

The impact and control of biofouling in marine aquaculture: a review

Isla Fitridge^{a*}, Tim Dempster^{a,b}, Jana Guenther^b and Rocky de Nys^c

^a*Sustainable Aquaculture Laboratory – Temperate and Tropical (SALTT), Department of Zoology, University of Melbourne, 3010 Victoria, Australia;* ^b*Centre for Research-based Innovation in Aquaculture Technology (CREATE), SINTEF Fisheries and Aquaculture, 7465 Trondheim, Norway;* ^c*School of Marine and Tropical Biology, James Cook University, Townsville 4811, Australia*

(Received 3 April 2012; final version received 1 May 2012)

Biofouling in marine aquaculture is a specific problem where both the target culture species and/or infrastructure are exposed to a diverse array of fouling organisms, with significant production impacts. In shellfish aquaculture the key impact is the direct fouling of stock causing physical damage, mechanical interference, biological competition and environmental modification, while infrastructure is also impacted. In contrast, the key impact in finfish aquaculture is the fouling of infrastructure which restricts water exchange, increases disease risk and causes deformation of cages and structures. Consequently, the economic costs associated with biofouling control are substantial. Conservative estimates are consistently between 5–10% of production costs (equivalent to US\$ 1.5 to 3 billion yr⁻¹), illustrating the need for effective mitigation methods and technologies. The control of biofouling in aquaculture is achieved through the avoidance of natural recruitment, physical removal and the use of antifoulants. However, the continued rise and expansion of the aquaculture industry and the increasingly stringent legislation for biocides in food production necessitates the development of innovative antifouling strategies. These must meet environmental, societal, and economic benchmarks while effectively preventing the settlement and growth of resilient multi-species consortia of biofouling organisms.

Keywords: aquaculture; antifouling; fish; shellfish; fouling; net; sea-cage

Introduction

Aquaculture is a globally important industry providing essential food to a growing world population, with a critical role in the supply of protein to low income, food deficient countries. In 2009, aquaculture provided more than half of the fish consumed by humans, exceeding 55.7 million tonnes and a value of US\$ 105 billion (FAO 2010). Of the total economic value of aquaculture, marine shellfish and marine finfish represent over US\$ 31.4 billion (30%; FAO 2010) and these commercially cultivated species are either high value, or can be cultured intensively to ensure large biomass production. Commonly cultivated marine shellfish are oysters (*Crassostrea* spp., *Ostrea* spp.), mussels (*Mytilus* spp., *Perna* spp.) and scallops (*Placopecten* spp., *Chlamys* spp.), while the principal species reared in marine fish culture are salmonids (*Salmo salar*, *Oncorhynchus* spp.), mullets (*Mugil* spp., *Chanos chanos*), kingfish (*Seriola* spp.), tunas (*Thunnus* spp.), sea breams (*Sparus* spp., *Pagrus* spp.) and sea basses (*Dicentrarchus labrax*, *Lates* spp., *Lateolabrax japonicus*).

The production infrastructure for these species invariably consists of a complex assortment of

submerged components with cages, nets, floats and ropes. All of these structures serve as surfaces for biofouling. Shells in shellfish culture also provide an ideal and accessible biofouling surface. The presence of such large and varied surfaces provides for a broad diversity of epibiotic organisms to settle and grow. These marine algae and animals, collectively termed biofouling, are severely problematic to culture operations and can have significant economic impacts.

The direct economic costs of biofouling control to the aquaculture industry are substantial, with conservative estimates of 5–10% of production costs attributed to biofouling (Lane and Willemsen 2004). Globally, this equates to costs of US\$ 1.5 to 3 billion yr⁻¹. While the direct costs of biofouling control have been estimated for many aquaculture species (salmon: US\$ 0.03 and \$ 0.12 per kg of salmon produced; Olafsen 2006; scallops: 30% of final market price; Claereboudt et al. 1994; oysters: 20% of final market price; Enright 1993; Watson et al. 2009), the indirect effects of fouling on the production of cultured species remain largely unassessed. The production chain inefficiencies associated with biofouling are substantial,

*Corresponding author. Email: fitridge@unimelb.edu.au

Table 1. An overview of common fouling organisms in marine shellfish culture and their documented adverse impacts.

Fouling organism	Range of known impacts	Region	Shellfish species affected	Author(s)	
Chordata: Ascidiacea					
<i>Botryllus schlosseri</i>	Physical disruption to opening and closing of valves	Australia	<i>Mytilus edulis</i>	Takemura and Okutani (1955); Miyauti (1968); Alagarwami and Chellam (1976); Mohammad (1976); Dharmaraj et al. (1987); Chengxing (1990); Doroudi (1996); Carver et al. (2003); Coutts and Sinner (2004); Bourque et al. (2005); Guenther et al. (2006); Mallet and Carver (2006); Forrest et al. (2007); LeBlanc et al. (2007); Locke et al. (2007); Bonardelli (2008); Denny (2008); Ramsay et al. (2008); Daigle and Herbinger (2009); Gittenberger (2009); Rocha et al. (2009); Paetzold and Davidson (2010); Comeau et al. (2012)	
<i>Ciona intestinalis</i>		Brazil	<i>Perna canaliculus</i>		
<i>Dicarpa</i> sp.	Canada	<i>Perna perna</i>			
<i>Didemnum perlucidum</i>	Reduced size and/or condition	China	<i>Pinctada radiata</i>		
<i>Didemnum</i> sp.		Japan	(= <i>fucata</i>)		
<i>Didemnum vexillum</i>	Mortality	Netherlands	<i>Pinctada maxima</i>		
<i>Diplosoma</i> sp.	Competition for food	New Zealand	<i>Pinctada martensi</i>		
<i>Styela clava</i>		Norway	(= <i>fucata</i>)		
<i>Styela plicata</i>	Stock losses	Persian Gulf	<i>Pinctada fucata</i>		
Turbellaria: Polycladida					
<i>Imogine mcgrathi</i>	Mortality	Australia	<i>Crassostrea rhizophorae</i>	Littlewood and Marsbe (1990); Newman et al. (1993); Monteforte and Garcia-Gasca (1994); Pit and Southgate (2003)	
<i>Stylochus</i> sp.		Mexico	<i>Mytilus galloprovincialis</i>		
<i>Stylochus matatsai</i>			<i>Pinctada margaritifera</i>		
<i>Stylochus frontalis</i>			<i>Pinctada mazatlanica</i>		
Annelida: Polychaeta					
<i>Boccardia knoxi</i>	Blisters in nacreous layer	Arabian Gulf	<i>Haliotis</i> spp.	Crossland (1957); Mohammad (1972); Blake and Evans (1973); Alagarwami and Chellam (1976); Mohammad (1976); Dharmaraj and Chellam (1983); Velayudhan (1983); Dharmaraj et al. (1987); Arakawa (1990); Wada (1991); Doroudi (1996); Taylor et al. (1997); Campbell and Kelly (2002); Leonart et al. (2003)	
<i>Hydroides elegans</i>		Australia	<i>Mytilus edulis</i>		
<i>Polydora hoplura</i>	Weakened shell	Indian Ocean	<i>Pinctada fucata</i>		
<i>Polydora websteri</i>		Japan	<i>Pinctada margaritifera</i>		
<i>Polydora ciliata</i>	Mortality	Red Sea			
<i>Polydora vulgaris</i>		UK			
<i>Pomatoceros triquetter</i>		USA			
Algae					
<i>Cladophora</i> sp.	Shell erosion	Canada	<i>Mytilus edulis</i>		Mao Che et al. (1996); Garbary and Jess (2000); Naylor et al. (2001); Provan et al. (2005); Forrest and Blakemore (2006); Sharp et al. (2006); Wells et al. (2009)
<i>Codium fragile</i> spp. fragile	Lost stock	New Zealand	<i>Perna canaliculus</i>		
<i>Cyanobacteria</i>	Overgrowth		<i>Pinctada margaritifera</i>		
<i>Undaria pinnatifida</i>	Smothering				
Porifera					
<i>Callyspongia fibrosa</i>	Brittleness	Australia	<i>Chlamys islandica</i>	Korringa (1952); Crossland (1957); Evans (1969); Mohammad (1972); Alagarwami and Chellam (1976); Mohammad (1976); Thomas (1979); Dharmaraj and Chellam (1983); Velayudhan (1983); Dharmaraj et al. (1987); Pomponi and Meritt (1990); Barthel et al. (1994); Doroudi (1996); Mao Che et al. (1996); Wesche et al. (1997); Moase et al. (1999); Rosell et al. (1999); Fromont et al. (2005)	
<i>Cliona celata</i>		Hinge instability	French Polynesia		<i>Ostrea edulis</i>
<i>Cliona dissimilis</i>	Blister formation	Indian Ocean	<i>Pinctada fucata</i>		
<i>Cliona margaritiferae</i>		Shell damage	Persian Gulf		<i>Pinctada margaritifera</i>
<i>Cliona orientalis</i>	Shell deformity	Red Sea	<i>Pinctada margaritifera</i> var. <i>cumingii</i>		
<i>Cliona</i> sp.		Mortality			<i>Pinctada radiata</i>
<i>Cliona vastifica</i>					<i>Placopecten magellanicus</i>
<i>Pione velans</i>					
Mollusca: Bivalvia					
<i>Crassostrea</i> sp.	Physical disruption to opening and closing of valves	Australia	<i>Pinctada fucata</i>		Takemura and Okutani (1955); Crossland (1957); Alagarwami and Chellam (1976); Dharmaraj et al. (1987); Doroudi (1996); Taylor et al. (1997); Guenther et al. (2006)
<i>Lithophaga</i> sp.		India	<i>Pinctada margaritifera</i>		
<i>Martesia</i> sp.	Damage to shell	Indonesia	<i>Pinctada maxima</i>		
<i>Mytilus</i> sp.		Persian Gulf	<i>Pinctada radiata</i>		
<i>Pinctada</i> sp.	Recession of shell growth	Red Sea			
<i>Pinna</i> sp.					
<i>Pteria</i> sp.	Shell deformity				
<i>Saccostrea</i> sp.	Mortality				
	Competition for food and space				
Cnidaria: Hydrozoa					
<i>Amphisbetia bispinosa</i>	Smothering	Australia	<i>Adamussium colbecki</i>	Claereboudt et al. (1994); Cerrano et al. (2001); Heasman and de Zwart (2004); Getchis (2006); Guenther and de Nys	
<i>Ectopleura crocea</i>	Recession of shell growth	Canada	<i>Mizuhopecten yessoensis</i>		
<i>Ectopleura larynx</i>		Japan			

(continued)

Table 1. (Continued).

Fouling organism	Range of known impacts	Region	Shellfish species affected	Author(s)
<i>Eutima japonica</i> <i>Hydractinia angusta</i> <i>Obelia bidentata</i> <i>Tubularia</i> sp.	Devaluation Competition for food and space Stress Disruption to feeding Physical disruption to opening and closing of valves Facilitate settlement of other foulers Deter shellfish recruitment	New Zealand USA	<i>Mytilus edulis</i> <i>Mytilus galloprovincialis</i> <i>Perna canaliculus</i> <i>Placopecten magellanicus</i>	(2006); Baba et al. (2007); Fitridge (2011)
Arthropoda: Maxillopoda <i>Balanus amphitrite</i> <i>communis</i> <i>Balanus amphitrite variegates</i>	Physical disruption to opening and closing of valves Recession of shell growth Mortality	Arabian Gulf Australia India Indonesia Japan Persian Gulf	<i>Pinctada fucata</i> <i>Pinctada martensi</i> <i>Pinctada maxima</i> <i>Pinctada radiata</i>	Takemura and Okutani (1955); Miyauti (1968); Alagarswarmi and Chellam (1976); Mohammad (1976); Dharmaraj and Chellam (1983); Dharmaraj et al. (1987); Wada (1991); Doroudi (1996); Taylor et al. (1997); de Nys and Ison (2004)

and the overall impact and cost of biofouling in marine aquaculture is significantly underestimated.

To minimise these impacts, the aquaculture industry uses technologies and husbandry techniques to manage and control fouling communities. The composition of fouling communities and their effect in marine aquaculture is largely dictated by the properties of the fouling surface, and the protection and management of these surfaces is the key to biofouling control. In the shellfish industry the control of biofouling is centred around maintaining clean shells, as biofoulers have detrimental effects on the appearance and marketability and on the growth and condition of shellfish. While fouling organisms settle onto infrastructure such as ropes and floats causing breakages and costly repairs, their attachment to the surfaces of cultured shells is more problematic. In contrast, in the marine finfish industry cage nets and supporting infrastructure offer fouling organisms thousands of square meters of multifilament netting. The primary focus in fish culture therefore relates to the mitigation of net fouling, as this leads to compromised cage structure (Swift et al. 2006) and detrimental effects on fish health mainly through low flow-through of water, leading to poor dissolved oxygen availability. Consequently, the control of biofouling is a specific and complex problem within each industry sector, where the prevention and/or removal of fouling organisms requires the development of technologies and application methods to minimise the impacts on non-target organisms and the culture environment.

This review discusses the impact of biofouling on aquaculture species and operations across the entire

production chain, and critically assesses the effectiveness of methods currently in use, and in development, for the control of biofouling. The focus is specifically on marine shellfish and finfish as biofouling is ubiquitous and problematic in these production systems. As biofouling has fundamentally different effects in the shellfish and finfish production systems, these are separated throughout the review. Furthermore, rather than reporting a compendium of studies on marine biofouling, a comprehensive list of common fouling organisms and their impacts in aquaculture are provided in Table 1 for shellfish and in Table 2 for finfish.

Fouling communities in aquaculture

Biofouling on marine surfaces, including those provided by aquaculture structures and stationary stock, develops through a well known ecological process (reviewed in Maki and Mitchell 2002), whereby macrofouling derived from the spores and propagules of algae, and the larvae of invertebrates such as hydroids, ascidians, sponges, bryozoans, barnacles, bivalves and polychaetes, develops rapidly within days to weeks.

All biofouling communities vary temporally and spatially. Major temporal changes are driven by seasonality in marine invertebrate populations. The arrival of new recruits, periods of intense growth, or times of dormancy and regression, all impact on community development at different times of the year. Spatial variability in marine invertebrate

Table 2. An overview of common fouling organisms in marine finfish culture and their documented adverse impacts.

Fouling organism	Range of known impacts	Region	Fish species affected	Author(s)
Chordata: Ascidiacea <i>Asciidiella aspersa</i> <i>Botrylloides</i> sp. <i>Botryllus schlosseri</i> <i>Styela plicata</i> <i>Symplegma</i> sp. <i>Trididemnum</i> sp.	Cage deformation and structural fatigue Increased disease risk	Malaysia UK	<i>Epinephelus</i> sp. <i>Lates calcarifer</i> <i>Lutjanus</i> sp. <i>Salmo salar</i> <i>Siganus</i> sp.	Milne (1975b); Tan et al. (2002); Braithwaite et al. (2007)
Algae <i>Antithamnion</i> sp. <i>Ectocarpus</i> spp. <i>Enteromorpha</i> spp. Filamentous diatoms <i>Gracilaria</i> sp. <i>Ulva</i> spp.	Net occlusion Restriction of water exchange Poor water quality Limited oxygen availability Reduced waste metabolite removal Cage deformation and structural fatigue	Australia UK USA Malaysia	<i>Epinephelus</i> sp <i>Lates calcarifer</i> <i>Lutjanus</i> sp. <i>Oncorhynchus tshawytscha</i> <i>Salmo salar</i> <i>Siganus</i> sp. <i>Thunnus maccoyii</i>	Milne (1975a); Milne (1975b); Moring and Moring (1975); Hodson and Burke (1994); Cronin et al. (1999); Svane et al. (2006)
Mollusca: Bivalvia <i>Crassostrea</i> spp. <i>Electroma georgiana</i> <i>Modiolus</i> sp. <i>Mytilus edulis</i> <i>Perna viridis</i> <i>Pinctada</i> spp.	Net occlusion Cage deformation and structural fatigue	Australia Malaysia Singapore UK USA	<i>Epinephelus</i> sp <i>Lates calcarifer</i> <i>Lutjanus</i> sp. <i>Oncorhynchus tshawytscha</i> <i>Salmo salar</i> <i>Siganus</i> sp. <i>Thunnus maccoyii</i>	Milne (1975a); Milne (1975b); Moring and Moring (1975); Lee et al. (1985); Cronin et al. (1999); Braithwaite et al. (2007); Greene and Grizzle (2007)
Cnidaria:: Hydrozoa <i>Ectopleura larynx</i> <i>Obelia dichotoma</i> <i>Plumularia</i> sp. <i>Tubularia</i> sp.	Net occlusion Reduced water flow	Malaysia Norway USA	<i>Lates calcarifer</i> <i>Salmo salar</i>	Hodson et al. (2000); Guenther et al. (2009); Madin et al. (2009); Guenther et al. (2010); Carl et al. (2011); Guenther et al. (2011)

communities varies on both the small and large scale (Fraschetti et al. 2005) and between temperate and tropical waters. Variation is primarily driven by planktonic events, larval choices during attachment and settlement, and metamorphosis and mortality (Holloway and Keough 2002a, 2002b) that also correlate with differences in environmental conditions. For example, a diverse range of algae and marine invertebrates occur on fish cages in marine waters compared to the algal monocultures in brackish waters (Santhanam et al. 1983). In contrast, variation in biofouling within sites is predominantly driven by the availability of light and water flow and is often related to the depth and orientation of infrastructure (eg Cronin et al. 1999; Howes et al. 2007; Guenther et al. 2010). Fouling communities generally decrease in biomass and become less diverse in deeper waters (Cronin et al. 1999; Guenther et al. 2010).

Common fouling organisms in aquaculture settings

Although spatial and temporal differences exist in the overall composition and biomass of fouling communities, in general, a common suite of sessile, suspension-feeding organisms dominate. These include

diverse organisms including barnacles, bivalves, bryozoans, polychaetes, ascidians, hydroids, sponges and algae (Figure 1, Tables 1 and 2). A commonly occurring trait across most of these taxa is their 'invasiveness'. Many are cosmopolitan in their distribution, being frequently transferred around the globe by shipping, and possess an ability to survive and reproduce in a new location. An example of 'invasiveness' is the vase tunicate *Ciona intestinalis* (Figure 1a), now one of the most problematic fouling organisms in global mussel culture, particularly in north America (Edwards and Leung 2009). Although its native range is ambiguous due to its unresolved taxonomic status (Zhan et al. 2010), *C. intestinalis* has spread to aquaculture industries in temperate and tropical regions worldwide. It was first documented on the west coast of North America in the 1930s (Blum et al. 2007), and invaded the east coast of North America in 2004 (Ramsay et al. 2008). New populations have appeared over the past 50 years along the coastline of Australia, New Zealand, Asia, South Africa and South America (Therriault and Herborg 2008; Zhan et al. 2010). Given the ongoing change in global climate and factors that have facilitated the spread of *C. intestinalis* and other invasive biofouling



Figure 1. Common fouling organisms associated with aquaculture operations: (A) *Ciona intestinalis* (vase tunicate); (B) *Ectopleura crocea* (pink mouthed hydroid); (C) *Mytilus edulis* (blue mussel); (D) *Ectopleura larynx* (ringed tubularia).

organisms, there are compelling predictions for an increase in their spread (Stachowicz et al. 2002; Floerl et al. 2009; Sorte et al. 2010).

The impact of biofouling on aquaculture

While fouling community structure is spatially and temporally variable, the impact of fouling is, in nearly all cases, highly detrimental to aquaculture. Surprisingly, however, there are circumstances where biofouling is beneficial, or at least, does not affect production. For example, fouling can enhance shellfish growth (Dalby and Young 1993), increase primary production of phytoplankton and therefore food availability to shellfish (Lodeiros et al. 2002; Ross et al. 2002; Le Blanc et al. 2003), provide shellfish with protection against predation (Wahl et al. 1997; Manning and Lindquist 2003), facilitate the settlement of commercially farmed shellfish (Hickman and Sause 1984; Fitridge 2011) or mitigate disease risk (Paclibare et al. 1994). These examples, however, are the exception, and biofouling is primarily deleterious to the cost effective production of shellfish and fish.

Shellfish

The effects of biofouling of shell surfaces and equipment fall into five major categories: (1) physical damage by invasive organisms that bore into the shell (endoliths) or epibiotic calcareous organisms growing on the shell surface, affecting aesthetics; (2) mechanical interference of shell function due to colonisation of shells, particularly around the hinge and lip, affecting feeding ability and susceptibility to predators; (3) biological competition for resources such as food and space, affecting growth and condition; (4) environmental modification due to colonisation of culture infrastructure, leading to reduced water flow, waste build-up, decreased oxygen levels and reduced food availability. In addition, biodeposition and the spread of non-indigenous organisms can have deleterious effects on surrounding natural ecosystems; (5) increased weight from biofouling biomass on stock and equipment (eg panels, nets, ropes and floats), leading to greater production costs associated with extra maintenance requirements and loss of stock and equipment.

Physical damage

Physical shell damage occurs through the burrowing activities of endolithic organisms or from epibiotic calcareous tube dwelling polychaetes attached to the shell surface. Polychaete worms such as members of the genera *Polydora* and *Boccardia* penetrate and excavate shells, causing cavities, burrows, blisters and tunnels deep within the nacreous layer (Leonart et al. 2003; Silina 2006; Simon et al. 2006). The effects are very destructive (Kaehler 1999), with hinge instability, disruption of shell formation, fragility, brittleness and loss of thickness (Mao Che et al. 1996). The shell becomes substantially weakened and vulnerable to predators and parasites (Kaehler and McQuaid 1999; Stefaniak et al. 2005; Buschbaum et al. 2007; Thielges and Buschbaum 2007). An increased investment in energy expensive processes such as shell formation and regeneration ensues, causing reduced growth and reproductive output (Kaehler and McQuaid 1999; Stefaniak et al. 2005), a reduction in yield and quality and in extreme cases, mortality. Although less destructive to the structural integrity of the shell, tube dwelling polychaetes such as *Pomatoceros triquetter* and *Hydroides elegans*, are also damaging to shellfish culture. Fouled shellfish are considered visually unattractive and unappetising to consumers and are subsequently devalued or discarded, leading to substantial economic losses for growers (Campbell and Kelly 2002). In extreme cases, shellfish experience severe shell damage and mortality.

Mechanical interference

Mechanical interference from biofouling overgrowth can be so severe it compromises the opening of shellfish valves. Valve obstruction is often attributed to smothering fouling species, such as colonial tunicates, but also arises from three-dimensional, structure forming fouling species such as hydroids (eg *Ectopleura crocea*, Figure 1b), macroalgae and barnacles. Physical disruption to the opening and closing of valves and hinges results in ineffective feeding (de Sa et al. 2007). In oysters, interference competition has a major effect on respiration rates (Miyauti 1968) and can cause mortality (Dharmaraj et al. 1987). Internal parasitic fouling organisms are also problematic, causing impediment to feeding mechanisms and stress to shellfish. For example, the hydroid *Eutima japonica* inhabits juvenile scallops, reducing shell length growth by 43% and when accompanied by other stressors such as handling and transfers, may lead to mass mortalities (Baba et al. 2007).

Biological competition

Fouling species often compete with shellfish for food and space, resulting in decreased recruitment success, inhibited growth and reduced product value (Adams et al. 2011). Food availability strongly influences shellfish growth (Southgate and Beer 2000; Watson et al. 2009) and competition for food resources between shellfish and biofouling organisms can be significant (Le Blanc et al. 2003). Fouling organisms are primarily filter feeders and although the strength of their competitive interaction depends upon resource limitation and the species present, many foulers compete with farmed shellfish for food. The tunicate *C. intestinalis* and the mussel *Mytilus edulis* are suspension feeders with overlapping preferences in the size range of particles they consume (Daigle and Herbingier 2009). These organisms have very similar clearance rates and as such food competition may be substantial (Petersen 2007). Similarly, in oyster aquaculture, tunicates compete for phytoplankton, causing reduced growth (Rissgård et al. 1995). In addition to food competition, shellfish may experience competition for space and are particularly vulnerable to interference competition from overgrowth. For example, *Ectopleura larynx* can smother scallop shells and attach their shells together (Claereboudt et al. 1994), and overgrowth by colonial ascidians can reduce the feeding ability of mussels (Lesser et al. 1992).

Environmental modification

Biofouling affects aquaculture environments by reducing water flow and changing the concentrations of

waste products. In oyster culture, biofouling reduces water currents and exchange, leading to rapid food depletion (Yukihira et al. 1998). Conversely, biofouling increases food availability to shellfish through enhanced net primary production (Lodeiros et al. 2002; Ross et al. 2002; Le Blanc et al. 2003). Biofoulers also greatly contribute to the already high biodeposition beneath aquaculture farms (Stenton-Dozey et al. 2001). For example, Giles et al. (2006) report that of the total deposition under a farm, only 14% can be attributed to mussel biodeposits, suggesting that the remaining 86% is deposited by other sources including biofouling. Similarly, the presence of *C. intestinalis* on cultured mussel lines increases biodeposition by a factor of two when compared to mussel lines without tunicate fouling (McKindsey et al. 2009). Biodeposition can significantly modify nutrient dynamics in the surrounding ecosystem, leading to an altered benthic community structure (Giles et al. 2006; Weise et al. 2009). In addition, the introduction of non-indigenous fouling species, which are thought to use aquaculture infrastructure as reservoirs to facilitate their spread, can have significant ecological effects on surrounding natural habitats (Ruesink et al. 2005; Rius et al. 2011). For example, *C. intestinalis*, a common non-indigenous fouling species in aquaculture settings, can fundamentally change the composition of sessile communities by depressing local species diversity and altering community assembly processes (Blum et al. 2007).

Increased weight and drag

Biofouling adds significant weight and drag to shellfish culture infrastructure, rapidly becoming a management issue. The need for additional flotation and repairs to equipment leads to subsequent increases in operational costs. In one of the few studies quantitatively measuring fouling in pearl culture, nets used to culture pearl oysters increased 5-fold in weight over a 6 month period due to heavy settlement by barnacles (Dharmaraj and Chellam 1983). Biofouling organisms cause increased drag through reduced water exchange (Claereboudt et al. 1994; Adams et al. 2011), and their presence can cause stock to drop from lines due to their additional weight, particularly in mussel culture (Mallet and Carver 2006). For example, heavy infestations of *C. intestinalis* add in excess of 10 kg m⁻¹ of culture rope to commercial mussel lines, causing compromised attachment of mussel byssal threads and subsequent crop losses of 50–60% (Ramsay et al. 2008). While biofouling of equipment is important, it is secondary to the impact on the cultured animals themselves. However, this effect is reversed in finfish culture systems.

Fish

Biofouling growth on fish cages and infrastructure has three main negative effects: (1) restriction of water exchange due to the growth of fouling organisms causing net occlusion. When fish are held in high density in net pens, this leads to poor water quality as flushing is reduced. Lowered dissolved oxygen levels result and the removal of excess feed and waste is inhibited; (2) disease risk due to fouling communities acting as reservoirs for pathogenic microorganisms harboured by macro- or microbial fouling species on cage netting, or lowered dissolved oxygen levels from poor water exchange increasing the stress levels of fish, lowering immunity and increasing vulnerability to disease; (3) cage deformation and structural fatigue due to the extra weight imposed by fouling. The maintenance and loss of equipment directly contributes to production costs for the industry.

Restriction of water exchange

Occlusion of netting mesh and the subsequent restriction of water flow into and out of the cage environment is the key impact of biofouling on aquaculture nets. The flow of water through cages can be more than halved with significant biofouling loads (Gormican 1989). Flow also decreases when cages are aligned in the current (Inoue 1972). When cages are aligned in a series, and when netting becomes fouled, the effects combine synergistically to reduce water exchange (Aarsnes et al. 1990). Net pen sizes for salmonid aquaculture are increasing (Jensen et al. 2010) and nets are now held in the sea for the whole production cycle. Therefore, the effects of biofouling on water exchange are expected to become more severe because larger cages and nets have a smaller surface area to volume ratio and hence reduced rates of water exchange compared to smaller nets (Lader et al. 2008).

Water exchange replenishes dissolved oxygen (DO) and removes excess feed and waste. Maintaining DO levels is key to effective production (Oppedal et al. 2011a, 2011b) and low DO levels are problematic in modern production settings (Johansson et al. 2006, 2007). Reduced DO levels inside cages, and clear relationships between DO levels and short-term water exchange are well documented. As stocking densities increase, DO consumption increases (Oppedal et al. 2011a, 2011b). Consequently, a combination of low current flow and significant mesh occlusion, and a high stocking density of fish, will reduce DO rapidly (Johansson et al. 2006). Mortalities due to anoxia have been recorded in heavily fouled nets. Oxygen concentrations of $>7 \text{ mg l}^{-1}$ are recommended for salmon farming, whilst concentrations of $<5 \text{ mg l}^{-1}$ negatively impact on feeding, fish growth and respiration

(Remen et al. 2012) and levels of $<2 \text{ mg l}^{-1}$ can result in mortality. Whilst oxygen levels within cages are primarily controlled by water exchange, oxygen production or consumption by fouling communities can affect DO levels (Cronin et al. 1999).

Disease risk

Fouling organisms and microbial communities on cage netting can present a health risk to cultured species by harbouring pathogenic microorganisms. Viral pathogens of finfish accumulate and persist for long periods within shellfish. Viruses isolated from bivalves and identified as finfish pathogens include 13p2 reovirus, the chum salmon virus, JOV-1 Japanese oyster virus, infectious pancreatic necrosis strains and infectious hematopoietic necrosis virus (Leong and Turner 1979; Meyers 1984). In addition, a number of bacterial agents that cause disease in finfish are common to bivalve tissues (eg *Vibrio* spp.). The occurrence of netpen liver disease (NLD) in caged fish is linked to the consumption of fouling organisms by the cultured species (Kent 1990; Andersen et al. 1993). NLD was thought to be caused by a hepatotoxin that may be produced by algae during summer (Kent 1990). The toxin isolated from affected liver tissue has been identified as microcystin-LR, a protein phosphatase inhibitor (Andersen et al. 1993). The fouling biota of the salmon cage is a reservoir for microcystin and the disease is likely to be contracted by feeding on net biota (Andersen et al. 1993).

Fish farms can also facilitate parasite life cycles by increasing the host density and promoting transmission from wild to cultured stocks and *vice versa*. Infection by *Gilquinia squali* metacestodes has been implicated in the deaths of Chinook salmon smolts at fish farms in British Columbia (Kent et al. 1991) where an unidentified crustacean which lives within the cage biofouling community likely acts as an intermediate host, and transfer to the definitive host (or the farmed salmon) occurs directly through ingestion (Kent et al. 1991). The life cycle of *Cardicola forsteri*, a major blood fluke pathogen of southern bluefin tuna (*Thunnus maccoyi*) in Australian aquaculture cages has an intermediate life history stage within polychaete biofoulers attached to the net pens, with other biofouling species acting as a reservoir of this parasite (Cribb et al. 2011).

Cage deformation and structural fatigue

Exposure to currents causes net cages to change their shape by deflection and deformation. The extent of the change in shape depends on current velocity, original shape and construction of the cage, placement weights, type of netting, and level of biofouling (Fredheim

2005; Lader et al. 2008). Increased mesh occlusion increases drag forces on netting; current-induced forces on a fouled net may be 12.5 times that of a clean net (Milne 1970). Consequently, unless cages are heavily weighted, the shape of the cage may be severely deformed by current flows of $0.5\text{--}1\text{ m s}^{-1}$, reducing the effective cage volume by 45–80% (Osawa et al. 1985; Aarsnes et al. 1990). Reduced cage volumes impact on DO consumption, ammonia production will increase per unit volume, and crowding will stress the cultured fish (Lader et al. 2008).

Fouling biomass also increases static load on nets up to 200-fold (Milne 1972 in Beveridge 2004), and horizontal drag forces on cage netting can be increased by up to three times by common fouling hydroids and mussels (Swift et al. 2006). Highly deformed nets increase structural stresses on the cage at specific points, with a two to six-fold increase in horizontal forces in the cage corners (Tomi et al. 1979). Cage designers and operators need to account for these increased loads in the design of cage floatation and mooring systems or devastating net failures result which lead to escapes of fish (Jensen et al. 2010).

The control of biofouling in aquaculture

The negative and significant impacts that biofouling has on viability and profitability of aquaculture has necessitated a long and persistent effort in biofouling control. Historically, the aquaculture industry has borrowed antifouling (AF) technologies from other marine industries which focus on chemical AF technologies. AF paints to control biofouling are commonly used on surfaces in marine transport, oil and gas industries (Yebra et al. 2004; de Nys and Guenther 2009; Dürr and Watson 2010). These paints leach biocidal compounds such as heavy metals and organic biocides onto the surface, producing a thin, toxic layer which prevents the onset of biofouling. However, many of the chemicals and heavy metals involved are recognized as dangerous in the environment, with detrimental effects on the survival and growth of shellfish (Paul and Davies 1986; reviewed by Fent 2006) and fish (Lee et al. 1985; Short and Thresher 1986; Bruno and Ellis 1988) and this has prompted an effort to prevent or mitigate biofouling in aquaculture through alternative methods. Consequently, biofouling control remains one of the most difficult challenges and costly production issues facing the aquaculture industry.

Shellfish

Methods to avoid, mitigate or prevent the effects of biofouling in shellfish culture fall into five broad

categories: (1) avoidance of natural recruitment to prevent settlement and growth of biofouling; (2) physical removal ranging from scrubbing and brushing to chemical dips and sprays; (3) biocontrol using natural species; (4) coatings on shells; (5) control and protection for equipment using antifouling coatings and organic biocides.

Avoidance of natural recruitment

Understanding the larval and settlement biology of problematic biofouling organisms offers the opportunity to manage an appropriate annual schedule of mitigation regimes to minimise colonisation by fouling species (Willis et al. 2011; Dunham and Marshall 2012). Avoidance techniques within farm practices provide a natural strategy to prevent or minimise larval recruitment of fouling organisms. For example, temporarily removing shellfish from the depth level favoured by fouling organisms during the peak period of settlement enables fewer larvae to colonise (Arakawa 1990). This strategy is questionable where fouling pressure is persistent, such as tropical regions, but can be a sensible and effective strategy for regions where fouling is predictable and seasonal. However, even then the practice may be ineffective at reducing fouling biomass (Le Blanc et al. 2003), prompting further techniques to decrease fouling settlement and growth by increasing stocking density of cultivated mussels during fouling episodes or by decreasing stocking density ('re-socking') of mussels after fouling episodes (Ramsay et al. 2008).

Physical removal

Given the adverse effects of chemical antifoulants on shellfish, the control of biofouling in shellfish culture must rely almost exclusively on the removal of fouling organisms. Methods of fouling removal, and the frequency and degree of effort required, are commonly dictated by the fouling composition or intensity of fouling outbreak at a given site (de Nys and Ison 2008; Mallet et al. 2009).

Air exposure of shellfish and associated infrastructure affected by biofouling has varying degrees of success depending on the composition of the fouling community (eg hard vs soft bodied organisms) and the varying sensitivities of shellfish species to air exposure (Gervis and Sims 1992). For example, calcareous organisms such as tube worms and barnacles can retain their internal moisture for long periods of time, so may be less affected. Similarly, some tunicates with a tough, leathery morphology can survive air exposure for many hours (Le Blanc et al. 2007), and under

humid conditions, some algal species exposed to air can remain viable for several weeks (Forrest and Blakemore 2006).

Power washing to remove fouling organisms using mechanical equipment is a common method, with few negative implications for shellfish. It can improve the condition of oysters through increased growth in shells that are handled and cleaned regularly compared to uncleaned shells (Taylor et al. 1997). Washing reduces some organisms such as algal gametophytes (Forrest and Blakemore 2006) and reduces the abundance of some solitary tunicates by up to 80% (Mallet and Carver 2006). However, there are problems associated with its use to mitigate fouling by some colonial organisms, which may undergo fragmentation (Hopkins et al. 2011) and recolonise nearby infrastructure (Paetzold and Davidson 2010). Manual (non-mechanised) cleaning with knives, brushes and water pressure is generally used by the pearl oyster industry in countries such as French Polynesia, Japan and China (Mao Che et al. 1996).

Immersing fouled shellfish and infrastructure in freshwater is a simple, cheap and environmentally friendly technique, with few detrimental effects on the cultured shellfish (Denny 2008). Shellfish are tolerant of freshwater immersion to a limited degree by tightly closing their valves. This technique has been used to treat incursions of many fouling organisms, based on the principle that fouling organisms are more sensitive to treatment. For example, immersion of Akoya pearl oysters in fresh water effectively controls polychaete infestations without inducing oyster mortality (Velayudhan 1983). However, this method is ineffective in completely eliminating some fouling taxa, including various tunicates (Carver et al. 2003; Denny 2008), and can require exposure times of minutes to days depending on the life stage of the target organism (eg algal plantlets vs gametophytes; Forrest and Blakemore 2006). Exposures to brine solutions are similarly inconsistent, with the possibility of rapid mortality of some algal species through osmotic stress (Sharp et al. 2006), but poor success against some tunicates (Carver et al. 2003).

Heat treatment has been used to successfully combat problematic biofouling in many marine industries (eg Perepelizin and Boltovskoy 2011), and is appealing due to its benign environmental effects and ease of application (Rajagopal et al. 1995). Although calcareous taxa such as tube worms and barnacles can be more resistant to heated water (Blakemore and Forrest 2007), a range of common algal and invertebrate fouling organisms are negatively affected (Forrest and Blakemore 2006; Blakemore and Forrest 2007), although the technique can lead to some shellfish mortality (Carver et al. 2003).

Both spray and immersion techniques have been implemented extensively using acidic and alkaline chemicals. In mussel culture, low concentrations of acetic acid are particularly successful against soft-bodied tunicates and against algae (Le Blanc et al. 2007; Denny 2008; Piola et al. 2010), whether applied by immersion or spray techniques. However, some mussel mortality may be experienced (Carver et al. 2003; Le Blanc et al. 2007) and the application of acetic acid also affects non-target organisms and hampers naturally occurring biocontrol (Paetzold et al. 2008). Other acids used less commonly but with some success on tunicates are silicic, formic and citric acid (Denny 2008). The most common alkaline substance in use is lime, and treatment has been conducted using both quicklime (calcium oxide) and hydrated lime (calcium hydroxide). Lime is effective against tunicates (Carver et al. 2003; Denny 2008), but less successful against other fouling species (Piola et al. 2010). Chlorination using chlorine bleach kills arbitrarily, so its use as an effective eradication treatment is considered tenuous (Williams and Schroeder 2004). It has proven efficient against a range of fouling organisms (Denny 2008; Piola et al. 2010), yet has been found to have no impact on some tunicates (Carver et al. 2003).

Biological control

Biological control, where predation of pest species by other marine organisms is used to manage fouling levels, is a useful management strategy in small-scale shellfish culture. Natural control mechanisms negate the need for costly physical and chemical treatments, and are safer for the health and wellbeing of the shellfish and the growers. Examples from oyster culture include the use of periwinkles (Enright et al. 1983; Cigarria et al. 1998), crabs (Ross et al. 2004) and sea urchins (Lodeiros and García 2004; Ross et al. 2004; Epelbaum et al. 2009). However, ensuring mobile organisms such as these remain on culture infrastructure for extended time periods is challenging, particularly in mussel culture (Comeau et al. 2012). This may require modification of culture techniques such as the addition of protective cages around mussel socks for retention (Epelbaum et al. 2009). The use of biocontrol in large scale shellfish culture is therefore tenuous.

Coatings

The development of coatings technology to mitigate biofouling in shipping and on other marine infrastructure has incited developments in shell coating technology within the shellfish industry. Coating of live pearl oysters with a biodegradable, wax-based, impervious, non-toxic coating, were successful in treating

oysters heavily infected with boring clionid sponges (de Nys and Ison 2004). Surface integrity lasts for 2 to 3 months after which it degrades. Its use may negate the need to cull infected oysters, but is unsuitable as a long-term AF control. However, coatings can be designed that can be effective in either reducing fouling, or alternatively facilitating the removal of fouling organisms during mechanical cleaning. This can then reduce the frequency of cleaning with significant reduction in infrastructure and operational costs (de Nys and Horne 2003; de Nys and Ison 2008).

Control and protection for equipment

Fouling prevention strategies for culture equipment such as ropes, floats, panels, nets and trays have traditionally used heavy metals including copper, nickel and tin. Unlike tributyltin and nickel, copper-based coatings remain in use despite their negative impacts on developing vertebrates and invertebrates (Oliva et al. 2007), and their ability to concentrate in shellfish tissues (Changsheng et al. 1990). The use of copper on equipment is discussed in detail below as this is the most common method of deterring the settlement and growth of fouling organisms on equipment used in finfish aquaculture. In a similar manner to equipment used in finfish culture, there are few if any alternatives available, given that low surface energy coatings are only effective under flow. Low surface energy coatings may, however, facilitate the release of fouling communities under regular physical cleaning, which is the main method for biofouling control in shellfish aquaculture, and as such may be an effective co-treatment option. Application and resilience under operational conditions are key criteria to successfully develop this approach for shellfish culture systems.

Fish

Commercial fish farm operations usually employ a multifaceted approach to controlling net fouling. This includes: (1) net changing and cleaning to remove fouling organisms and maintain water exchange; (2) chemical antifoulants such as copper to deter the recruitment of fouling organisms; and most recently (3) biological control using herbivorous fish or invertebrates to graze biofouling from the net surfaces.

Net changing and cleaning

Fish farmers in temperate and tropical regions frequently change or clean net pens to maintain water exchange when biofouling loads are heavy (5–8 days in

summer in Australia: Hodson and Burke 1994; 8–14 days in Japan: Milne 1979; 14 days in Malaysia: Lee et al. 1985; 3–4 weeks in Canada: Menton and Allen 1991). Large meshed cages are changed or cleaned less frequently because of the greater amount of fouling required to occlude the mesh (tuna cages of 60–90 mm mesh cleaned every 6 months: Cronin et al. 1999). If the fouling is restricted to the upper area of the cage, the frequency of cleaning can sometimes be delayed by raising the top few metres of the net out of the water (Needham 1988). Net changing incurs a major cost to the industry, necessitating the purchase of a large number of nets and provision of dedicated net-changing and cleaning teams. Moreover, frequent net changing risks damage or loss of stock, and disturbs the feeding regimes of fish which may lower growth rates. Net changing is labour and capital-intensive, and boat-mounted hydraulic cranes are needed for large cages. Changed nets are usually left to compost for 1–2 weeks on-shore, followed by cleaning with high-pressure water hoses or automated washing machines (Cronin et al. 1999; Olafsen 2006). Washing procedures and net handling frequently damage netting and reduce its life-span. Consequently, after cleaning, nets are repaired.

As an alternative to net replacement, nets can be cleaned *in situ*, primarily with cleaning discs on Remote Operating Vehicles, or manually by divers. Underwater net cleaners are now in widespread use (eg Tasmania: Hodson et al. 1997; Norway: Guenther et al. 2009). Over half of Norway's salmon farms now undertake regular *in situ* cleaning (Olafsen 2006). Although frequent mechanical cleaning is expensive, the combination of this with other strategies can reduce biofouling control costs by up to 50% per m² of netting (CRAB 2004–2007). *In situ* cleaning is now almost fully automated and the dominant removal strategy in the largest fish farms. Problems remain however in that fouling remnants are invariably left after cleaning (Greene and Grizzle 2007), some of which can regrow quickly (Guenther et al. 2010). The washing process can also trigger larval release which leads to rapid recolonisation of nets (Carl et al. 2011), as well as fragmentation and regrowth of some colonial organisms (Carl et al. 2011; Hopkins et al. 2011). *In situ* cleaning may therefore be required frequently. Furthermore, brushing increases fouling problems because it scratches the mesh creating loose filaments, the morphology of which are ideal settlement substrata for some fouling species such as mussels (eg *Mytilus edulis*, Figure 1c; Alfaro and Jeffs 2002) and hydroids (eg *Ectopleura larynx*, Figure 1d; Carl et al. 2011). An alternative to washing may be concentrated, short term exposure of fouling species *in situ* to heated seawater or acetic acid solutions,

which may kill the organisms and negate the need for harsh brushing (Guenther et al. 2011).

Chemical antifoulants

As copper is highly toxic to many marine invertebrates, particularly their larval stages, copper coatings have a long history of approved use in mariculture. For example, in 2005 a total of 261 tonnes of copper was sold to the aquaculture industry in Norway. Copper adds ~20–25% to the cost of a knotless nylon cage (Beveridge 2004). In temperate regions, nets must be coated each year, but the application of copper AF paint gives good protection for 6 months and is effective during summer when fouling is worst (reviewed in Braithwaite and McEvoy 2005; Braithwaite et al. 2007; reviewed in de Nys and Guenther 2009).

Copper has negative impacts on non-target organisms including macroalgae (Andersson and Kautsky 1996; Bond et al. 1999), microalgae (Lim et al. 2006), clams (Munari and Mistri 2007) and fish (Mochida et al. 2006). Relatively low concentrations of copper are harmful to fish and diverse effects have been reported from several toxicity studies (Brooks et al. 2008; Brooks and Waldock 2009; Thomas and Brooks 2010). Copper leaches out of impregnated nets into the water column and elevated concentrations of copper inside treated salmon pens have been recorded after net installation (Brooks 2000; Brooks and Mahnken 2003; Thomas and Brooks 2010). While some studies indicate that salmon raised in copper-treated nets do not bioaccumulate copper in muscle or liver tissue (Peterson et al. 1991; Solberg et al. 2002), industry best practice is to introduce fish into nets 1 month after newly coated nets are in position, to minimise any potential for bioaccumulation.

There are environmental concerns that copper bioaccumulates in sediments around fish farms and in non-target organisms (Miller 1998). Intestinal copper levels in the green sea urchin *Strongylocentrotus droebrachiensis* are elevated at salmon aquaculture sites (Chou et al. 2003), and copper bioaccumulates in the hepatopancreas of lobsters sampled near salmon farms (Chou et al. 2000). Given recent evidence on the effects of dissolved organic carbon (DOC) on the bioavailability of copper and its impacts on non-target species, the use of copper in areas with high levels of DOC may not be as detrimental as perceived. This is an area of ongoing and topical research (Brooks et al. 2008; Brooks and Waldock 2009; Thomas and Brooks 2010).

Copper is also used as the active ingredient in metal based nets. The use of copper alloys to construct nets is not new; however, recent innovations in the construction of nets with copper-zinc, copper-nickel and copper-silicon alloys has spurred renewed interest by

fish farmers in their use in Chile, Australia, Japan and elsewhere. Despite the promising nature of this technology, there is no published evidence of the effects of copper nets on biofouling and possible benefits such as reductions in fish pathogens and increased oxygen levels in cages due to better water flow. Biofouling appears minimal on copper nets, but their use in the industry is hindered by their weight, failure and breakage through corrosion and relative expense compared to standard nylon mesh. New techniques to construct light-weight mesh alloys may drive greater use of this technology by industry as benefits begin to outweigh costs.

Importantly however, the perception of using copper as an AF compound, be it in a coating or with a net, is undesirable in an industry selling a food product from a 'clean and green' marketing perspective. Most countries are now reducing their use of copper-based AF. The European Commission is proposing to give copper a R50/R53 classification, based on the 67/548/EEC directive on dangerous substances, which recognizes that copper is toxic to aquatic organisms and may cause long-term adverse effects in the environment. The Norwegian aquaculture industry is moving towards a reduction in copper use, based on public perception of copper treatments having negative environmental impacts (Sandberg and Olafsen 2006).

Worldwide, there are a number of other biocides currently being used as antifoulants, albeit not necessarily in mariculture (Konstantinou 2006; Brooks and Waldock 2009; Thomas 2009), which are candidates to supplement or replace the use of copper as an antifoulant. The most commonly used biocides include Irgarol 1051 and Sea-Nine 211 (isothiazolinones) (Konstantinou 2006; Thomas 2009). Coatings using isothiazolinones as the sole biocide class have been successfully tested in Australia (Svane et al. 2006) but there is little peer-reviewed literature on the efficacy of other biocides trialled in an aquaculture context.

All countries have enforced their own national legislation regarding AF paint biocides, with a diverse range of requirements. The European Union's (EU) Biocidal Products Directive (BPD) is currently reviewing all European AF paint biocides (98/8/EC), in order to harmonise legislation between countries and control the production, marketing and use of biocidal products, for the protection of humans and the environment (Pereira and Ankjaergaard 2009; Thomas 2009). To phase out the use of traditional, hazardous AF coatings based on heavy metals such as copper, the general trend in global AF research and development has therefore shifted to the creation of agents that are both effective and environmentally benign, as a consequence of their chemistry (non-toxic coatings) or their physical properties (eg fouling-release coatings

and non-leaching biocides) (Callow and Callow 2009; Pereira and Ankaergeraard 2009; Scardino 2009; Webster and Chisholm 2010).

Biological control

An increase in profitability and sustainability could be achieved by the use of herbivorous fish or invertebrates to control fouling, yet to date attempts to do so have been largely small-scale or experimental in nature. The biological control concept is constrained by the variation in types of algal and invertebrate fouling, which suggests that only herbivores and omnivores with a broad dietary range will be successful control agents. Furthermore, it is likely that continuous grazing will provide an environment which selects for inedible species, thus only reducing the frequency of net changing. Biological control using herbivorous fish has to date only been effective in small cages (Kuwa 1984); no examples of this strategy exist for modern, large-scale fish farms. Invertebrate detritivores, such as the red sea cucumber *Parastichopus californicus*, have reduced fouling in salmon mariculture, although maintaining their position on the sides of cages is difficult in wave affected areas (Ahlgren 1998) where most salmon aquaculture occurs. The advantage of biological control with sea cucumbers is that they are a commercial crop in their own right, with strong demand in Asia (Conand and Sloan 1989). However, regardless of value, the use of biocontrol with invertebrates is experimental with significant challenges.

New strategies to control and mitigate biofouling in aquaculture

The development of AF technologies for aquaculture is underpinned by the development of new AF solutions for the marine transport industry where costs for biofouling are high. There are six recommended criteria for AF strategies in the aquaculture industry (Lewis 1994). Strategies should: (1) be effective against a broad range of fouling taxa; (2) be environmentally benign; (3) have no negative effects on the cultured species; (4) leave no residues in the cultured species; (5) be able to withstand on-shore handling and cleaning; and (6) be economically viable. These strategies need to underpin the development of new technologies for the large-scale prevention of fouling in both shellfish and fish production.

Shellfish

While many control strategies involve treatments after fouling communities have established, an alternate strategy to manage biofouling could be based on more

accurate predictions of the occurrence of fouling episodes (Cyr et al. 2007). Prediction may enable avoidance and is a feasible option in many environments, especially where infrastructure can be moved in synchrony with fouling settlement peaks. In addition, with the production of hatchery reared mussel larvae, farmers can deploy their larval collecting ropes outside 'normal' collecting times, which may coincide with low fouling settlement periods. Most studies on biofouling in aquaculture, and particularly shellfish culture, have taken place in temperate regions and fewer data exist for tropical regions, where fouling pressure is constant and growth is rapid.

Control of biofouling will be facilitated through further research on spatial and temporal variation in the larval and settlement biology of fouling species, and their development on both shells and equipment. Determining key points for disruption of the settlement and metamorphosis process will assist development of new AF technologies. However, this will need to be tempered with an acknowledgement that such strategies are only likely to be effective where fouling is already seasonal and largely mono-specific. Ultimately, non-toxic alternatives to AF paints and coatings, that deter fouling episodes, are required and are a focus for research. For example, a novel technique, the application of food grade oil to farm buoys, ropes and floats, reduced fouling by algae and tunicates in mussel culture by more than 90% (Bakker et al. 2011). Fouling prevention rather than mitigation is obviously desirable, both ecologically and economically.

Farmed shellfish suffer more from endolithic biofouling than natural populations (Mao Che et al. 1996), suggesting that culturing techniques and fouling removal practices wear away the protective shell periostracum more quickly (Mao Che et al. 1996). While the periostracum does not deter all fouling species, it is broadly effective against boring organisms. Management of husbandry and cleaning regimes to prevent the removal of this natural coating would optimise the fouling resistant properties of shells and extend their efficacy (Mao Che et al. 1996; Guenther et al. 2006). Hard fouling such as barnacles, tube worms and bivalves are particularly difficult and costly to remove. The development of inert barrier based man-made coatings which prevent fouling organisms from settling and facilitate their removal could provide broader spectrum deterrence to fouling (de Nys and Ison 2004). When coated on pearl oysters, waxes and polyurethanes offer both deterrence and enhanced removal of fouling organisms (de Nys and Horne 2003). Similarly, low surface energy coatings are constantly improving with increased resilience and decreased flow required for the release of fouling organisms (Townsin and Anderson 2009). For

example, release of fouling is said to occur at speeds as low as 10 knots. The broader shellfish industry would benefit by understanding the capacity of these coatings (derived from the marine transport industry) in delivering AF alternatives that meet the six criteria for success. Within this context, there are mechanisms that may enhance the efficacy of low surface energy coatings in deterring the initial settlement of fouling organisms by manipulating the topography of the low energy surface (Callow et al. 2002, reviewed by Magin et al. 2010). The development of novel surface microtopographies, many with a bio-inspired design, into low surface energy coatings may inhibit the settlement and growth of specific fouling organisms, and also facilitate their release (Scardino 2009; Aldred et al. 2010; Magin et al. 2010; Scardino and De Nys 2011).

While physical and mechanical cleaning is the corner stone of many large shellfish industries such as pearl oysters, the development of effective and inexpensive technology to remove biofouling mechanically is a key area of research in shellfish culture. For example, low-cost tools which mount outside traditional oyster stacks and move around the stack with currents and waves resulted in 16 times less fouling than traditional oyster stacks (Sala and Lucchetti 2008). Similarly, the novel addition of artificial growth medium (expanded clay aggregate) to basket cockle culture enclosures significantly reduced shell deformities and barnacle fouling as well as reducing fouling by tube worms, overall fouling rate, and fouling intensity (Dunham and Marshall 2012).

Biocontrol is another focus for research. Biocontrol is attractive as it can augment aquaculture industries when the species used for biological control also have commercial value, and may provide a potential complementary product through polyculture (Ross et al. 2004). Of particular focus are sea urchins, which may provide long-term financial benefits due to the availability of a diverse range of edible species with commercial value and their closed life cycle (reviewed in Lawrence 2007). While this methodology is unlikely to have broad spectrum use in highly mechanised industries, it warrants investment and consideration, with significant scope to deliver innovation and value.

Fish

The control of fouling on nets and other fish farm structures is largely restricted to a limited range of products which release copper and/or zinc and/or additional booster biocides. As metal and biocide based technologies are removed from the market, with a clear driver being the EU Biocides Directive (Pereira and Ankjaergaard 2009), the aquaculture industry may

have to return to the traditional methods of net changes and washing. New products with a focus on fouling-release technologies based on low-surface energy coatings, texturing and surface-bound compounds could be developed. Fouling-release technologies rely on hydrodynamic forces to remove fouling organisms with poor adhesion to the fouling-release surface making them less suitable for aquaculture (see above). As the technology for vessels improves, the transfer (trickle-down) of technology to aquaculture industries will occur. New approaches for marine shipping and infrastructure are targeting well-documented pharmaceuticals (Pinori et al. 2011), bioactives (Dahlström and Elwing 2006; Pinori et al. 2011), and commercially available enzymes (Pettitt et al. 2004; Aldred et al. 2008) as antifoulants, or innovations with existing technologies such as copper (Vucko et al. 2012). These approaches may prove productive if they can be specifically tailored to aquaculture, however, they still involve a chemical entity and their use will attract close scrutiny of any chemical effects on cultured organisms.

Non-toxic coatings

Biocide-free, low surface energy siloxane elastomers and fluoropolymers may provide a non-toxic alternative to control biofouling in aquaculture given the step-wise improvements in their efficacy in the marine transport industry (Lewis 2009; Townsin and Anderson 2009; Magin et al. 2010; Webster and Chisholm 2010). These 'fouling-release' coatings aim at reducing or preventing the adhesion of fouling. Silicone-based paints are a non-toxic alternative to biocidal paints for ships' hulls, where the speed of the vessel produces the hydrodynamic shear required to remove weakly adhered fouling (Yebra et al. 2004; Townsin and Anderson 2009; Webster and Chisholm 2010). Although the hydrodynamic forces are much reduced in a 'stationary' aquaculture environment, nets and panels coated with non-toxic silicone coatings reduce the initial stages of fouling development and make it easier to clean the net of fouling that does accumulate (Hodson et al. 2000; Terlizzi et al. 2000). In addition, simple, but effective methods using an air-bubble curtain in conjunction with fouling-release coatings may also prove effective on aquaculture infrastructure (Scardino et al. 2009). A number of commercial products are available for aquaculture and the use of air bubble curtains is likely to yield commercial outcomes of great interest to the aquaculture industry in the medium to short-term as practical issues such as cost-effective coating of aquaculture nets are addressed. There are also further developments in the field of fouling-release technologies using the principles

of super-hydrophobicity (Genzer and Efimenko 2006; Marmur 2006; Callow and Callow 2009; Scardino 2009). However, the commercial development of these technologies and their application to stationary aquaculture infrastructure will require a longer time frame.

Non-leaching biocides

Biocides irreversibly bound to the AF coating surface or net are known as non-leaching biocides. While this approach limits environmental contamination, it has not been successfully pursued. The techniques have been used effectively against bacterial biofouling on biomedical devices (Hume et al. 2004; Zhu et al. 2008) and this is an area of technical promise with the move towards legislation restricting antifouling technologies to non-release mechanisms.

Conclusion

The occurrence of biofouling in marine aquaculture is a significant management issue resulting in increased operational expenses and deleterious impacts on the species being cultured. Surprisingly, for an issue with such high impact in a growing global industry, sparse information exists on its effects and costs. For example, the focus on biofouling in cage culture has been skewed to more modern advanced aquaculture industries, such as the Northern hemisphere salmon industry, with little quantitative information on fouling in new aquaculture regions and in the tropics where fouling community development is most rapid. The expansion of tropical aquaculture and the trend towards greater use of offshore sites both present new challenges in understanding the impacts of fouling and implementing successful control measures. Given the limited choice of products currently available, quantitative studies on the spatial and temporal variation of fouling species, and the effects of husbandry techniques and farm management on fouling development, are essential to assist the industry to choose the most cost effective and practical methods for fouling control, both now and into the future. In terms of control, the mechanical removal of biofouling remains dominant in shellfish and fish culture, and copper coatings on fish nets are the only consistently effective form of biofouling prevention at an industrial scale. Future developments need to rely on incremental improvements in these fundamental platform technologies until there is a step-change in the development of non-toxic, low surface energy coatings. Low surface energy coatings fit all of the key criteria for a long term fouling control mechanism that meets strict legislative frameworks around the environment and food products. The development of robust low surface energy

coatings that prevent fouling and facilitate its release at low water flows have the potential to transform biofouling control in aquaculture either independently, or in conjunction with mechanical cleaning. Notably, the development of biofouling technologies will always be led by larger, more valuable maritime industries, and the most advanced of these rely on moving structures to facilitate fouling release. However, as low surface energy coatings are developed and modified to provide fouling release at lower release velocities their application to aquaculture has the potential to transform the manner in which biofouling is controlled. Therefore, while the aquaculture industry remains a step behind other maritime industries in control methods it can also benefit from the broader research effort across maritime industries to solve a cosmopolitan, persistent and complex problem, biofouling.

Acknowledgements

The authors thank Michael Sievers and anonymous reviewers for their comments on the manuscript.

References

- Aarsnes JV, Rudi H, Loland G. 1990. Current forces on cage, net deflection. In: Institution of Civil Engineers. Engineering for offshore fish farming. Proceedings of a conference organised by the Institute of Civil Engineers; 17–18 October 1990; Glasgow. London (UK): Thomas Telford Ltd, p. 137–152.
- Adams CM, Shumway SE, Whitlatch RB, Getchis T. 2011. Biofouling in marine molluscan shellfish aquaculture: a survey assessing the business and economic implications of mitigation. *J World Aquacult Soc* 42:242–252.
- Ahlgren MO. 1998. Consumption and assimilation of salmon net pen fouling debris by the red sea cucumber *Parastichopus californicus*: implications for polyculture. *J World Aquacult Soc* 29:133–139.
- Alagarwami K, Chellam A. 1976. On fouling and boring organisms and mortality of pearl oysters in the farm at Veppalodai, Gulf of Mannar. *Indian J Fish* 23:10–22.
- Aldred N, Phang IY, Comlan SL, Clare AS, Vancso GJ. 2008. The effects of a serine protease, Alcalase[®], on the adhesives of barnacle cyprids (*Balanus amphitrite*). *Biofouling* 24:97–107.
- Aldred N, Scardino A, Cavaco A, de Nys R, Clare AS. 2010. Attachment strength is a key factor in the selection of surfaces by barnacle cyprids (*Balanus amphitrite*) during settlement. *Biofouling* 26:287–299.
- Alfaro AC, Jeffs AG. 2002. Small-scale mussel settlement patterns within morphologically distinct substrata at Ninety Mile Beach, northern New Zealand. *Malacologia* 44:1–15.
- Andersen RJ, Luu HA, Chen DZX, Homes CFB, Kent ML, Le Blanc F, Taylor FJR, Williams DE. 1993. Chemical and biological evidence links microcystins to salmon netpen liver disease. *Toxicon* 31:1315–1325.
- Andersson A, Kautsky L. 1996. Copper effects on reproductive stages of Baltic Sea *Fucus vesiculosus*. *Mar Biol* 125: 171–176.

- Arakawa KY. 1990. Competitors and fouling organisms in the hanging culture of the Pacific oyster, *Crassostrea gigas* (Thunberg). *Mar Behav Physiol* 17:67–94.
- Baba K, Miyazono A, Matsuyama K, Kohno S, Kubota S. 2007. Occurrence and detrimental effects of the bivalve-inhabiting hydroid *Eutima japonica* on juveniles of the Japanese scallop *Mizuhopecten yessoensis* in Funaka Bay, Japan: relationship to juvenile massive mortality in 2003. *Mar Biol* 151:1977–1987.
- Bakker JA, Paetzold C, Quijon PA, Davidson J. 2011. The use of food grade oil in the prevention of vase tunicate fouling on mussel aquaculture gear. *Manag Biol Invas* 2: 15–25.
- Barthel D, Sundet J, Barthel KG. 1994. The boring sponge *Cliona vastifica* in a subarctic population of *Chlamys islandica*. An example of balanced commensalism? In: van Soest RWM, van Kempen TMG, Braekman JC, editors. *Sponges in time and space*. Rotterdam (The Netherlands): AA Balkema. p. 289–296.
- Beveridge M. 2004. *Cage aquaculture*. Oxford (UK): Blackwell Publishing Ltd. 368pp.
- Blake JA, Evans JW. 1973. *Polydora* and related genera as borers in mollusk shells and other calcareous substrates. *Veliger* 15:235–249.
- Blakemore KA, Forrest BM. 2007. Heat treatment of marine fouling organisms. Prepared for Golder Associates (NZ) Ltd. Nelson (New Zealand): Cawthron Institute. Cawthron Report No. 1300.
- Blum JC, Chang AL, Liljestrom M, Schenk ME, Steinberg MK, Ruiz GM. 2007. The non-native solitary ascidian *Ciona intestinalis* (L.) depresses species richness. *J Exp Mar Biol Ecol* 342:5–14.
- Bonardelli J. 2008. Antacid – your mussels’ best friend. *Fish Farm Int* September:48–49.
- Bond PR, Brown MT, Moate RM, Gledhill M, Hill SJ, Nimmo M. 1999. Arrested development in *Fucus spiralis* (Phaeophyceae) germlings exposed to copper. *Eur J Phycol* 34:513–521.
- Bourque D, Le Blanc AR, Landry T, McNair N, Davidson J. 2005. Tunicate infested mussel aquaculture sites in Prince Edward Island, Canada. *J Shellfish Res* 24:1261.
- Braithwaite RA, McEvoy LA. 2005. Marine biofouling on fish farms and its remediation. *Adv Mar Biol* 47: 215–252.
- Braithwaite RA, Carrascosa MCC, McEvoy LA. 2007. Biofouling of salmon cage netting and the efficacy of a typical copper-based antifoulant. *Aquaculture* 262:219–226.
- Brooks KM. 2000. Determination of copper loss rates from Flexgard XI™ treated nets in marine environments and evaluation of the resulting environmental risks. Report to the Ministry of Environment for the BC Salmon Farmers Association. Vancouver (BC): British Columbia Salmon Farmers Association. 24 pp.
- Brooks KM, Mahnken CVW. 2003. Interactions of Atlantic salmon in the Pacific Northwest environment. III. Accumulation of zinc and copper. *Fish Res* 62:295–305.
- Brooks S, Waldock M. 2009. The use of copper as a biocide in marine antifouling paints. In Hellio C, Yebra D, editors. *Advances in marine antifouling coatings and technologies*. Cambridge (UK): Woodhead Publishing Ltd. p. 492–515.
- Brooks SJ, Bolam T, Tolhurst L, Bassett J, La Roche J, Waldock M, Barry J, Thomas KV. 2008. Dissolved organic carbon reduces the toxicity of copper to germlings of the macroalga, *Fucus vesiculosus*. *Ecotoxicol Environ Saf* 70:88–98.
- Bruno DW, Ellis AE. 1988. Histopathological effects in Atlantic salmon, *Salmo salar* L., attributed to the use of tributyltin antifoulant. *Aquaculture* 72:15–20.
- Buschbaum C, Buschbaum G, Schrey T, Thieltges DW. 2007. Shell-boring polychaetes affect gastropod shell strength and crab predation. *Mar Ecol Prog Ser* 329: 123–130.
- Callow JA, Callow ME. 2009. Advanced nanostructured surfaces for the control of marine biofouling: the AMBIO project. In Hellio C, Yebra D, editors. *Advances in marine antifouling coatings and technologies*. Cambridge (UK): Woodhead Publishing Ltd. p. 647–663.
- Callow ME, Jennings AR, Brennan AB, Seegert CE, Gibson A, Wilson L, Feinberg A, Baney R, Callow JA. 2002. Microtopographic cues for settlement of zoospores of the green fouling alga *Enteromorpha*. *Biofouling* 18: 237–245.
- Campbell DA, Kelly MS. 2002. Settlement of *Pomatoceros triqueter* (L.) in two Scottish Lochs, and factors determining its abundance on mussels grown in suspended culture. *J Shellfish Res* 21:519–527.
- Carl C, Guenther J, Sunde LM. 2011. Larval release and attachment modes of the hydroid *Ectopleura larynx* on aquaculture nets in Norway. *Aquacult Res* 42:1056–1060.
- Carver CE, Chisholm A, Mallet AL. 2003. Strategies to mitigate the impact of *Ciona intestinalis* (L.) biofouling on shellfish production. *J Shellfish Res* 22:621–631.
- Cerrano C, Puce S, Chiantore M, Bavestrello G, Cattaneo-Vietti R. 2001. The influence of the epizoid hydroid *Hydractinia angusta* on the recruitment of the Antarctic scallop *Adamussium colbecki*. *Polar Biol* 24:577–581.
- Changsheng Z, Bingyin S, Yunbi H, Xianggui X. 1990. Effects of JS-876, a copper-tin compounded anti-fouling agent, on growth of the scallop *Pecten maximus*. *J Oceanogr Huanguai Bohai Seas* 8:40–46. (Chinese with English abstract).
- Chengxing Z. 1990. Ecology of ascidians in Daya Bay. In Huang Z, editor. *Collected works on marine ecology in Daya Bay*. Beijing (China): Ocean Publishing Press. p. 397–403.
- Chou CL, Paon LA, Moffat JD, Zwicker B. 2000. Copper contamination and cadmium, silver, and zinc concentrations in the digestive glands of American lobster (*Homarus americanus*) from the Inner Bay of Fundy, Atlantic Canada. *Bull Environ Contam Toxicol* 65:470–477.
- Chou CL, Haya K, Paon LA, Moffat JD. 2003. Metals in the green sea urchin (*Strongylocentrotus droebachiensis*) as an indicator for the near-field effects of chemical wastes from salmon aquaculture sites in New Brunswick, Canada. *Bull Environ Contam Toxicol* 70:948–956.
- Cigarria J, Fernandez J, Magadan LP. 1998. Feasibility of biological control of algal fouling in intertidal oyster culture using periwinkles. *J Shellfish Res* 17:1167–1169.
- Claereboudt MR, Bureau D, Côté J, Himmelman JH. 1994. Fouling development and its effect on the growth of juvenile giant scallops (*Placopecten magellanicus*) in suspended culture. *Aquaculture* 121:327–342.
- Comeau LA, Sonier R, Hanson JM. 2012. Seasonal movements of Atlantic rock crab (*Cancer irroratus* Say) transplanted into a mussel aquaculture site. *Aquacult Res* 43:509–517.
- Conand C, Sloan NA. 1989. World fisheries for echinoderms. In: Cadey JF, editor. *Marine invertebrate fisheries: their assessment and management*. New York (NY): John Wiley and Sons. p. 647–663.

- Coutts ADM, Sinner J. 2004. An updated benefit-cost analysis of management options for *Didemnum vexillum* in Queen Charlotte Sound. Report prepared for Marlborough District Council. Nelson (New Zealand): Cawthron Institute. Cawthron Report No.925.
- CRAB (Collective Research on Aquaculture Biofouling, EU Project COLL-CT-2003-500536-CRAB) (2004–2007) Strategy factsheet: mechanical cleaning; [cited 2012 Mar]. Available from www.crabproject.com
- Cribb TH, Adlard RD, Hayward CJ, Bott NJ, Ellis D, Evans D, Nowak BF. 2011. The life cycle of *Cardicola forsteri* (Trematoda: Aporocotylidae), a pathogen of farmed southern bluefin tuna, *Thunnus maccoyi*. Int J Parasitol 41:861–870.
- Cronin ER, Cheshire AC, Clarke SM, Melville AJ. 1999. An investigation into the composition, biomass and oxygen budget of the fouling community on tuna aquaculture farm. Biofouling 13:279–299.
- Crossland C. 1957. The cultivation of the mother-of-pearl oyster in the Red Sea. Aust J Freshwater Mar Res 8:111–130.
- Cyr C, Myrand B, Cliche G, Desrosiers G. 2007. Weekly spat collection of sea scallop, *Placopecten magellanicus*, and undesirable species as a potential tool to predict an optimal deployment period of collectors. J Shellfish Res 26:1045–1054.
- Dahlström M, Elwing H. 2006. Adrenoceptor and pharmacoeactive compounds as putative antifoulants. In Fusetani N, Clare AS, Volume Editors. Antifouling compounds. Prog Mol Subcell Biol 42:171–202.
- Daigle RM, Herbinger CM. 2009. Ecological interactions between the vase tunicate (*Ciona intestinalis*) and the farmed blue mussel (*Mytilus edulis*) in Nova Scotia, Canada. Aquat Invas 4:177–187.
- Dalby JE, Young CM. 1993. Variable effects of ascidian competitors on oysters in a Florida epifaunal community. J Exp Mar Biol Ecol 167:47–57.
- Denny CM. 2008. Development of a method to reduce the spread of the ascidian *Didemnum vexillum* with aquaculture transfers. ICES J Mar Sci 65:805–810.
- de Nys R, Horne M. 2003. Antifouling solutions for the Australian pearling industry. Project No. 2003/206. Final Report to the Fisheries Research and Development Corporation. Townsville (Qld): James Cook University, School of Marine and Tropical Biology. 140 pp.
- de Nys R, Ison O. 2004. Evaluation of antifouling products developed for the Australian pearl industry. Project No 2000/254. Final Report to the Fisheries Research and Development Corporation. Townsville (Qld): James Cook University. 114 pp.
- de Nys R, Ison O. 2008. Biofouling. In: Southgate PC, Lucas J, editors. The pearl oyster. Oxford (UK): Elsevier. p. 527–553.
- de Nys R, Guenther J. 2009. The impact and control of biofouling in marine finfish aquaculture. In: Hellio C, Yebra D, editors. Advances in marine antifouling coatings and technologies. Cambridge (UK): Woodhead Publishing Ltd. p. 177–221.
- de Sa FS, Nalesso RC, Paresgue K. 2007. Fouling organisms on *Perna perna* mussels: is it worth removing them? Braz J Oceanogr 55:155–161.
- Dharmaraj S, Chellam A. 1983. Settlement and growth of barnacle and associated fouling organisms in pearl culture farm in the Gulf of Mannar. Proc Symp on Coastal Aquaculture, Cochin, India, 1980. Part 2: Molluscan Culture. Cochin (India): Marine Biological Association of India. p. 608–613. Available from <http://eprints.cmfri.org.in/2306/>
- Dharmaraj S, Chellam A, Velayudhan TS. 1987. Biofouling, boring and predation of pearl oyster. In: Alagaraswami K, editor. Pearl culture. Central Marine Fisheries Research Institute special publication No 39. Cochin (India): CMFRI. p. 92–97.
- Doroudi M. 1996. Infestation of pearl oysters by boring and fouling organisms in the northern Persian Gulf. Indian J Mar Sci 25:168–169.
- Dunham A, Marshall RD. 2012. Using stocking density modifications and novel growth medium to control shell deformities and biofouling in suspended culture of bivalves. Aquaculture 324:234–241.
- Dürr S, Watson DI. 2010. Biofouling and antifouling in aquaculture. In: Dürr S, Thomason JC, editors. Biofouling. Oxford (UK): Wiley-Blackwell. p. 267–287.
- Edwards PK, Leung B. 2009. Re-evaluating eradication of nuisance species: invasion of the tunicate, *Ciona intestinalis*. Front Ecol Environ 7:326–332.
- Enright C. 1993. Control of fouling in bivalve aquaculture. World Aquacult 24:44–46.
- Enright C, Krailo D, Staples L, Smith M, Vaughan C, Ward D, Gaul P, Borgese E. 1983. Biological control of fouling algae in oyster aquaculture. J Shellfish Res 3:41–44.
- Epelbaum A, Pearce CM, Barker DJ, Paulson A, Therriault TW. 2009. Susceptibility of non-indigenous ascidian species in British Columbia (Canada) to invertebrate predation. Mar Biol 156:1311–1320.
- Evans JW. 1969. Borers in the shell of the sea scallop, *Placopecten magellanicus*. Am Zool 9:775–782.
- FAO. 2010. The state of world fisheries and aquaculture, Food and Agriculture Organization of the United Nations. Data for 2009, accessed February 2012.
- Fent K. 2006. Worldwide occurrence of organotin from antifouling paints and effects in the aquatic environment. In: Konstantinou I, editor. Antifouling paint biocides. The Handbook of Environmental Chemistry 5.0. Berlin (Germany): Springer-Verlag. p. 71–100.
- Fitridge I. 2011. The ecology of hydroids (Hydrozoa: Cnidaria) in Port Phillip Bay, Australia, and their impacts as fouling species in longline mussel culture. PhD thesis. Department of Zoology, The University of Melbourne, Australia. 147pp.
- Floerl O, Inglis G, Dey KL, Smith A. 2009. The importance of transport hubs in stepping-stone invasions. J Appl Ecol 46:37–45.
- Forrest BM, Blakemore KA. 2006. Evaluation of treatments to reduce the spread of a marine plant pest with aquaculture transfers. Aquaculture 257:333–345.
- Forrest BM, Hopkins GA, Dodgshun TJ, Gardner JPA. 2007. Efficacy of acetic acid treatments in the management of marine biofouling. Aquaculture 262:319–332.
- Fraschetti S, Terlizzi A, Terlizzi A, Benedetti-Cecchi L. 2005. Patterns of distribution of marine assemblages from rocky shores: evidence of relevant scales of variation. Mar Ecol Prog Ser 296:13–29.
- Fredheim A. 2005. Current forces on net structures. PhD thesis. Department of Marine Technology, Norwegian University of Science and Technology, Trondheim, Norway. 64 pp.
- Fromont J, Craig R, Rawlinson L, Alder J. 2005. Excavating sponges that are destructive to farmed pearl oysters in Western and Northern Australia. Aquacult Res 36:150–162.
- Garbary DJ, Jess CB. 2000. Current status of the invasive green alga *Codium fragile* in eastern Canada. J Phycol 36:23.

- Genzer J, Efimenko K. 2006. Recent developments in superhydrophobic surfaces and their relevance to marine fouling: a review. *Biofouling* 22:339–360.
- Gervis MH, Sims NA. 1992. The biology and culture of pearl oysters (*Bivalvia*: Pteriidae). *ICLARM Stud Rev* 21. 49 pp.
- Getchis TS. 2006. What's putting some aquaculturists in a 'foul' mood? Fouling organisms are taking their toll on marine aquaculture. *Wrack Lines* 5:8–10.
- Giles H, Pilditch CA, Bell DG. 2006. Sedimentation from mussel (*Perna canaliculus*) culture in the Firth of Thames, New Zealand: impacts on sediment oxygen and nutrient fluxes. *Aquaculture* 261:125–140.
- Gittenberger A. 2009. Invasive tunicates on Zealand and Prince Edward Island mussels, and management practices in The Netherlands. *Aquat Invas* 4:279–281.
- Gormican SJ. 1989. Water circulation, dissolved oxygen, and ammonia concentrations in fish net-cages. MSc Thesis. University of British Columbia, Canada. 62 pp.
- Greene JK, Grizzle RE. 2007. Successional development of fouling communities on open ocean aquaculture fish cages in the western Gulf of Maine, USA. *Aquaculture* 262:289–301.
- Guenther J, de Nys R. 2006. Differential community development of fouling species on the pearl oyster *Pinctada fucata*, *Pteria penguin* and *Pteria chinensis* (*Bivalvia*, Pteriidae). *Biofouling* 22:163–171.
- Guenther J, de Nys R, Southgate PC. 2006. The effects of age and shell size of the Akoya pearl oyster *Pinctada fucata* (*Bivalvia*, Pteriidae) on the accumulation of fouling organisms. *Aquaculture* 253:366–373.
- Guenther J, Carl C, Sunde LM. 2009. The effects of colour and copper on the settlement of the hydroid *Ectopleura larynx* on aquaculture nets in Norway. *Aquaculture* 292: 252–255.
- Guenther J, Misimi E, Sunde LM. 2010. The development of biofouling, particularly the hydroid *Ectopleura larynx*, on commercial salmon cage nets in Mid-Norway. *Aquaculture* 300:120–127.
- Guenther J, Fitridge I, Misimi E. 2011. Potential antifouling strategies for marine finfish aquaculture: the effects of physical and chemical treatments on the settlement and survival of the hydroid *Ectopleura larynx*. *Biofouling* 27: 1033–1042.
- Heasman K, de Zwart E. 2004. Preliminary investigation on *Amphisbetia bispinosa* colonisation on mussel farms in the Coromandel. Report prepared for the New Zealand Mussel Industry Council. Nelson (New Zealand): Cawthron Institute. 7 pp.
- Hickman NJ, Sause BL. 1984. Culture of the blue mussel (*Mytilus edulis planulatus*) in Port Phillip Bay, Victoria Australia. III: Larval settlement. Report No. 75. Victoria (Australia): Marine Science Laboratories (Fisheries Victoria). 25 pp.
- Hodson SL, Burke C. 1994. Microfouling of salmon-cage netting: a preliminary investigation. *Biofouling* 8: 93–105.
- Hodson SL, Lewis TE, Burke CM. 1997. Biofouling of fish-cage netting: efficacy and problems of in situ cleaning. *Aquaculture* 152:77–90.
- Hodson SL, Burke CM, Bissett AP. 2000. Biofouling of fish-cage netting: the efficacy of a silicone coating and the effect of netting colour. *Aquaculture* 184:277–290.
- Holloway MG, Keough MJ. 2002a. An introduced polychaete affects recruitment and larval abundance of sessile invertebrates. *Ecol Appl* 12:1803–1823.
- Holloway MG, Keough MJ. 2002b. Effects of an introduced polychaete, *Sabella spallanzanii*, on the development of epifaunal assemblages. *Mar Ecol Prog Ser* 236:137–154.
- Hopkins GA, Forrest BM, Piola RF, Gardner JPA. 2011. Factors affecting survivorship of defouled communities and the effect of fragmentation on establishment success. *J Exp Mar Biol Ecol* 396:233–243.
- Howes S, Herbinger CM, Darnell P, Vercaemer B. 2007. Spatial and temporal patterns of recruitment of the tunicate *Ciona intestinalis* on a mussel farm in Nova Scotia, Canada. *J Exp Mar Biol Ecol* 342:85–92.
- Hume EBH, Baveja J, Muir B, Schubert TL, Kumar N, Kjelleberg S, Griesser HJ, Thissen H, Read R, Poole-Warren LA, et al. 2004. The control of *Staphylococcus epidermidis* biofilm formation and in vivo infection rates by covalently bound furanones. *Biomaterials* 25:5023–5030.
- Inoue H. 1972. On water exchange in a net cage stocked with the fish, Hamachi. *Bull Jap Soc Sci Fish* 38:167–176 (Abstracts and illustrations in English).
- Jensen Ø, Dempster T, Thorstad E, Uglem I, Fredheim A. 2010. Escapes of fish from Norwegian sea-cage aquaculture: causes, consequences and prevention. *Aquacult Environ Interact* 1:71–83.
- Johansson D, Juell J-E, Oppedal F, Stiansen J-E, Ruohonen K. 2007. The influence of the pycnocline and cage resistance on current flow, oxygen flux and swimming behaviour of Atlantic salmon (*Salmo salar* L.) in production cages. *Aquaculture* 265:271–287.
- Johansson D, Ruohonen K, Kiessling A, Oppedal F, Stiansen J-E, Kelly M, Juell J-E. 2006. Effect of environmental factors on swimming depth preferences of Atlantic salmon (*Salmo salar* L.) and temporal and spatial variations in oxygen levels in sea cages at a fjord site. *Aquaculture* 254:594–605.
- Kaehler S. 1999. Incidence and distribution of phototrophic shell-degrading endoliths of the brown mussel, *Perna perna*. *Mar Biol* 135:505–514.
- Kaehler S, McQuaid CD. 1999. Lethal and sub-lethal effects of phototrophic endoliths attacking the shell of the intertidal mussel *Perna perna*. *Mar Biol* 135:497–503.
- Kent ML. 1990. Netpen liver disease (NLD) of salmonid fishes reared in sea water: species susceptibility, recovery and probable cause. *Dis Aquat Org* 8:21–28.
- Kent ML, Margolis L, Fournie JW. 1991. A new eye disease in pen-reared Chinook salmon causes by metacestodes of *Gilquinia squali* (Trypanorhyncha). *J Aquat Anim Health* 3:134–140.
- Konstantinou IK. 2006. Antifouling paint biocides. The handbook of environmental chemistry. Berlin (Germany): Springer-Verlag. 266 pp.
- Korringa P. 1952. Recent advances in oyster biology. *Quart Rev Biol* 27:266–308.
- Kuwa M. 1984. Fouling organisms on floating cage of wire netting and the removal by *Oplegnathus* sp. cultured with other marine fish. *Bull Jap Soc Sci Fish* 50:1635–1640 (in Japanese).
- Lader P, Dempster T, Fredheim A, Jensen Ø. 2008. Current induced net deformations in full-scale sea-cages for Atlantic salmon (*Salmo salar*). *Aquacult Eng* 38:52–65.
- Lane A, Willemsen PR. 2004. Collaborative effort looks into biofouling. *Fish Farming Int* September 2004: 34–35.
- Lawrence JM. 2007. Edible sea urchins: biology and ecology. 2nd ed. *Developments in aquaculture and Fisheries Science* Volume 37. Amsterdam (The Netherlands). Elsevier Press. 529 pp.

- Le Blanc AR, Landry T, Miron G. 2003. Fouling organisms of the blue mussel *Mytilus edulis*: their effect on nutrient uptake and release. *J Shellfish Res* 22:633–638.
- Le Blanc AR, Davidson J, Tremblay R, McNiven M, Landry T. 2007. The effect of anti-fouling treatments for the clubbed tunicate on the blue mussel, *Mytilus edulis*. *Aquaculture* 264:205–213.
- Lee HB, Lim LC, Cheong L. 1985. Observations on the use of antifouling paint in netcage fish farming in Singapore. *Singapore J Primary Ind* 13:1–12.
- Leong J, Turner S. 1979. Isolation of waterborne infectious hematopoietic necrosis virus. *Fish News* 8:vi–viii.
- Lesser MP, Shumway SE, Cucci T, Smith J. 1992. Impact of fouling organisms on mussel rope culture: interspecific competition for food among suspension-feeding invertebrates. *J Exp Mar Biol Ecol* 165: 91–102.
- Lewis JA. 1994. Biofouling and fouling protection: a defence perspective. In: Kjelleberg S, Steinberg P, editors. *Biofouling: problems and solutions – Proceedings of an international workshop*. Sydney (Australia): University of New South Wales. p. 39–43.
- Lewis JA. 2009. Non silicone biocide-free antifouling solutions. In Hellio C, Yebra D, editors. *Advances in marine antifouling coatings and technologies*. Cambridge (UK): Woodhead Publishing Ltd. p. 709–724.
- Lim CY, Yoo YH, Sidhartan M, Ma CW, Bang IC, Kim JM, Lee KS, Park NS, Shin HW. 2006. Effects of copper (I) oxide on growth and biochemical compositions of two marine microalgae. *J Environ Biol* 27:461–466.
- Littlewood DTJ, Marsbe LA. 1990. Predation on cultivated oysters, *Crassostrea rhizophorae* (Guilding), by the polyclad turbellarian flatworm, *Stylochus* (*Stylochus*) *frontalis* Verrill. *Aquaculture* 88:145–150.
- Lleonart M, Handlinger J, Powell M. 2003. Spionid mudworm infestation of farmed abalone (*Haliotis* spp.). *Aquaculture* 221:85–96.
- Locke A, Hanson JM, Ellis KM, Thompson J, Rochette R. 2007. Invasion of the southern Gulf of St Lawrence by the clubbed tunicate (*Styela clava* Herdman): potential mechanisms for invasions of Prince Edward Island estuaries. *J Exp Mar Biol Ecol* 342:69–77.
- Lodeiros C, García N. 2004. The use of sea urchins to control fouling during suspended culture of bivalves. *Aquaculture* 231:293–298.
- Lodeiros C, Pico D, Prieto A, Narvaez N, Guerra A. 2002. Growth and survival of the pearl oyster *Pinctada imbricata* (Roding 1758) in suspended and bottom culture in the Golfo de Cariaco, Venezuela. *Aquacult Int* 10:327–338.
- Madin J, Chong VC, Basri B. 2009. Development and short-term dynamics of macrofouling assemblages on fish-cage nettings in a tropical estuary. *Estuar Coast Shelf Sci* 83: 19–29.
- Magin CM, Cooper SP, Brennan AB. 2010. Non-toxic antifouling strategies. *Mater Today* 13:36–44.
- Maki JC, Mitchell R. 2002. Biofouling in the marine environment. In: Bitton G, editor. *Encyclopedia of environmental microbiology*. New York (NY): John Wiley and Sons. p. 610–619.
- Mallet AL, Carver CE. 2006. Incorporating the New Zealand Tunicate Treatment Technology into a tunicate management strategy for Indian Point Marine Farms. Report prepared for Aquaculture Association of Nova Scotia. Dartmouth (Nova Scotia): Mallet Research Services. 21 pp.
- Mallet AL, Carver CE, Hardy M. 2009. The effect of floating bag management strategies on biofouling, oyster growth and biodeposition levels. *Aquaculture* 287:315–323.
- Manning LM, Lindquist N. 2003. Helpful habitant or pernicious passenger: interactions between an infaunal bivalve, an epifaunal hydroid and three potential predators. *Oecologia* 134:415–422.
- Mao Che L, Le Campion-Alsumard T, Boury-Esnault N, Payri C, Golubic S, Bezac C. 1996. Biodegradation of shells of the black pearl oyster, *Pinctada margaritifera* var. *cumingii*, by microborers and sponges of French Polynesia. *Mar Biol* 126:509–519.
- Marmur A. 2006. Super-hydrophobicity fundamentals: implications to biofouling prevention. *Biofouling* 22:107–115.
- McKindsey CW, Lecuona M, Huot M, Weise AM. 2009. Biodeposit production and benthic loading by farmed mussels and associated tunicate epifauna in Prince Edward Island. *Aquaculture* 295:44–51.
- Menton DJ, Allen JH. 1991. Spherical (Kiel) and square steel cages: first year of comparative evaluations at St Andrews, NB. *Bull Aquacult Assoc Canada* 91:111–113.
- Meyers TR. 1984. Marine bivalve molluscs as reservoirs of viral finfish pathogens: significance to marine and anadromous finfish culture. *Mar Fish Rev* 46:14–17.
- Miller B. 1998. An assessment of sediment copper and zinc concentrations in marine caged fish farms in SEPA West region. Stirling (UK): Scottish Environmental Protection Authority, 77 pp.
- Milne PH. 1970. Fish farming: A guide to the design and construction of net enclosures. Marine Research, No. 1. Department of Agriculture and Fisheries for Scotland. Edinburgh (Scotland): HMSO. 31 pp.
- Milne PH. 1975a. Fouling of marine cages – Part One. *Fish Farming Int* 2:15–19.
- Milne PH. 1975b. Fouling of marine cages – Part Two. *Fish Farming Int* 2:18–21.
- Milne PH. 1979. Selection of sites and design of cages, fishpens and net enclosures for aquaculture. In: Pillay TVR, Dill WA, editors. *Advances in Aquaculture*. Oxford (UK): Fishing News Books Ltd. p. 416–423.
- Miyauti T. 1968. Studies on the effect of shell cleaning in pearl culture – III. The influence of fouling organisms upon the oxygen consumption in the Japanese pearl oysters. *Nihon Seitai Gakkai Shi* (Jap J Ecol.) 18:40 (in Japanese with English abstract).
- Moase PB, Wilmont A, Parkinson SA. 1999. *Cliona* – an enemy of the pearl oyster, *Pinctada maxima* in the west Australian pearling industry. *SPC Pearl Oyster Inform Bull* 13:27–28.
- Mochida K, Ito K, Harino H, Kakuno A, Fuji K. 2006. Acute toxicity of pyrethrin antifouling biocides and joint toxicity with copper to red sea bream (*Pagrus major*) and toy shrimp (*Heptacarpus futilirostris*). *Environ Toxicol Chem* 25:3058–3064.
- Mohammad M-BM. 1972. Infestation of the pearl oyster *Pinctada margaritifera* (Linne) by a new species of *Polydora* in Kuwait, Arabian Gulf. *Hydrobiologia* 39: 463–477.
- Mohammad M-BM. 1976. Relationship between biofouling and growth of the pearl oyster *Pinctada fucata* (Gould) in Kuwait, Arabian Gulf. *Hydrobiologia* 51:129–138.
- Monteforte M, Garcia-Gasca A. 1994. Spat collection studies on pearl oysters *Pinctada mazatlanica* and *Pteria sterna* (Bivalvia, Pteriidae) in Bahia de La Paz, South Baja California, Mexico. *Hydrobiologia* 291:21–34.

- Moring JR, Moring KA. 1975. Succession of net biofouling material and its role in the diet of pen-cultured Chinook salmon. *Prog Fish Cult* 37:27–30.
- Munari C, Mistri M. 2007. Effect of copper on the scope for growth of clams (*Tapes philippinarum*) from a farming area in the Northern Adriatic Sea. *Mar Environ Res* 64: 347–357.
- Naylor RL, Williams SL, Strong DR. 2001. Aquaculture – a gateway for exotic species. *Science* 294:1655–1656.
- Needham T. 1988. Sea water cage culture of salmonids. In: Laird LM, Needham T, editors. *Salmon and trout farming*. Chichester (UK): Ellis Horwood Ltd. p. 117–154.
- Newman LJ, Cannon RG, Govan H. 1993. *Stylochus (Imogene) matatasi* n. sp. (Platyhelminthes, Polycladida): pest of cultured giant clams and pearl oysters from Solomon Islands. *Hydrobiologia* 257:185–189.
- Olafsen T. 2006. Cost analysis of different antifouling strategies. SINTEF Fisheries and Aquaculture, SFH80 A066041, ISBN 82-14-03947-9, 23 pp. (in Norwegian).
- Oliva M, Carmen Garrido MD, Perez E, Gonzalez De Canales ML. 2007. Evaluation of acute copper toxicity during early life stages of gilthead, *Sparus aurata*. *J Environ Sci Health A* 42:525–533.
- Oppedal F, Dempster T, Stien L. 2011a. Environmental drivers of Atlantic salmon behaviour in sea-cages: a review. *Aquaculture* 311:1–18.
- Oppedal F, Vågseth T, Dempster T, Juell J-E, Johansson D. 2011b. Fluctuating sea-cage environments modify the effects of stocking densities on the production and welfare of Atlantic salmon (*Salmo salar* L.). *Aquaculture* 315: 361–368.
- Osawa Y, Tawara Y, Taketomi H. 1985. Studies on behaviour of fish cages against flow of water. On relationship between volume of fish cages and current velocity. *Bull Natl Res Inst Fish Eng (Jpn)* 6:297–321 (in Japanese).
- Paclibare JO, Evelyn TPT, Albright LJ, Prospero-Porta L. 1994. Clearing of the kidney disease bacterium *Renibacterium salmoninarum* from seawater by the blue mussel *Mytilus edulis*, and the status of the mussel as a reservoir of the bacterium. *Dis Aquat Org* 18:129–133.
- Paetzold SC, Davidson J. 2010. Viability of golden star tunicate fragments after high-pressure water treatment. *Aquaculture* 303:105–107.
- Paetzold SC, Davidson J, Giberson D. 2008. Responses of *Mitrella lunata* and *Caprella* spp., potential tunicate micropredators, in Prince Edward Island estuaries to acetic acid anti-fouling treatments. *Aquaculture* 285:96–101.
- Paul JD, Davies IM. 1986. Effects of copper and tin-based antifoulant on the growth of cultivated scallops (*Pecten maximus*) and oyster (*Crassostrea gigas*). *Aquaculture* 54: 191–203.
- Pereira M, Ankjaergaard C. 2009. Legislation affecting anti-fouling products. In Hellio C, Yebra D, editors. *Advances in marine antifouling coatings and technologies*. Cambridge (UK): Woodhead Publishing Ltd. p. 240–259.
- Perepelizin PV, Boltovskoy D. 2011. Thermal tolerance of *Limnoperna fortunei* to gradual temperature increase and its applications for biofouling control in industrial and power plants. *Biofouling* 27:667–674.
- Petersen JK. 2007. Ascidian suspension feeding. *J Exp Mar Biol Ecol* 342:127–137.
- Peterson LK, D'Auria JM, McKeown BA, Moore K, Shum M. 1991. Copper levels in the muscle and liver tissue of farmed chinook salmon, *Oncorhynchus tshawytscha*. *Aquaculture* 99:105–115.
- Pettitt ME, Henry SL, Callow ME, Callow JA, Clare AS. 2004. Activity of commercial enzymes on settlement and adhesion of cypris larvae of the barnacle *Ballanus amphitrite*, spores of the green alga *Ulva linza*, and the diatom *Navicula perimuta*. *Biofouling* 20:299–311.
- Pinori E, Berglin M, Brive LM, Hulander M, Dahlström M, Elwing H. 2011. Multi-seasonal barnacle (*Balanus improvisus*) protection achieved by trace amounts of a macrocyclic lactone (ivermectin) included in rosin-based coatings. *Biofouling* 27:941–953.
- Pioli RF, Dunmore RA, Forrest BM. 2010. Assessing the efficacy of spray-delivered 'eco-friendly' chemicals for the control and eradication of marine fouling pests. *Biofouling* 26:187–203.
- Pit JH, Southgate PC. 2003. Fouling and predation: how do they affect growth and survival of the blacklip pearl oyster, *Pinctada margaritifera*, during nursery culture? *Aquacult Int* 11:545–555.
- Pomponi SA, Meritt DW. 1990. Distribution and life history of the boring sponge *Cliona truitti* in the upper Chesapeake Bay. In: Rutzler K, editor. *New perspectives in sponge biology*. Third Int Conf on the Biology of Sponges, 1985. Washington (DC): Smithsonian Institution Press. p. 384–413.
- Provan J, Murphy S, Maggs CA. 2005. Tackling the invasive history of the green alga *Codium fragile* ssp. tomentosoides. *Mol Ecol* 14:189–194.
- Rajagopal S, van der Velde G, Jansen J. 1995. Thermal tolerance of the invasive oyster *Crassostrea gigas*: feasibility of heat treatment as an antifouling option. *Water Res* 39:4335–4342.
- Ramsay A, Davidson J, Landry T, Stryhn H. 2008. The effect of mussel seed density on tunicate settlement and growth for the cultured mussel, *Mytilus edulis*. *Aquaculture* 275: 194–200.
- Remen M, Oppedal F, Torgersen T, Imsland AK, Olsen RE. 2012. Effects of cyclic environmental hypoxia on physiology and feed intake of post-smolt Atlantic salmon: Initial responses and acclimation. *Aquaculture* 326–329:148–155.
- Rissgård HU, Christensen PB, Olesen NJ, Petersen JK, Møller MM, Anderson P. 1995. Biological structure in a shallow cove (Kertinge Nor, Denmark). Control by benthic nutrient fluxes and suspension-feeding ascidians and jellyfish. *Ophelia* 41:329–344.
- Rius M, Heasman KG, McQuaid CD. 2011. Long-term coexistence of non-indigenous species in aquaculture facilities. *Mar Pollut Bull* 62:2395–2403.
- Rocha RM, Kremer LP, Baptista MS, Metri R. 2009. Bivalve cultures provide habitat for exotic tunicates in southern Brazil. *Aquat Invas* 4:195–205.
- Rosell D, Uriz MJ, Martin D. 1999. Infestation by excavating sponges on the oyster (*Ostrea edulis*) populations of the Blanes littoral zone (north-western Mediterranean Sea). *J Mar Biol Assoc UK* 79:409–413.
- Ross KA, Thorpe JP, Brand AR. 2004. Biological control of fouling in suspended scallop cultivation. *Aquaculture* 229: 99–116.
- Ross KA, Thorpe JP, Norton TA, Brand AR. 2002. Fouling in scallop cultivation: help or hindrance? *J Shellfish Res* 21:539–547.
- Ruesink JL, Lenihan HS, Trimble AC, Heiman KW, Micheli F, Byers JE, Kay MC. 2005. Introduction of non-native oysters: ecosystem effects and restoration implications. *Annu Rev Ecol Syst* 36:643–689.
- Sala A, Lucchetti A. 2008. Low-cost tool to reduce biofouling in oyster longline culture. *Aquacult Eng* 39:53–58.

- Sandberg MG, Olafsen T. 2006. Overview of laws and regulations regarding antifouling methods in fish farming. SINTEF Fisheries and Aquaculture Report SFH80 A066001. Trondheim (Norway): SINTEF Fisheries and Aquaculture. 35 pp.
- Santhanam R, Srikrishnadhas B, Natarajan P. 1983. Fouling problems in cages and pens. In: Proc Natl Seminar on Cage and Pen Culture, Fisheries College, Tamil Nadu Agricultural University, Tuticorin. Cochin (India): Tamil Nadu Agricultural University. p. 143–147.
- Scardino AJ. 2009. Surface modification approaches to control marine biofouling. In Hellio C, Yebra D, editors. Advances in marine antifouling coatings and technologies. Cambridge (UK): Woodhead Publishing Ltd. p. 664–692.
- Scardino AJ, De Nys R. 2011. Mini-review: Biomimetic models and bioinspired surfaces for fouling control. *Biofouling* 27:73–86.
- Scardino AJ, Fletcher LE, Lewis JA. 2009. Fouling control using air bubble curtains: protection for stationary vessels. *J Mar Eng Technol* A13:3–10.
- Sharp GJ, Macnair N, Campbell E, Butters A, Ramsay A, Semple R. 2006. Fouling of mussel (*Mytilus edulis*) collectors by algal mats: dynamics, impacts and symptomatic treatment in P.E.I. Canada. *Science Asia* 32:87–97.
- Short JW, Thrower FP. 1986. Accumulation of butyltin in mussel of Chinook salmon reared in sea pens treated with tri-*n*-butyltin. *Mar Pollut Bull* 17:542–545.
- Silina AV. 2006. Tumor-like formations on the shells of Japanese scallops *Patinopecten yessoensis*. *Mar Biol* 148: 833–840.
- Simon CA, Ludford A, Wynne S. 2006. Spionid polychaetes infesting cultured abalone *Haliotis midae* in South Africa. *Afr J Mar Sci* 28:167–171.
- Solberg CB, Saethre L, Julshamn K. 2002. The effect of copper-treated net pens on farmed salmon (*Salmo salar*) and other marine organisms and sediments. *Mar Pollut Bull* 45:126–132.
- Sorte CJB, Williams SL, Carlton JT. 2010. Marine range shifts and species introductions: comparative spread rates and community impacts. *Glob Ecol Biogeog* 19: 303–316.
- Southgate PC, Beer AC. 2000. Growth of black lip pearl oyster (*Pinctada margaritifera*) juveniles using different nursery culture techniques. *Aquaculture* 187: 97–104.
- Stachowicz, JJ, Terwin JR, Whitlatch RB, Osman RW. 2002. Linking climate change and biological invasions: ocean warming facilitates nonindigenous species invasions. *P Natl Acad Sci USA* 99:15497–15500.
- Stefaniak LM, McAtee J, Shulman MJ. 2005. The cost of being bored: effects of a clionid sponge on the gastropod *Littorina littorea*. *J Exp Mar Biol Ecol* 327: 103–114.
- Stenton-Dozey J, Probyn T, Busby A. 2001. Impact of mussel (*Mytilus galloprovincialis*) raft-culture on benthic macrofauna, in situ oxygen uptake, and nutrient fluxes in Saldanha Bay, South Africa. *Can J Fish Aquat Sci* 58: 1021–1031.
- Svane I, Cheshire A, Barnett J. 2006. Test of an antifouling treatment on tuna fish-cages in Boston Bay, Port Lincoln, South Australia. *Biofouling* 22:209–219.
- Swift MR, Fredriksson DW, Unrein A, Fullerton B, Patursson O, Baldwin K. 2006. Drag force acting on biofouled net panels. *Aquacult Eng* 35:292–299.
- Takemura Y, Okutani T. 1955. Notes on animals attached to the shells of the silver-lip oyster, *Pinctada maxima* (Jameson), collected from the 'East' fishing ground of the Arafura Sea. *Nippon Suisan Gakkaishi* (Bull Jap Soc Fish Sci) 21:92–101 (in Japanese).
- Tan CK, Nowak BF, Hodson SL. 2002. Biofouling as a reservoir of *Neoparamoeba pemaquidensis* (Page, 1970), the causative agent of amoebic gill disease in Atlantic salmon. *Aquaculture* 210:49–58.
- Taylor JJ, Southgate PC, Rose RA. 1997. Fouling animals and their effect on the growth of silverlip pearl oysters, *Pinctada maxima* (Jameson) in suspended culture. *Aquaculture* 153:31–40.
- Terlizzi A, Conte E, Zupo V, Mazzella L. 2000. Biological succession on silicone fouling release surfaces: long term exposure tests in the harbour of Ischia, Italy. *Biofouling* 15:327–342.
- Therriault TW, Herborg L-M. 2008. Predicting the potential distribution of the vase tunicate *Ciona intestinalis* in Canadian waters: informing a risk assessment. *ICES J Mar Sci* 65:788–794.
- Thieltges DW, Buschbaum C. 2007. Vicious circle in the intertidal: Facilitation between barnacles epibionts, a shell boring polychaete and trematode parasites in the periwinkle *Littorina littorea*. *J Exp Mar Biol Ecol* 340: 90–95.
- Thomas K. 2009. The use of broad-spectrum organic biocides in marine antifouling paints. In Hellio C, Yebra D, editors. Advances in marine antifouling coatings and technologies. Cambridge (UK): Woodhead Publishing. p. 522–553.
- Thomas KV, Brooks S. 2010. The environmental fate and effects of antifouling paint biocides. *Biofouling* 26:73–88.
- Thomas PA. 1979. Boring sponges destructive to economically important molluscan beds and coral reefs in Indian seas. *Indian J Fish* 26:163–200.
- Tomi W, Naiki K, Yamada Y. 1979. Investigations into technical development of mariculture on commercial scale applied to offshore region. Proceedings of the Japan – Soviet Joint Symposium on Aquaculture. Tokyo (Japan): Tokai University. p. 111–120.
- Towns RL, Anderson CD. 2009. Fouling control coatings using low surface energy, foul release technology. In Hellio C, Yebra D, editors. Advances in marine antifouling coatings and technologies. Cambridge (UK): Woodhead Publishing Ltd. p. 693–708.
- Velayudhan TS. 1983. On the occurrence of shell boring polychaetes and sponges on the pearl oyster *Pinctada fucata* and control of boring organisms. Proc Symp on Coastal Aquaculture, Cochin, India, 1980. Part 2: Molluscan Culture. Cochin (India): Marine Biological Association of India. p. 614–618. Available from <http://eprints.cmfri.org.in/2308/>
- Vucko MJ, King PC, Poole AJ, Carl C, Jahedi MZ, de Nys R. 2012. Cold spray metal embedment: an innovative antifouling technology. *Biofouling* 28:239–248.
- Wada KT. 1991. The pearl oyster, *Pinctada fucata* (Gould) (Family Pteriidae). In: Menzel W, editor. Estuarine and marine bivalve mollusk culture. Boca Raton (FL): CRC Press. p. 245–260.
- Wahl M, Hay ME, Enderlein P. 1997. Effects of epibiosis on consumer-prey interactions. *Hydrobiologia* 355: 49–59.

- Watson DI, Shumway SE, Whitlatch RB. 2009. Biofouling and the shellfish industry. In: Shumway SE, Rodrick GE, editors. Shellfish safety and quality. Cambridge (UK): Woodhead Publishing. p. 317–336.
- Webster DC, Chisholm BJ. 2010. New directions in antifouling technology. In: Dürr S, Thomason JC, editors. Biofouling. Oxford (UK): Wiley-Blackwell. p. 366–387.
- Weise AM, Cromey CJ, Callier MD, Archambault P, Chamberlain J, McKindsey CW. 2009. Shellfish-DEPO-MOD: Modelling the biodeposition from suspended shellfish aquaculture and assessing benthic effects. *Aquaculture* 288:239–253.
- Wells FE, McDonald JI, Huisman J. 2009. Introduced marine species in Western Australia. Fisheries occasional publication No. 57. Perth (WA): Department of Fisheries. 97 pp.
- Wesche SJ, Adlard RD, Hooper JNA. 1997. The first incidence of clionid sponges (Porifera) from the Sydney rock oyster *Saccostrea commercialis* (Iredale and Roughley, 1933). *Aquaculture* 157:173–180.
- Williams SL, Schroeder SL. 2004. Eradication of the invasive seaweed *Caulerpa taxifolia* by chlorine bleach. *Mar Ecol Prog Ser* 272:69–76.
- Willis JE, Stewart-Clark S, Greenwood SJ, Davidson J, Quijon PA. 2011. A PCR-based assay to facilitate early detection of *Diplosoma listerianum* in Atlantic Canada. *Aquat Invas* 6:7–16.
- Yebra DM, Kiil S, Dam-Johansen K. 2004. Antifouling technology – past, present and future steps towards efficient and environmentally friendly antifouling coatings. *Prog Org Coat* 50:75–104.
- Yukihira H, Klumpp DW, Lucas JS. 1998. Effects of body size on suspension feeding and energy budgets of the pearl oysters *Pinctada margaritifera* and *P. maxima*. *Mar Ecol Prog Ser* 170:119–130.
- Zhan A, MacIsaac HJ, Cristescu ME. 2010. Invasion genetics of the *Ciona intestinalis* species complex: from regional endemism to global heterogeneity. *Mol Ecol* 19:4678–4694.
- Zhu H, Kumar A, Ozkan J, Bandara R, Ding A, Perera I, Steinberg P, Kumar N, Lao W, Griesser SS, et al. 2008. Fimbrolide-coated antimicrobial lenses: their in vitro and in vivo effects. *Optometry Vision Sci* 85:292–300.