940s and has since increased in distribution and abundance. *Ficopomatus enigmaticus* is now observed in all estuaries along the Argentinian coastline (Orensanz et al. 2002; Obenat et al. 2006; pers. comm. Schwindt). In the 1960s, field studies described well-established populations in the Mar Chiquita lagoon, located at the northern end of the Argentinian coastline. Subsequently, this lagoon became the most studied area for *F. enigmaticus* incursion in South America. Unlike in the Po River estuary, Italy, where *F. enigmaticus* populations grow into elongated and large fringing reefs, *F. enigmaticus* reefs at the Mar Chiquita lagoon are more or less separate structures of up to 0.5 m in height and 7 m in diameter (Figure 8) (Orensanz et al. 2002; Schwindt et al. 2004b; Montefalcone et al. 2022). By 1999, reef density in the Mar Chiquita lagoon had reached an average of 89 reefs/ha (Figure 9), an increase of 18 reefs/ha since the 1970s. In some areas of the lagoon, up to 370 individual worm reefs can be found per hectare (Schwindt et al. 2004a, 2004b). Overall, 86.3% (3968 ha) of the area of Mar Chiquita lagoon is occupied by *F. enigmaticus* (Schwindt et al. 2001).

Because of multidirectional currents, the reef mass in the Mar Chiquita lagoon grows as a circular isolated reef rather than a linear reef (such as in Italy). Furthermore, the growth of the overall reef mass at this location is limited by the low occurrence of 'nuclei' (see above), such as mollusc shells, glass bottles, reef fragments and other

hard structures (Obenat & Pezzani 1994; Thomas & Thorp 1994; Schwindt & Iribarne 2000; Schwindt et al. 2001, 2004a; Luppi & Bas 2002; Peria & Pernet 2019).



Figure 8 *Ficopomatus enigmaticus* reefs at the Mar Chiquita lagoon, Argentina; hat used as reference has a height of 10 cm. Source: Schwindt & Iribane (2000), figure 1, p. 74. Photo credit: A Bortolus.



Figure 9 Aerial view of *Ficopomatus enigmaticus* reefs at the Mar Chiquita lagoon, Argentina. Each 'dot' is a reef. Source: Cohen (2011); Photo credit: A. Bortolus.

*Ficopomatus enigmaticus* reefs around Argentina are thought to have considerable environmental impacts. They function as large sediment traps and retain particles that would otherwise be transported into the ocean. Furthermore, the niches created by their complexity result in changes to the original assemblage composition of lagoon habitats and regional species distributions (Orensanz et al. 2002; Schwindt et al. 2001; Bazterrica et al. 2011; Bruschetti et al. 2011).

First attempts at manual removal of *F. enigmaticus* reefs from the Mar Chiquita lagoon were made about 30 years ago. Unfortunately, these attempts resulted in a net increase in reefs, as reef fragments created by the removal initiative were left behind and functioned as new reef nuclei. A second attempt was made 10 years later, when a 310 m 'path' was cleared through the lagoon's reef matrix by the local tourism industry and recreational fishermen. This path requires ongoing maintenance to prevent regrowth, which is associated with significant cost (pers. comm. Schwindt).

### 3.5. Australia

In Australia, *F. enigmaticus* was first observed at Sydney's Cooks River in 1910, but was not described until the 1950s (Dew 1959; Styan et al. 2017). However, recent assessments suggest that the species was actually introduced in the 1930s, likely from the coast of India (ten Hove & Weerdenburg 1978; Pollard & Hutchings 1990; Liñero-Arana & Díaz-Díaz 2012; Bastida-Zavala et al. 2017). Consequently, there is uncertainty regarding the timing of the arrival of *F. enigmaticus*. Based on recent studies, the current extension of *F. enigmaticus* appears to be limited to the south Australian coastline between Perth and Sydney. However, the current distribution of *F. enigmaticus* is based on the limited number of available records, rather than being informed by any geographical or environmental delimiters (Styan et al. 2017).

Adequate information is available for populations in the Lower Lakes, South Australia, for example, Lake Alexandrina and Coorong near Adelaide. Aerial imagery of the Mundoo Channel, Coorong has been used to describe the growth of *F. enigmaticus* reef structures since the 1970s. By 2003, reefs measuring up to 250 m<sup>2</sup> were present in the Mundoo Channel. While surveys in 2008 reported a decline in reef size, which was potentially caused by an elevated saltwater influx from the open coast (Dittmann et al. 2009; Bengner et al. 2010), most of the reefs observed in the Mundoo Channel in 1989 are still present. Notably, during a dry summer in 2007/2008, the water level in the Lower Lakes dropped below sea level. This led to increased seawater influx and elevated salinities and resulted in a 23 km upstream extension of *F. enigmaticus*' local recruitment range. By 2009, 288 ha of Lake Alexandrina (total area 58,000 ha) were covered by worm reefs (Dittmann et al. 2009). Subsequently, recruits of *F. enigmaticus* appeared up to 32.5 km upstream from the Golwa Barrage (a man-made land barrier). The total extent of *F. enigmaticus* populations around the Lower Lakes has been estimated as 6320 ha (Bengner et al. 2010).

As in Argentina, *F. enigmaticus* in the Lower Lakes of South Australia utilise mollusc, crab and turtle shells as nuclei for new reefs (Bengner et al. 2010). It is also suggested that turtle shells function as an additional distribution mechanism for this serpulid (Figure 10). Extensive colonisation of shells by worms resulted in the death of turtles, thus local efforts were made by the community to clean the shells of resident turtles (Bengner et al. 2010). Shells of the bivalve *Velesunio ambiguus* Phillippi, 1847 (billabong mussel, Figure 11) also seem to attract *F. enigmaticus* recruits, possibly making areas with high mussel densities particularly prone to extensive formations of worm reefs (Bengner et al. 2010; Dittmann et al. 2019).

In addition to California, at least two coexisting genotypes of *F. enigmaticus* have been identified in Australia (Styan et al. 2017). As identified in the North American populations, this could be the result of multiple introductions and may increase the tolerance of the overall population to stressors (Roman & Darling 2007).



Figure 10 *Ficopomatus enigmaticus* recruits on the shell of a turtle at the Lower Lakes, Australia. Source: Bengert et al. (2010), figure 3, p. 7; Photo credit: K. Bartley and B. Cowan.



Figure 11 *Ficopomatus enigmaticus* settled on a shell of *Vesunio ambiguus* at the Lower Lakes, Australia. Source: Bengert et al. (2010), figure 6, p. 9; Photo credit: S. Dittmann.

### 3.6. Summary of insights from global locations subject to *Ficopomatus enigmaticus* invasion

Based on our communication and correspondence with global experts and our review of the available literature, we conclude that most observations regarding the global, regional and local spread of *F. enigmaticus* are opportunistic and untargeted. As a consequence, the true distribution and rate of spread of this species is most likely underestimated. An additional challenge is that the worm's initial taxonomic misidentification resulted in a confused and unreliable understanding of its environmental requirements and ecology, particularly with regard to its reproductive biology and recruitment seasonality.

The environmental impacts of *F. enigmaticus* are understudied across the species' and genus' current range and remain largely inconclusive. In Europe, for example, where the majority of study efforts of *F. enigmaticus* have been concentrated, some populations are seen as beneficial, while others only 500 to 1000 km away are regarded as high-impact invaders. Geographically replicated ecological studies are therefore required to reliably identify and quantify the impacts and potential ecosystem services of *F. enigmaticus* in coastal ecosystems.

The lack of clarity regarding *F. enigmaticus*' impacts has likely contributed to the low number of attempts to manage local and regional populations. Most initiatives are not mentioned in the literature, but rather have been conveyed to us via personal communication with regional experts. Moreover, as these initiatives have primarily involved small-scale efforts by the public or local tourism operators, there is no robust information available regarding their scale (intensity and duration), cost or level of success.

### 3.7. Recommendations for HBRC

Despite the lack of published information on the population dynamics, impacts and attempted eradication or control of non-indigenous *F. enigmaticus* populations worldwide, our review presents several important conclusions.

First, from the information provided to us by HBRC and our site visits, it appears that the extent of *F. enigmaticus* infestations around the Hawke's Bay region is relatively small compared to invasive populations in other parts of the world. This is a significant advantage for the consideration and implementation of potential population control measures.

Second, the control attempts for global *F. enigmaticus* populations have generally been unsuccessful. However, these attempts seem to have been undertaken sporadically, at a relatively small scale and not in a sustained manner following a

medium- to long-term strategy. We consider that the lack of reported success overseas should not cause concern for the New Zealand context, and population control of *F. enigmaticus* in the Hawke's Bay region may be possible.

Third, there are a number of helpful findings from the previous control attempts and the information gathered and reported in this review can be used to inform potential management approaches for *F. enigmaticus* in the Hawke's Bay region. For example, control measures should not be undertaken when worms may release gametes or larvae, and control measures in soft-sediment environments need to ensure that no reef material / fragments are generated or, if unavoidable, left behind, as these can act as nuclei for the formation of new reefs. There are also indications (although not based on rigorous data) that variations in eutrophication and salinity levels may influence population dynamics of this species. The incorporation of these and other conclusions into HBRC's approach would strengthen the chances of successfully managing the *F. enigmaticus* populations in the Hawke's Bay region.

In conclusion, the information gathered during this review suggests that population control attempts in the Hawke's Bay region should not be ruled out. Instead, we recommend that HBRC's original strategy should be given primary importance, resulting in the following activities and outputs:

1. Recruitment monitoring for *F. enigmaticus*. A trial phase for method and protocol development was commenced by HBRC in December 2022.
2. Preparation of a feasibility assessment that examines optional approaches against a range of criteria and recommends methods and tactics for addressing invasive worm reefs around the Ahuriri estuary and Clive River (if this approach is undertaken by Council). This phase is already funded (via the MBIE EnviroLink scheme) and due on 31 March 2023.
3. A meeting with HBRC to discuss our recommendations (from item 2) and develop an agreed strategy for HBRC regarding *F. enigmaticus* population control.

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## 5. APPENDICES

Table A.1 Global distribution of *Ficopomatus enigmaticus* compiled by Dittman et al. (2009), table 1, p. 8, with updated references and distribution range (in blue letters) and further comments. References from original table can be found in Dittmann et al. (2009).

Continent	Country or region	Source	Comment	
Europe	Baltic Sea	Rasmussen 1958; Leppakoski & Olenin 2000	Within the last century and with the exception of Ireland, <i>Ficopomatus enigmaticus</i> was only able to establish aggregations in natural environments south of Swansea and Emsworth (UK) (Kilty and Guiry 1973; Thomas and Thorp 1994; Thorp 1994). Any established population north of this region was found warm water effluent of power stations or similar (ten Hove 1974; van der Velde et al. 1993). Only within the last two decades has <i>F. enigmaticus</i> become established in estuaries of the Baltic Sea as a result of temperature increases associated with climate change (Weitzel 2021).	
	Denmark	Wesenberg-Lund 1941; Rasmussen 1958; Hartmann- Schröder 1971; Jensen & Knudsen 2005		
	Germany	Hartmann-Schröder 1967, 1971; Kühl 1977		
	Netherlands	Wolff 1968, 1969; ten Hove 1974; Vaas 1975; Velde et al. 1993		
	Belgium	Leloup & Lefevere 1952		
	France	Fauvel 1923, 1933; Fischer 1925; Maury 1937; Bordet 1939; Remy 1948; Petit & Rullier 1952, 1956; Aleem 1952; Euzet & Poujol 1963; Rullier 1943, 1948, 1955b		
	England	Monro 1924; Tebble 1953, 1956; Naylor 1959; Markowski 1962; Gee 1963; Nelson-Smith 1967; Harris 1970; Dixon 1977, 1980, 1981; Thorp 1987, 1994; Thomas & Thorp 1994; Joyce et al. 2005; see Zibrowius & Thorp 1989 and Eno et al. 1997		
	Ireland	Kilty & Guiry 1973		
	Spain	Rioja 1923, 1924, 1931; Fischer-Piette 1951; Martinez-Taberner et al. 1993; Fornos et al. 1997		Research from the Balearic Islands suggests that <i>F. enigmaticus</i> reefs at least double the sedimentation rate (Fornós et al. 1997).
	Portugal	Freitas at al. 1994		
	Azores	Costa et al. 2019	First record in the Macaronesia region, possible introduction through migratory birds into Landlock saltmarsh.	
	Italy	Lindegg 1934; Cognetti 1954; Rullier 1955a; Sichel 1965; Granda & Sabelli 1973; Bianchi 1981, 1983a, 1983b; Bianchi et al. 1984, 1995; Aliani et al. 1995; Bianchi & Morri 1996, 2001; Ambrogi 2000; Bertozzi et al. 2002	Particularly in the Po River estuary (northern Italy), reefs of <i>F. enigmaticus</i> are seen as beneficial to the environment due to increases in oxygenation and biodiversity (Bianchi and Morri, 1996; Giangrande et al. 2020).	
	Albania	Shumka et al. 2014		
	Croatia	Despalatović et al. 2013	In Croatia, <i>F. enigmaticus</i> facilitate the recruitment of the invasive bivalve <i>Arcuatula senhousia</i> Benson, 1842 and increase sedimentation. However, <i>F. enigmaticus</i> populations are seen as favourable along Italy's northern Adriatic coastline; 500 km southwest in the Adriatic Sea, researchers described this species as problematic due to ecological and nuisance impacts in estuaries (Despalatović et al. 2013).	
	Greece	Bogdanos & Satsmadjis 1992		
	Turkey	Ergen 1976		
	Bulgaria (Black Sea)	Marinov 1960	Particularly in the Black Sea (including Romania), <i>F. enigmaticus</i> is seen as beneficial due to their ability to filter and withstand pollution while increasing habitat diversity and biodiversity. In 2016, biogenic reefs of <i>F. enigmaticus</i> were included in the European Red List of Habitats (Gubbay et al. 2016; Micu et al. 2016).	
	Russia (Black Sea)	Soldatova & Turpaeva 1960; Turpaeva 1961; Turpaeva et al. 1963; Shurova & Losovskaya 2003		
	Romania	Micu et al. 2016		
	Ukraine	Micu et al. 2016		
Georgia	Micu et al. 2016			
Caspian Sea	Bogoroditskiy 1963; Kasymov 1982			

Table A.1 continued: Global distribution of *Ficopomatus enigmaticus* compiled by Dittman et al. (2009), table 1, p. 8, with updated references and distribution range (in blue letters) and further comments. References from original table can be found in Dittmann et al. (2009).

Continent	Country or region	Source	Comment
Africa	Tunis	Seurat 1927; Heldt 1944; Vuillemin 1952, 1954, 1958, 1964; Zibrowius 1978; Keene 1980; Zaouali & Baeten 1983; Ben Charrada 1995; Diawara et al. 2008	Abundance of <i>F. enigmaticus</i> may be linked to the local influx of organic matter a reduction in water temperature (Diawara et al. 2008).
	Egypt	Kirkegaard 1959; Zibrowius 1973	
	West Africa	Samaan & Aleem 1972; Ghobashy & Ghobashy 2005	Similar to the initial recorded appearance of <i>F. enigmaticus</i> in Nigeria, there is also a possibility that the discovery of worms in West Africa may have been the congener <i>F. ushakovia</i> (Dittmann et al. 2009; Hill 1967).
	Côte d'Ivoire	Rullier 1955c	
	South Africa	Day 1951; Stewart & Davies 1986; Davies et al. 1989	The appearance of <i>F. enigmaticus</i> in South Africa is widely accepted; however, due to the wide distribution across different temperature zones, it is conceivable that more than one species of the genus <i>Ficopomatus</i> is present; however further examination is required. Contradicting views persist in South Africa regarding the impacts versus benefits of reefs formed by <i>Ficopomatus</i> spp.
Asia	Japan	Kajihara et al. 1976; Okamoto et al. 1995; Okamoto & Watanabe 1997; Nishi 2003; Iwasaki et al. 2004	The currently most accepted hypothesis is that the whole genus <i>Ficopomatus</i> has its origins in the Indo-Pacific (Fauvel 1932; Pollard & Hutchings 1990; Bastida-Zavala 2017). Hence, its distribution throughout Asia is likely under reported.
Australasia	Australia	Monro 1938b; Allen 1953; Dew 1959; Straughan 1966, 1971 1972a; Geddes & Butler 1984; Pollard & Hutchings 1990; Hewitt 2002; Johnston & Keough 2003; Hewitt et al. 2004	
	New Zealand	Read & Gordon 1991; Probert 1993; Forrest et al. 1997; Cranfield et al. 1998; Hayward & Morley 2005; Inglis et al. 2006a, 2006b; Kelly 2008	
North America	USA (Pacific Coast)	California: Smith & Carlton 1975; Morris et al. 1980; Cohen & Carlton 1995; Heiman 2006; Heiman et al. 2008; Pernet et al. 2016; Peria & Pernet 2019; Yee et al. 2019	
	USA (Atlantic Coast)	New Jersey: Hoagland & Turner 1980	
		Maryland: Ruiz et al. 2000; Jewett et al. 2005	
		Texas: Hartman 1952; ten Hove & Weerdenburg 1978	
		Florida: Bastida-Zavala et al. 2017	
South Carolina: Bastida-Zavala et al. 2017			
South America	Uruguay	Monro 1938a; Muniz et al. 2005a; Borthagaray et al. 2006	
	Argentina	Rioja 1943; Orensanz & Estivariz 1971; Schwindt 1997; Obenat & Pezzani 1989, 1994; Spivak et al. 1994; Schwindt & Iribarne 1998, 2000; Obenat 2001; Schwindt et al. 2001; Luppi & Bas 2002; Schwindt et al. 2004a, 2004b; Obenat et al. 2006; Bruschetti et al. 2008; Bazterrica et al. 2011; Bruschetti et al. 2011	

Table A.2 Questionnaire sent to international experts on *Ficopomatus enigmaticus* to help with preparation for discussions via video conferences. For our colleagues from Mexico, we used a questionnaire with the same questions but referring to *F. ushakovi* and *F. miamiensis*.

1.	Geographic area and first record of <i>F. enigmaticus</i> in this area: -
2.	Is <i>F. enigmaticus</i> perceived as a problem to this area?  If yes, how soon following its first record did it reach problem status?  What are the species' local/regional impacts on environment, infrastructure or other aspects?
3.	What is the current extent of the population?
4.	Did you examine the temperature and salinity range in which <i>F. enigmaticus</i> reproduces in your area (and if yes, what is it)?
5.	Did you examine recruitment of <i>F. enigmaticus</i> in your area? If yes, please provide some information on seasonality, substrates affected tidal height and other aspects.
6.	How far upstream (from the coast) did you encounter <i>F. enigmaticus</i> populations?
7.	Did you notice any effects of freshwater influx on <i>F. enigmaticus</i> population or recruitment?
8.	Did you notice any effects on <i>F. enigmaticus</i> populations by the occurrence of organic or inorganic pollution?
9.	Were there attempts to remove or otherwise treat <i>F. enigmaticus</i> populations/reefs in the area? If yes, which methods were used, when how frequently and for how long?  How effective would you say were these interventions, and what factors do you think contributed to the observed level of success (or lack of success)?
10.	Do you have any additional advice for anybody engaging in future control of <i>F. enigmaticus</i> populations?

Table A.3 Studied populations: list of countries and regions reviewed in this report, and information on population size and mitigation strategies (if any).

Country	First record	Biggest observed population at	Size of biggest observed population	Impacts	Control attempts
United Kingdom	London 1921	Millpond at Emsworth (West Sussex)	NA	Fouling on ship hulls, marina infrastructure, power stations.	1937: Small worm population discovered at Weymouth harbour in water body adjacent to freshwater lakes. Infested surfaces were treated with antifouling paint followed by increasing salinity in waterbodies between May and September to hinder larval development. Thereafter, the gradual return to freshwater appeared to kill the adult population.  1972: <i>Ficopomatus enigmaticus</i> was discovered on vertical walls at the Tilbury Power Station. For one year, the organisms were exposed daily to chlorine (0.5 ppm). This treatment did not seem to not affect the population (Dixon 1977, p. 65).
Spain	Spain 1923	Albufera at Menorca	NA	Fouling on ship hulls and pumps. Doubling sedimentation rates.	NA
Croatia	?	Neretva River Delta	NA	Supports recruitment of other non-native species such as <i>Arcuatula senhousia</i> . Increase in sedimentation.	NA
Italy	?	Po River Delta	200 ha (2000)	Increased oxygenation, increased biodiversity.	NA
South Africa	? 1951	Zandvlei estuary	0.6 ha (2014)	Prevents waterflow and recreational use. Improved water quality through filtration. Change in fauna and flora composition of the estuary.	2015 & 2017: manual removal of approx. 30 m <sup>2</sup> of reefs, but no persistent effect. Currently, population decline in Berg River, Milnerton Lagoon and Zandvlei is without explanation, but could potentially be caused by a long dry spell.
Tunisia	Tunis 1921	Lake of Tunis	NA	Increase sedimentation and eutrophication, removal of oxygen and nutrient leads to larger algae bloom.	Population significantly reduced in 2008 and was potentially caused by oligotrophic environment after environmental policy changes.

Table A.3 continued: Studied populations: list of countries and regions reviewed in this report, and information on population size and mitigation strategies (if any).

Country	First record	Biggest observed population at	Size of biggest observed population	Impacts	Control attempts
<b>Argentina</b>	Quequén estuary in 1943 (approx. 38°33'S 58°42'W)	Mar Chiquita lagoon (37°37'S 57°18'W)	~3900 ha	Affecting flora and fauna communities by providing substrate and shelter to certain species including predators, increased biodiversity, also more non-native species. Reefs function as sediment traps: negative effects on tourism, difficult for navigation and fishing.	Before 1980, reefs were broken apart during a control attempt. Fragments remained in the water body and founded new reefs. Since the 1990s, a path of around 310 m length is regularly cleared (by local industry) to allow recreational usage.
<b>USA</b>	San Fransico Bay 1920	NA	NA	Fouling on equipment. Facilitates the recruitment of other non-native species.	NA
<b>Australia</b>	Cooks River (Sydney), 1910	Lower Lakes (South Australia)	6320 ha	Fouling on shellfish, crabs and turtles, can potentially be fatal for host organism.	NA

## 6. REFERENCES

- Arteaga-Flórez C, Fernández-Rodríguez V, Londoño-Mesa MH 2014. First record of the polychaete *Ficopomatus uschakovi* (Pillai, 1960) (Annelida, Serpulidae) in the Colombian Caribbean, South America. *Zookeys* 371: 1–11.  
<https://doi.org/10.3897/zookeys.371.5588>
- Banse K 1986. Vertical distribution and horizontal transport of planktonic larvae of echinoderms and benthic polychaetes in an open coastal sea. *Bulletin of Marine Science* 39(2): 162–175.
- Bastida-Zavala JR 2008. Serpulids (Annelida: Polychaeta) from the Eastern Pacific, including a brief mention of Hawaiian serpulids. *Zootaxa* 1722: 1–61.
- Bastida-Zavala JR, McCann LD, Keppel E, Ruiz GM 2017. The fouling serpulids (Polychaeta: Serpulidae) from United States coastal waters: an overview. *European Journal of Taxonomy* 344: 1–76.  
<https://doi.org/10.5852/ejt.2017.344>
- Bayne BL 1964. The responses of the larvae of *Mytilus edulis* L. to light and to gravity. *Oikos* 15: 162–174.
- Bayne BL, Hawkins JS, Navarro E 1988. Feeding and digestion in suspension-feeding bivalve molluscs: the relevance of physiological compensations. *American Zoologist* 28(1): 147–159. <https://www.jstor.org/stable/3883226>
- Bazterrica MC, Botto F, Iribarne O 2011. Effects of an invasive reef-building polychaete on the biomass and composition of estuarine macroalgal assemblages. *Biological Invasions* 14: 765–777.  
<https://doi.org/10.1007/s10530-011-0115-7>
- Benger S, Dittmann S, Bolton T, Brown E, Taylor S, Cameron S 2010. Current tubeworm (*Ficopomatus enigmaticus*) and freshwater mussel (*Velesunio ambiguus*) distribution in the lower lakes and capabilities of tubeworm reproduction under changing environmental conditions. Final Report for SA Water. Flinders University of South Australia.
- Bertness MD, Gaines SD, Yeh SM 1998. Making mountains out of barnacles: the dynamics of acorn barnacle hummocking. *Ecology* 79: 1382–1394.  
[https://doi.org/10.1890/0012-9658\(1998\)079\[1382:MMOBT\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1998)079[1382:MMOBT]2.0.CO;2)
- Bertness MD, Leonard GH, Levine JM, Bruno JF 1999. Climate-driven interactions among rocky intertidal organisms caught between a rock and a hot place. *Oecologia* 120: 446–450. <https://doi.org/10.1007/s004420050877>
- Bhaud M, Duchêne J, Arago L, Cedex B 1995. Change from planktonic to benthic development: is life cycle evolution an adaptive answer to the constraints of dispersal? *Oceanologica Acta* 19: 335–346.

- Bianchi CN, Morri C 1996. *Ficopomatus* “reefs” in the Po River Delta (Northern Adriatic): their constructional dynamics, biology and influences on the brackish-water biota. *Marine Ecology* 17: 51–66.
- Bianchi CN, Morri C 2001. The battle is not to the strong: serpulid reefs in the Lagoon of Orbetello (Tuscany, Italy). *Estuarine, Coastal and Shelf Science* 53: 215–220. <https://doi.org/10.1006/ecss.2001.0793>
- Boicourt WC 1982. Estuarine larval retention mechanisms on two scales. In: Kennedy VS ed. *Estuarine comparisons*. New York: Academic Press. pp. 445–457.
- Boidron-Métairon IF 1995. Larval nutrition. In: McEdward L ed. *Ecology of marine invertebrates larvae*. Boca Raton, Florida: CRC Press. pp. 223–248.
- Borthagaray AI, Clemente JM, Boccardi L, Brugnoli E, Muniz P 2006. Impacto potencial de invasión de *Ficopomatus enigmaticus* (Fauvel) (Polychaeta: Serpulidae) en la Laguna de Rocha, Uruguay. *Pan-American Journal of Aquatic Sciences* 1: 57–65.
- Brenner M, Fraser D, Van Nieuwenhove K, O’Beirn F, Buck BH, Mazurie J, Thorarinsdottir G, Dolmer P, Sanchez-Mata A, Strand O, Flimlin G, Miossec L, Kamermans P 2014. Bivalve aquaculture transfers in Atlantic Europe. Part B: environmental impacts of transfer activities. *Ocean and Coastal Management* 89: 139–146.
- Brundu G, Magni P 2021. Context-dependent effect of serpulid reefs on the variability of soft-bottom macrobenthic assemblages in three Mediterranean lagoons (Sardinia, Italy). *Estuarine, Coastal and Shelf Science* 262: 107589. <https://doi.org/10.1016/j.ecss.2021.107589>
- Bruschetti M., 2019. Role of reef-building, ecosystem engineering polychaetes in shallow water ecosystems. *Diversity* 11(9): 168. <https://doi.org/10.3390/D11090168>
- Bruschetti M, Bazterrica C, Fanjul E, Luppi T, Iribarne O 2011. Effect of biodeposition of an invasive polychaete on organic matter content and productivity of the sediment in a coastal lagoon. *Journal of Sea Research* 66: 20–28. <https://doi.org/10.1016/j.seares.2011.04.007>
- Bruschetti M, Luppi T, Fanjul E, Rosenthal A, Iribarne O 2008. Grazing effect of the invasive reef-forming polychaete *Ficopomatus enigmaticus* (Fauvel) on phytoplankton biomass in a SW Atlantic coastal lagoon. *Journal of Experimental Marine Biology and Ecology* 354(2): 212–219. <https://doi.org/10.1016/j.jembe.2007.11.009>
- Bruschetti M, Luppi T, Iribarne O 2015. Effect of an invasive filter-feeder on the zooplankton assemblage in a coastal lagoon. *Journal of the Marine Biological Association of the United Kingdom* 96: 1201–1210. <https://doi.org/10.1017/S0025315415001320>

- Bulter RA, Chen H-C, Ebert EE, Hahn KO, Houk JL, McMullen JD, Tegner MJ, Thompson T, Yoo SK 1989. Handbook of culture of abalone and other marine gastropods. Boca Raton, Florida: CRC Press. 348 p.
- Burfeind DD, Pitt KA, Connolly RM, Byers JE 2013. Performance of non-native species within marine reserves. *Biological Invasions* 15: 17–28.  
<https://doi.org/10.1007/s10530-012-0265-2>
- CABI 2013. CABI compendium: invasive species. <http://www.cabi.org/isc/>
- Callaway R, Shinn AP, Grenfell SE, Bron JE, Burnell G, Cook EJ, Crumlish M, Culloty S, Davidson K, Ellis RP, Flynn KJ, Fox C, Green DM, Hays GC, Hughes AD, Johnston E, Lowe CD, Lupatsch I, Malham S, Mendzil AF, Nickell T, Pickerell T, Rowley AF, Stanley MS, Tocher DR, Turnbull JF, Webb G, Wootton E, Shields RJ 2012. Review of climate change impacts on marine aquaculture in the UK and Ireland. *Aquatic Conservation: Marine and Freshwater Ecosystems* 22: 389–421. <https://doi.org/10.1002/aqc.2247>
- Chapman ND, Moore CG, Harries DB, Lyndon AR 2007. Recruitment patterns of *Serpula vermicularis* L. (Polychaeta, Serpulidae) in Loch Creran, Scotland. *Estuarine, Coastal and Shelf Science* 73: 598–606.  
<https://doi.org/10.1016/j.ecss.2007.03.001>
- Charles M, Faillettaz R, Desroy N, Fournier J, Costil K 2018. Distribution, associated species and extent of biofouling “reefs” formed by the alien species *Ficopomatus enigmaticus* (Annelida, Polychaeta) in marinas. *Estuarine, Coastal and Shelf Science* 212: 164–175.  
<https://doi.org/10.1016/j.ecss.2018.07.007>
- Coe WR 1932a. Alternation of sexuality in oysters. *American Naturalist* 68: 236–251.  
<https://doi.org/10.1086/280542>
- Coe WR 1932b. Sexual phases in the American oyster (*Ostrea virginica*). *Biological Bulletin* 63(3): 419–441. <https://doi.org/10.2307/1537344>
- Coe WR 1934. Sexual rhythm in the pelecypod mollusk *Teredo*. *Science* 80: 192.  
<https://doi.org/10.1126/science.80.2069.192.a>
- Cohen AN 2011. Exotics guide: non-native marine species of the North American Pacific Coast. Richmond, California: Center for Research in Aquatic Bioinvasions; Oakland, California: San Francisco Estuary Institute. Revised September 2011. [https://www.exoticsguide.org/ficopomatus\\_enigmaticus](https://www.exoticsguide.org/ficopomatus_enigmaticus) (accessed 12 December 2022).
- Cohen AN, Harris LH, Bingham BL, Carlton JT, Chapman JW, Lambert CC, Lambert G, Ljubenkov JC, Murray SN, Rao LC, Reardon K, Schwindt E 2000. Project report for the Southern California Exotics Expedition 2000: a rapid assessment survey of exotic species in sheltered coastal waters. Oakland, California: San Francisco Estuary Institute. 23 p.



- Connell JH 1961. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthalamus stellatus*. *Ecology* 42(4): 710–723.
- Costa AC, Parente MI, de Frias Martins AM 2019. The arrival of the invasive tubeworm *Ficopomatus enigmaticus* (Fauvel, 1923) (Annelida: Serpulidae) to the Azores, possibly via migratory birds. *BioInvasions Records* 8(2): 242–251. <https://doi.org/10.3391/bir.2019.8.2.05>
- Costello KE, Lynch SA, O’Riordan RM, McAllen R, Culloty SC 2021. The importance of marine bivalves in invasive host-parasite introductions. *Frontiers in Marine Science* 8: 1–14. <https://doi.org/10.3389/fmars.2021.609248>
- Costlow JD, Bookhout CG 1971. The effect of cyclic temperature on larval development in the mud-crab *Rhithropanopeus harrisii*. In: Crisp DJ ed. Fourth European Marine Biology Symposium. London: Cambridge University Press. pp. 211–220.
- Cotter E, O’Riordan RM, Meyers AA 2003. A histological study of reproduction in the serpulids *Pomatoceros triqueter* and *Pomatoceros lamarckii* (Annelida: Polychaeta). *Marine Biology* 142: 905–914. <https://doi.org/10.1007/s00227-002-0987-2>
- Counihan RT, Mcnamara DC, Souter DC, Jebreen EJ, Preston NP, Johnson CR, Degan BM 2001. Pattern, synchrony and predictability of spawning of the tropical abalone *Haliotis asinina* from Heron Reef, Australia 213: 193–202. <https://www.jstor.org/stable/24864212>
- Cranfield HJ, Gordon DP, Willan RC, Marshall BA, Battershill CN, Francis MP, Nelson WA, Glasby CJ, Read GB 1998. Adventive marine species in New Zealand. Technical Report No. 34. Wellington, NZ: NIWA. 48 p.
- Cronin TW, Forward RBJ 1986. Vertical migration cycles of crab larvae and their role in larval dispersal. *Bulletin of Marine Science* 39(2): 192–201.
- Davidson IC, Zabin CJ, Chang AL, Brown CW, Sytsma MD, Ruiz GM 2010. Recreational boats as potential vectors of marine organisms at an invasion hotspot. *Aquatic Biology* 11: 179–191. <https://doi.org/10.3354/ab00302>
- Davies BR, Stuart V, de Villiers M 1989. The filtration activity of a serpulid polychaete population (*Ficopomatus enigmaticus* (Fauvel) and its effects on water quality in a coastal marina. *Estuarine, Coastal and Shelf Science* 29(6): 613–620. [https://doi.org/10.1016/0272-7714\(89\)90014-0](https://doi.org/10.1016/0272-7714(89)90014-0)
- Despalatović M, Cukrov M, Cvitković I, Cukrov N, Žuljević A 2013. Occurrence of non-indigenous invasive bivalve *Arcuatula senhousia* in aggregations of non-indigenous invasive polychaete *Ficopomatus enigmaticus* in Neretva river delta on the eastern Adriatic coast. *Acta Adriatica* 54(2): 213–220.
- Dew B 1959. Serpulidae (Polychaeta) from Australia. *Records of the Australian Museum* 25(2): 19–56. <https://doi.org/10.3853/j.0067-1975.25.1959.654>

- Diawara M, Zouari-Tlig S, Rabaoui L, Ben Hassine OK 2008. Impact of management on the diversity of macrobenthic communities in Tunis north lagoon: systematics. *Cahiers de Biologie Marine* 49(1) 1–16.
- Dinamani P 1986. Potential disease-causing organisms associated with mantle cavity of Pacific oyster *Crassostrea gigas* in northern New Zealand. *Diseases of Aquatic Organisms* 2: 55–63. <https://doi.org/10.3354/dao002055>
- Dittmann S, Rolston A, Benger SN, Kupriyanova EK 2009. Habitat requirements, distribution and colonisation of the tubeworm *Ficopomatus enigmaticus* in the Lower Lakes and Coorong. Report for the South Australian Murray-Darling Basin Natural Resources Management Board, Adelaide. 99 p.
- Dixon DR 1977. The energetics of the brackish water Serpulid polychaete *Mercierella enigmatica* (Fauvel). Unpublished PhD thesis, University of London, London.
- Dixon DR 1981. Reproductive biology of the serpulid *Ficopomatus (Mercierella) enigmaticus* in the Thames Estuary, SE England. *Journal of the Marine Biological Association of the United Kingdom* 61(3): 805–815. <https://doi.org/10.1017/S0025315400048220>
- Doğan A, Öztürk B, Bakır BB, Önen M 2014. Additions to the knowledge of the molluscs of the Aegean Sea with three species: *Crepidula fornicata* (Linnaeus, 1758), *Anadara polii* (Mayer, 1868) and *Arcuatula senhousia* (Benson in Cantor, 1842). *Turkish Journal of Fisheries and Aquatic Sciences* 14: 255–260.
- Donovan DA, Bingham BL, From M, Fleisch AE, Loomis ES 2003. Effects of barnacle encrustation on the swimming behaviour, energetics, morphometry, and drag coefficient of the scallop *Chlamys hastata*. *Journal of the Marine Biological Association of the United Kingdom* 83(4): 813–819. <https://doi.org/10.1017/S0025315403007847h>
- Etchegoin JA, Merlo MJ, Parietti M 2012. The role of the invasive polychaete *Ficopomatus enigmaticus* (Fauvel, 1923) (Serpulidae) as facilitator of parasite transmission in Mar Chiquita coastal lagoon (Buenos Aires, Argentina). *Parasitology* 139(11): 1506–1512. <https://doi.org/10.1017/S0031182012000820>
- Fauchald K, Jumars PA 1979. The diet of worms: a study of polychaete feeding guilds. *Oceanography and Marine Biology* 17: 193–284.
- Fauvel P 1932. Annelida Polychaeta of the Indian Museum, Calcutta. *Memoirs of the Indian Museum* 12: 1–262.
- Fernald RL, Hermans CO, Lacalli TC, Wilson WH, Woodin, SA 1987. Phylum Annelida, class Polychaeta. In: Strathman MF ed. *Reproduction and development of marine invertebrates of the northern Pacific Coast*. Seattle, Washington: University of Washington Press. pp. 138–195.
- Fornós JJ, Forteza V, Martínez-Taberner A 1997. Modern polychaete reefs in Western Mediterranean lagoons: *Ficopomatus enigmaticus* (Fauvel) in the

- Albufera of Menorca, Balearic Islands. *Palaeogeography, Palaeoclimatology, Palaeoecology* 128: 175–186. [https://doi.org/10.1016/S0031-0182\(96\)00045-4](https://doi.org/10.1016/S0031-0182(96)00045-4)
- Gabilondo R, Graham H, Caldwell GS, Clare AS 2013. Laboratory culture and evaluation of the tubeworm *Ficopomatus enigmaticus* for biofouling studies. *Biofouling* 29(7): 869–878. <https://doi.org/10.1080/08927014.2013.810214>
- Galimany E, Freeman CJ, Lunt J, Domingos A, Sacks P, Walters L 2017. Feeding competition between the native oyster *Crassostrea virginica* and the invasive mussel *Mytella charruana*. *Marine Ecology Progress Series* 564: 57–66. <https://doi.org/10.3354/meps11976>
- Gee JM 1967. Growth and breeding of *Spirobis rupestris* (Polychaeta: Serpulidae). *Journal of Zoology* 152: 235–244.
- Ghazala S, Muzammil A 2002. Gametogenic patterns of the larviparous oyster *Ostrea nomades* from Karachi, Pakistan (northern Arabian Sea). *Aquaculture Research* 33(13): 1049–1058. <https://doi.org/10.1046/j.1365-2109.2002.00769.x>
- Ghiselin MT 1969. The evolution of hermaphroditism among animals. *Quarterly Review of Biology* 44(2): 189–208. <https://doi.org/10.1086/406066>
- Ghiselin MT 1974. Love's labor divided, or, the union and separation of the sexes. In: Ghiselin MT ed. *The economy of nature and the evolution of sex*. Berkeley, Los Angeles: University of California Press. pp. 99–137.
- Giangrande A 1997. Polychaete reproductive patterns, life cycles and life histories: an overview. *Oceanography and Marine Biology* 35: 323–386.
- Giangrande A, Geraci S, Belmonte G 1994. Life cycle and life history diversity in marine invertebrates and the implication in community dynamics. *Oceanography and Marine Biology* 32: 305–333.
- Giangrande A, Pierri C, Del Pasqua M, Gravili C, Gambi MC, Gravina MF 2020. The Mediterranean in check: biological invasions in a changing sea. *Marine Ecology* 41(2): e12583. <https://doi.org/10.1111/maec.12583>.
- Grubert MA 2005. Factors influencing the reproductive development and early life history of blacklip (*Haliotis rubra*) and greenlip (*H. laevigata*) abalone. Unpublished PhD thesis, University of Tasmania, Launceston, Australia.
- Grubert MA, Ritar AJ 2004a. The effect of temperature on the embryonic and larval development of blacklip (*Haliotis rubra*) and greenlip (*H. laevigata*) abalone. *Invertebrate Reproduction & Development*. 45(3): 197–203. <https://doi.org/10.1080/07924259.2004.9652591>
- Grubert MA, Ritar AJ 2004b. Temperature effects on the dynamics of gonad and oocyte development in captive wild-caught blacklip (*Haliotis rubra*) and greenlip (*H. laevigata*) abalone. *Invertebrate Reproduction & Development* 45(3): 185–196. <https://doi.org/10.1080/07924259.2004.9652590>

- Grubert MA, Ritar AJ 2005. The effect of temperature and conditioning interval on the spawning success of wild-caught blacklip (*Haliotis rubra*, Leach 1814) and greenlip (*H. laevigata*, Donovan 1808) abalone. *Aquaculture Research* 36: 654–665. <https://doi.org/10.1111/j.1365-2109.2005.01269.x>
- Gubbay S, Sanders N, Haynes T, Janssen JAM, Airoidi L, Battelli C, Lipej L, Turk R, Dolenc-Orbanić N 2016. European red list of habitats: Part 1. Marine habitats. Luxembourg: Publications Office of the European Union. 46 p.
- Hannan CA 1984. Planktonic larvae may act like passive particles in turbulent near bottom flows. *Limnology and Oceanography* 29(5): 1108–1116. <https://doi.org/10.4319/lo.1984.29.5.1108>
- Havenhand JN 1995. Evolutionary ecology of larval types. In: McEdward L ed. *Ecology of marine invertebrate larvae*. Boca Raton, Florida: CRC Press. pp. 79–122.
- Havenhand JN, Svane I 1991. Roles of hydrodynamics and larval behaviour in determining spatial aggregation in the tunicate *Ciona intestinalis*. *Marine Ecology Progress Series* 68(3): 271–276.
- Hayward B, Morley MS 2005. Intertidal life of the Tamaki Estuary and its entrance. Technical Publication No. 373. Auckland, NZ: Auckland Regional Council. 71 p.
- Hayward BW, Grenfell HR, Sabaa AT, Morley MS 2008. Ecological impact of the introduction to New Zealand of Asian date mussels and cordgrass – the foraminiferal, ostracod and molluscan record. *Estuaries and Coasts* 31: 941–959. <https://doi.org/10.1007/s12237-008-9070-7>
- Heiman K, Vidargas N, Micheli F 2008. Non-native habitat as home for non-native species: comparison of communities associated with invasive tubeworm and native oyster reefs. *Aquatic Biology* 2: 47–56. <https://doi.org/10.3354/ab00034>
- Heller J 1993. Hermaphroditism in molluscs. *Biological Journal of the Linnean Society* 48(1): 19–42. <https://doi.org/10.1111/j.1095-8312.1993.tb00874.x>
- Hernroth BE, Baden SP 2018. Alteration of host-pathogen interactions in the wake of climate change – increasing risk for shellfish associated infections? *Environmental Research* 161: 425–438. <https://doi.org/10.1016/j.envres.2017.11.032>
- Hewitt CL, Campbell ML, Thresher RE, Martin RB, Boyd S, Cohen BF, Currie DR, Gomon MF, Keough MJ, Lewis JA, Lockett MM, Mays N, McArthur MA, O'Hara TD, Poore GCB, Ross DJ, Storey MJ, Watson JE, Wilson RS 2004. Introduced and cryptogenic species in Port Phillip Bay, Victoria, Australia. *Marine Biology* 144: 183–202. <https://doi.org/10.1007/s00227-003-1173-x>
- Hill M 1967. The life cycles and salinity tolerance of the serpulids *Mercierella enigmatica* Fauvel and *Hydroides uncinata* (Philippi) at Lagos, Nigeria. *Journal of Animal Ecology* 36(2): 303–321. <https://doi.org/10.2307/2914>

- Hoagland KE 1984. Use of the terms protandry, protogyny and hermaphroditism in malacology. *Americal Malacological Bulletin* 3: 85–88.
- Hoagland KE, Turner RD 1980. Range extensions of teredinids (shipworms) and polychaetes in the vicinity of a temperate-zone nuclear generating station. *Marine Biology* 58: 55–64.
- Hoegh-Guldberg O, Pearse JS 1995. Temperature, food availability, and the development of marine invertebrate larvae. *Americal Zoologist* 35(4): 415–425. <https://doi.org/10.1093/icb/35.4.415>
- Huchette S, Paillard C, Clavier J, Day R 2006. Shell disease: abnormal conchiolin deposit in the abalone *Haliotis tuberculata*. *Diseases of Aquatic Organisms* 68(3): 267–271. <https://doi.org/10.3354/dao068267>
- Hung O, Thiagarajan V, Wu R, Qian P 2005. Effect of ultraviolet radiation on biofilms and subsequent larval settlement of *Hydroides elegans*. *Marine Ecology Progress Series* 304: 155–166. <https://doi.org/10.3354/meps304155>
- Inglis G, Gust N, Fitridge I, Floerl O, Woods C, Hayden B, Fenwick G 2006a. Whangarei Harbour (Whangarei Port and Marsden Point): baseline survey for non-indigenous marine species (Research Project ZBS 2000/04). *Biosecurity New Zealand Technical Paper No. 2005/16*. Wellington, NZ: Ministry of Agriculture and Forestry. 68 p. plus appendices.
- Inglis G, Gust N, Fitridge I, Floerl O, Woods C, Hayden B, Fenwick G 2006b. Port of Auckland: baseline survey for non-indigenous marine species (Research Project ZBS 2000/04). *Biosecurity New Zealand Technical Paper No. 2005/08*. Wellington, NZ: Ministry of Agriculture and Forestry. 91 p.
- Johnston EL, Keough MJ 2003. Competition modifies the response of organisms to toxic disturbance. *Marine Ecology Progress Series* 251: 15–26. <https://doi.org/10.3354/meps251015>
- Jones CG, Lawton JH, Shachak M 1994. Organisms as ecosystem engineers. *Oikos* 69(3): 373. <https://doi.org/10.2307/3545850>
- Jones CG, Lawton JH, Shachak M 1997. Positive and negative effects of organisms as physical ecosystem engineers. *Ecology* 78(7): 1946–1957. [https://doi.org/10.1890/0012-9658\(1997\)078\[1946:PANEOO\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1997)078[1946:PANEOO]2.0.CO;2)
- Juchault P 2002. Hermaphroditism and gonochorism: a new hypothesis on the evolution of sexuality in crustacea. *Comptes Rendus l'Académie des Sciences. Series III: Sciences de la Vie* 322(5): 423–427. [https://doi.org/10.1016/s0764-4469\(99\)80078-x](https://doi.org/10.1016/s0764-4469(99)80078-x)
- Jumars PA, Dorgan KM, Lindsay SM 2015. Diet of worms emended: an update of polychaete feeding guilds. *Annual Review of Marine Science* 7: 497–520. <https://doi.org/10.1146/annurev-marine-010814-020007>

- Katsanevakis S, Wallentinus I, Zenetos A, Leppäkoski E, Çinar ME, Oztürk B, Grabowski M, Golani D, Cardoso AC 2014. Impacts of invasive alien marine species on ecosystem services and biodiversity: a pan-European review. *Aquatic Invasions* 9(4): 391–423. <https://doi.org/10.3391/ai.2014.9.4.01>
- Keene WCJ 1980. The importance of a reef-forming polychaete, *Mercierella enigmatica* Fauvel, in the oxygen and nutrient dynamics of a hypereutrophic subtropical lagoon. *Estuarine and Coastal Marine Science* 11(2): 167–178. [https://doi.org/10.1016/S0302-3524\(80\)80039-9](https://doi.org/10.1016/S0302-3524(80)80039-9)
- Kelly S 2008. Environmental condition and values of Mangere Inlet, Whau Estuary and Tamaki Estuary. Prepared by Coast and Catchment Ltd. Auckland Regional Council Technical Report No. 031. 130 p.
- Kilty GM, Guiry MD 1973. *Mercierella enigmatica* Fauvel (Polychaeta: Serpulidae) from Cork Harbour. *Irish Naturalists' Journal* 17(11): 379–381.
- Konrad CP 2014. Approaches for evaluating the effects of bivalve filter feeding on nutrient dynamics in Puget Sound, Washington. U.S. Geological Survey Scientific Investigations Report 2013-5237. 22 p.
- Kupriyanova EK 2003. Live history evolution in Serpulimorph polychaetes: a phylogenetic analysis. *Hydrobiologia* 496: 105–114. <https://doi.org/10.1023/A:1026128411461>
- Kupriyanova EK, Macdonald TA, Rouse GW 2006. Phylogenetic relationships within Serpulidae (Sabellida, Annelida) inferred from molecular and morphological data. *Zoologica Scripta* 35(5): 421–439. <https://doi.org/10.1111/j.1463-6409.2006.00244.x>
- Kupriyanova EK, Nishi E, ten Hove HA, Rzhavsky AV 2001. Life-history patterns in serpulimorph polychaetes: ecological and evolutionary perspectives. *Oceanography and Marine Biology* 39: 1–101.
- Kupriyanova EK, ten Hove HA, Sket B, Zakšek V, Trontelj P, Rouse GW 2009. Evolution of the unique freshwater cave-dwelling tube worm *Marifugia cavatica* (Annelida: Serpulidae). *Systematics and Biodiversity* 7(4): 389–401. <https://doi.org/10.1017/S1477200009990168>
- Leighton P 2008. Abalone hatchery manual: aquaculture explained. Abalone File No. 25. Irish Sea Fisheries Board. 88 p.
- Leone DE 1970. The maturation of *Hydroides dianthus*. *Biological Bulletin* 138(3): 306–315. <https://doi.org/10.2307/1540214>
- Liñero-Arana I, Díaz-Díaz Ó 2012. Presence of the exotic polychaete *Ficopomatus uschakovi* (Polychaeta: Serpulidae) in Venezuela: description and comments on its distribution. *Interciencia* 37: 234–237.
- Luppi TA, Bas CC 2002. The role of the invasive polychaete *Ficopomatus enigmaticus* Fauvel 1923 (Polychaeta: Serpulidae) reefs in the recruitment of *Cyrtograpsus*

- angulatus* Dana 1851 (Brachyura : Grapsidae) in the Mar Chiquita coastal lagoon, Argentina. *Ciencias Marinas* 28(4): 319–330.  
<https://doi.org/10.7773/cm.v28i4.242>
- Manahan DT 1983. The uptake and metabolism of dissolved amino acids by bivalve larvae. *Biological Bulletin* 164(2): 236–250. <https://doi.org/10.2307/1541142>.
- Manahan DT 1990. Adaptations by invertebrate larvae for nutrient acquisition from seawater. *Integrative & Comparative Biology* 30(1): 147–160.  
<https://doi.org/10.1093/icb/30.1.147>
- Marsden JR 1988. Light responses of the larva of the serpulid polychaete *Galeolaria caespitosa*. *Marine Biology* 99: 397–407. <https://doi.org/10.1007/BF02112133>
- Marsden JR 1994. Vertical movements and distribution of planktonic larvae of the serpulid polychaete *Spirobranchus polycerus* (Schmarda): effects of changes in hydrostatic pressure. *Journal of Experimental Marine Biology and Ecology* 176(1): 87–105.
- McCormick TB, Navas G, Buckley LM, Biggs C 2016. Effect of temperature, diet, light, and cultivation density on growth and survival of larval and juvenile white abalone *Haliotis sorenseni* (Bartsch, 1940). *Journal of Shellfish Research* 35(4): 981–992. <https://doi.org/10.2983/035.035.0421>
- McQuaid KA, Griffiths CL 2014. Alien reef-building polychaete drives long-term changes in invertebrate biomass and diversity in a small, urban estuary. *Estuarine, Coastal and Shelf Science* 138: 101–106.  
<https://doi.org/10.1016/j.ecss.2013.12.016>
- Menge BA 1976. Organization of the New England rocky intertidal community: role of predation, competition, and environmental heterogeneity. *Ecological Monographs* 46(4): 355–393. <https://doi.org/10.2307/1942563>
- Micu D, Beal S, Mihneva V, Yokes B 2016. A5.61a Biogenic reefs of *Ficopomatus enigmaticus* on sheltered upper infralittoral rock. European red list of habitats – Marine: Black Sea Habitat Group. 9 p.
- Mileikovsky SA 1973. Speed of active movement of pelagic larvae of marine bottom invertebrates and their ability to regulate their vertical position. *Marine Biology* 23: 11–17. <https://doi.org/10.1007/BF00394107>
- Miranda NAF, Kupriyanova EK, Rishworth GM, Peer N, Bornman TG, Bird MS, Perissinotto R 2016. An invasive polychaete species found in living marine stromatolites. *Aquatic Invasions* 11: 257–266.  
<https://doi.org/10.3391/ai.2016.11.3.04>
- Montefalcone M, Oprandi A, Azzola A, Morri C, Bianchi CN 2022. Serpulid reefs and their role in aquatic ecosystems: a global review. *Advances in Marine Biology* 92: 1–52. <https://doi.org/10.1016/bs.amb.2022.06.001>

- Moyse J, Knight-Jones EW 1965. Biology of cirripede larvae. In: Proceedings of the Symposium on Crustacea: held at Ernakulam from January 12 to 15, 1965. pp. 595–611.
- Muniz P, Clemente J, Brugnoli E 2005. Benthic invasive pests in Uruguay: a new problem or an old one recently perceived? *Marine Pollution Bulletin* 50(9): 1014–1018. <https://doi.org/10.1016/j.marpolbul.2005.06.049>
- Noble M, Zabin C 2014. From big ships to small boats – the secondary spread of introduced species. Edgewater, Maryland: Smithsonian Environmental Research Center. <https://serc.si.edu/research/laboratories/marine-invasions-research/feature-stories/big-ships-small-boats---secondary> (accessed 12 December 2022).
- O'Donnell M 1986. The ecology and early life history of the intertidal tubeworm *Galeolaria caespitosa*. Unpublished PhD thesis, University of Sydney, Sydney, Australia.
- Obenat SM, Pezzani SE 1994. Life cycle and population structure of the polychaete *Ficopomatus enigmaticus* (Serpulidae) in Mar Chiquita coastal lagoon, Argentina. *Estuaries Part B* 17(1): 263–270. <https://doi.org/10.2307/1352574>
- Obenat SM, Spivak E, Orensanz JM 2006. Reproductive biology of the invasive reef-forming serpulid, *Ficopomatus enigmaticus*, in the Mar Chiquita coastal lagoon, Argentina. *Invertebrate Reproduction and Development* 49(4): 263–271. <https://doi.org/10.1080/07924259.2006.9652216>
- Olito C, Marshall DJ, Connallon T 2017. The evolution of reproductive phenology in broadcast spawners and the maintenance of sexually antagonistic polymorphism. *American Naturalist* 189(2): 153–169. <https://doi.org/10.1086/690010>
- Onitsuka T, Kawamura T, Horii T, Takiguchi N, Takami H, Watanabe Y 2007. Synchronized spawning of abalone *Haliotis diversicolor* triggered by typhoon events in Sagami Bay, Japan. *Marine Ecology Progress Series* 351: 129–138. <https://doi.org/10.3354/meps07150>
- Orensanz JM, Schwindt E, Pastorino G, Bortolus A, Casas G, Darrigran G, Elías R, López Gappa JJ, Obenat S, Pascual M, Penchaszadeh P, Luz Piriz M, Scarabino F, Spivak ED, Vallarino EA 2002. No longer the pristine confines of the world ocean: a survey of exotic marine species in the Southwestern Atlantic. *Biological Invasions* 4: 115–143.
- Paine RT 1974. Intertidal community structure: experimental studies on the relationship between an dominant competitor and its principal predator. *Oecologia* 15: 93–120. <https://doi.org/10.1007/bf00345739>
- Patti FP, Gambi MC 2001. Phylogeography of the invasive polychaete *Sabella spallanzanii* (Sabellidae) based on the nucleotide sequence of internal



- transcribed spacer 2 (ITS2) of nuclear rDNA. *Marine Ecology Progress Series* 215: 169–177.
- Peria J, Pernet B 2019. Tolerance to salinity and thermal stress by larvae and adults of the serpulid annelid *Ficopomatus enigmaticus*. *Invertebrate Biology* 138(4): e12271. <https://doi.org/10.1111/ivb.12271>
- Pernet B, Barton M, Fitzhugh K, Harris LH, Lizárraga D, Ohl R, Whitcraft CR 2016. Establishment of the reef-forming tubeworm *Ficopomatus enigmaticus* (Fauvel, 1923) (Annelida: Serpulidae) in southern California. *BioInvasions Records* 5(1): 13–19. <https://doi.org/10.3391/bir.2016.5.1.03>
- Pernet F, Lupo C, Bacher C, Whittington RJ 2016. Infectious diseases in oyster aquaculture require a new integrated approach. *Philosophical Transactions of the Royal Society B: Biological Sciences* 371. 1–9. <https://doi.org/10.1098/rstb.2015.0213>
- Pollard DA, Hutchings PA 1990. A review of exotic marine organisms introduced to the Australian region. II. Invertebrates and algae. *Asian Fisheries Science* 3: 223–250.
- Premoli MC, Sella G 1995. Sex economy in benthic polychaetes. *Ethology, Ecology & Evolution* 7(1): 27–48. <https://doi.org/10.1080/08927014.1995.9522968>
- Prevedelli D, N'Siala GM, Simonini R 2006. Gonochorism vs. hermaphroditism: relationship between life history and fitness in three species of *Ophryotrocha* (Polychaeta: Dorvilleidae) with different forms of sexuality. *Journal of Animal Ecology* 75(1): 203–212. <https://doi.org/10.1111/j.1365-2656.2006.01040.x>
- Probert PK 1993. First record of the introduced fouling tubeworm *Ficopomatus enigmaticus* (Polychaeta: Serpulidae) in Hawke Bay, New Zealand. *New Zealand Journal of Zoology* 20(1): 35–36. <https://doi.org/10.1080/03014223.1993.10423240>
- Qiu J, Qian P 1998. Combined effects of salinity and temperature on juvenile survival, growth and maturation in the polychaete *Hydroides elegans*. *Marine Ecology Progress Series* 168: 127–134. <https://doi.org/10.3354/meps168127>
- Raimondi PT 1988a. Rock type affects settlement, recruitment, and zonation of the barnacle *Chthamalus anisopoma* Pilsbury. *Journal of Experimental Marine Biology and Ecology* 123(3): 253–267. [https://doi.org/10.1016/0022-0981\(88\)90046-9](https://doi.org/10.1016/0022-0981(88)90046-9)
- Raimondi PT 1988b. Settlement cues and determination of the vertical limit of an intertidal barnacle. *Ecology* 69(2): 400–407. <https://doi.org/10.2307/1940438>
- Read GB, Gordon DP 1991. Adventive occurrence of the fouling serpulid *Ficopomatus enigmaticus* (Polychaeta) in New Zealand. *New Zealand Journal of Marine and Freshwater Research* 25(3): 269–273.

- Riedi MA 2012. Carbonate production by two New Zealand serpulids. Unpublished MSc thesis, University of Otago, Dunedin, New Zealand.
- Ritar AJ, Elliott NG 2004. Abalone aquaculture subprogram: the commercial control of spawning in temperate abalone. Fisheries Research and Development Corporation Project No. 2000/204 Final Report. Hobart, Tasmania: Tasmanian Aquaculture and Fisheries Institute. 105 p.
- Roman J, Darling JA 2007. Paradox lost: genetic diversity and the success of aquatic invasions. *Trends in Ecology & Evolution* 22(9): 454–464.  
<https://doi.org/10.1016/j.tree.2007.07.002>
- Rouse G, Fitzhugh K 1994. Broadcasting fables: is external fertilization really primitive? Sex, size, and larvae in sabellid polychaetes. *Zoologica Scripta* 23(4): 271–312. <https://doi.org/10.1111/j.1463-6409.1994.tb00390.x>
- Runham NW 1992. Mollusca. In: Adiyodi KG, Adiyodi RG eds. Reproductive biology of invertebrates. Volume 5: sexual differentiation and behaviour. Chichester, UK: J Wiley & Sons.
- Sánchez MI, Paredes I, Lebouvier M, Green AJ 2016. Functional role of native and invasive filter-feeders, and the effect of parasites: learning from hypersaline ecosystems. *PLoS One* 11: 1–19.  
<https://doi.org/10.1371/journal.pone.0161478>
- Schwindt E, Bortolus A, Iribarne OO 2001. Invasion of a reef-builder polychaete: direct and indirect impacts on the native benthic community structure. *Biological Invasions* 3: 137–149. <https://doi.org/10.1023/A:1014571916818>
- Schwindt E, De Francesco CG, Iribarne OO 2004a. Individual and reef growth of the invasive reef-building polychaete *Ficopomatus enigmaticus* in a south-western Atlantic coastal lagoon. *Journal of the Marine Biological Association of the United Kingdom* 84(5): 987–993.  
<https://doi.org/10.1017/S0025315404010288h>
- Schwindt E, Iribarne OO 2000. Settlement sites, survival and effects on benthos of an introduced reef-building polychaete in a SW Atlantic coastal lagoon. *Bulletin of Marine Science* 67(1): 73–82.
- Schwindt E, Iribarne OO, Isla FI 2004b. Physical effects of an invading reef-building polychaete on an Argentinean estuarine environment. *Estuarine, Coastal and Shelf Science* 59(1): 109–120. <https://doi.org/10.1016/j.ecss.2003.06.004>.
- Sella G, Ramella L 1999. Sexual conflict and mating systems in the dorvilleid genus *Ophryotrocha* and the dinophilid genus *Dinophilus*. *Hydrobiologia* 402: 203–213. <https://doi.org/10.1023/A:1003748710921>
- Shafer DJ, Sherman TD, Wyllie-Echeverria S 2007. Do desiccation tolerances control the vertical distribution of intertidal seagrasses? *Aquatic Botany* 87(2): 161–166. <https://doi.org/10.1016/j.aquabot.2007.04.003>

- Shanks A 1983. Surface slicks associated with tidally forced internal waves may transport pelagic larvae of benthic invertebrates and fishes shoreward. *Marine Ecology Progress Series* 13: 311–315. <https://doi.org/10.3354/meps013311>
- Shoukry A, Hafez M 1979. Studies on the biology of the mediterranean fruit fly *Ceratitis capitata*. *Entomologia Experimentalis et Applicata* 26(1): 33–39. <https://doi.org/10.1111/j.1570-7458.1979.tb02894.x>
- Shumka S, Kashta L, Cake A 2014. Occurrence of the nonindigenous tubeworm *Ficopomatus enigmaticus* (Fauvel, 1923) (Polychaeta: Serpulidae) on the Albanian coast of the Adriatic Sea. *Turkish Journal of Zoology* 38: 519–521. <https://doi.org/10.3906/zoo-1303-14>
- Stephenson TA, Stephenson A 1949. The universal features of zonation between tide-marks on rocky coasts. *Journal of Ecology* 37(2): 289–305. <https://doi.org/10.2307/2256610>
- Strathmann RR 1978. The evolution and loss of feeding larval stages of marine invertebrates. *Evolution* 32(4): 894–906. <https://doi.org/10.2307/2407502>
- Straughan D 1966. Australian brackish water serpulids (Annelida: Polychaeta). *Records of the Australian Museum* 27(5): 139–146. <https://doi.org/10.3853/j.0067-1975.27.1966.440>
- Straughan D 1968. Ecological aspects of serpulid fouling. *Australian Natural History* 16(2): 59–64.
- Straughan D 1972a. The influence of seasonal rainfall and water temperature on the population of *Mercierella enigmatica* Fauvel (Annelida: Polychaeta) in the Ross River estuary, North Queensland. *Journal of Experimental Marine Biology and Ecology* 9(2): 165–172. [https://doi.org/10.1016/0022-0981\(72\)90045-7](https://doi.org/10.1016/0022-0981(72)90045-7)
- Straughan D 1972b. Ecological studies of *Mercierella enigmatica* Fauvel (Annelida: Polychaeta) in the Brisbane River. *Journal of Animal Ecology* 41(1): 93–136. <https://doi.org/10.2307/3508>
- Streftaris N, Zenetos A 2006. Alien marine species in the Mediterranean – the 100 'worst invasives' and their impact. *Mediterranean Marine Science* 7(1): 87–118. <https://doi.org/10.12681/mms.180>
- Styan CA, McCluskey CF, Sun Y, Kupriyanova EK 2017. Cryptic sympatric species across the Australian range of the global estuarine invader *Ficopomatus enigmaticus* (Fauvel, 1923) (Serpulidae, Annelida). *Aquatic Invasions* 12(1): 53–65. <https://doi.org/10.3391/ai.2017.12.1.06>
- ten Hove HA 1974. Notes on *Hydroides elegans* (Haswell, 1883) and *Mercierella enigmatica* Fauvel, 1923, alien serpulid polychaetes introduced into the Netherlands. *Bulletin Zoologisch Museum* 4(6): 45–51.
- ten Hove HA, Weerdenburg JCA 1978. A generic revision of the brackish-water serpulid *Ficopomatus* Southern 1921 (Polychaeta: Serpulinae), including

- Mercierella* Fauvel 1923, *Sphaeropomatus* Treadwell 1934, *Mercierellopsis* Rioja 1945 and *Neopomatus* Pillai 1960. *Biological Bulletin* 154(1): 96–120. <https://doi.org/10.2307/1540777>
- Thomas NS, Thorp CH 1994. Cyclical changes in the fauna associated with tube aggregates of *Ficopomatus enigmaticus* (Fauvel). In: Actes de la 4eme Conference Internationale des Polychetes. Memoires du Museum National d'Histoire Naturelle. pp. 575–584.
- Thorp CH 1994. Population variation in *Ficopomatus enigmaticus* (Fauvel) (Polychaeta, Serpulidae) in a brackish water millpond at Emsworth, Wes Sussex, UK. In: Actes de la 4eme Conference Internationale des Polychetes. Memoires du Museum National d'Histoire Naturelle. pp. 585–591.
- Toonen RJ, Pawlik JR 2001. Settlement of the gregarious tube worm *Hydroides dianthus* (Polychaeta: Serpulidae). II. Testing the desperate larva hypothesis. *Marine Ecology Progress Series* 224: 115–131. <https://doi.org/10.3354/meps224115>
- Tovar-Hernández MA, Méndez N, Villalobos-Guerrero TF 2009. Fouling polychaete worms from the southern Gulf of California: Sabellidae and Serpulidae. *Systematics and Biodiversity* 7(3): 319–336. <https://doi.org/10.1017/S1477200009990041>
- Tovar-Hernández MA, Yáñez-Rivera B 2012. Ficha técnica y análisis de riesgo de *Ficopomatus miamiensis* (Treadwell, 1934) (Polychaeta: Serpulidae). In: Low-Pfeng AM, Recagno EMP eds. *Invertebrados exóticos marinos en El Pacifico Mexicano*. Mexico: Geomare AC, Inesemarnat. pp. 193–212.
- van der Velde G, van der Gaag M, ten Hove HA 1993. De exotische trompetkalkkokerworm [*Ficopomatus enigmaticus* (Fauvel)], een nieuwe kolonisorator in het Noordzeekanaal. *Het Zeepaard* 53(3): 62–70.
- Vanaverbeke J, Braeckman U, Cuveliers E, Courtens W, Huyse T, Lacroix G, Larmuseau M, Maes G, Provoost P, Rabaut M, Remerie T, Savina M, Soetaert K, Stienen E, Verstraete H, Volckaert F, Vincx M 2009. Understanding benthic, pelagic and airborne ecosystem interactions in shallow coastal seas, "Westbanks". Science for a Sustainable Development Final Report. Brussels: Belgian Science Policy Office. 82 p.
- Viana MT 2005. Abalone culture. In: *American Fisheries Society Symposium* 46. Bethesda, Maryland: American Fisheries Society. pp. 1–24.
- Wahl M 1996. Fouled snails in flow: potential of epibionts on *Littorina littorea* to increase drag and reduce snail growth rates. *Marine Ecology Progress Series* 138: 157–168. <https://doi.org/10.3354/meps138157>
- Wasson K, Zabin CJ, Bedinger L, Diaz MC, Pearse JS 2001. Biological invasions of estuaries without international shipping: the importance of intraregional

- transport. *Biological Conservation* 102(2): 143–153.  
[https://doi.org/10.1016/S0006-3207\(01\)00098-2](https://doi.org/10.1016/S0006-3207(01)00098-2)
- Watabe N 1990. Calcium phosphate structures in invertebrates and protozoans. In: Carter JG ed. *Skeletal biomineralization: patterns, processes and evolutionary trends*. New York: Van Nostrand Reinhold. pp. 35–44.
- Weitzel B 2021. Ecology of the invasive species *Ficopomatus enigmaticus* (Fauvel, 1923) in an estuary of the southern Baltic Sea. Unpublished thesis, University of Rostock, Rostock, Germany.
- Wolf RP 2020. PhD. Recruitment, settlement and ontogeny of the serpulid *Spirobranchus cariniferus* (Gray, 1843). Unpublished PhD thesis, Victoria University of Wellington, Wellington, New Zealand.
- Wolf RP 2022. Manual to study the recruitment of *Ficopomatus enigmaticus* (Fauvel, 1923) at the Clive River, Ahuriri estuary and related water bodies. Prepared for Hawke's Bay Regional Council. Cawthron Report No. 3826. 15 p. plus appendices.
- Wolf RP, Ruawai J 2020. Brood stock managing report: Community-based Pāua Recover & Education Project. May 2020. [9] p.
- Yee A, Mackie J, Pernet B 2019. The distribution and unexpected genetic diversity of the non-indigenous annelid *Ficopomatus enigmaticus* in California. *Aquatic Invasions* 14(2): 250–266. <https://doi.org/10.3391/ai.2019.14.2.06>
- Zuraw EA, Leone DE 1968. Laboratory culture of the tubeworm, *Hydroides* (*Eupomatus*) *dianthus* Verril [sic] 1873. Groton, Connecticut: General Dynamics, Electrical Boat Division.
- Zwerschke N, van Rein H, Harrod C, Reddin C, Emmerson MC, Roberts D, O'Connor NE 2018. Competition between co-occurring invasive and native consumers switches between habitats. *Functional Ecology* 32(12): 2717–2729.  
<https://doi.org/10.1111/1365-2435.13211>