

2018

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Citation/Publisher Attribution


Callier, M. D., Byron, C. J., Bengtson, D. A., Cranford, P. J., Cross, S. F., Focken, U.,...McKindsey, C. W. (2017). Attraction and repulsion of mobile wild organisms to finfish and shellfish aquaculture: a review. *Review in Aquaculture*, 10(4), 924-949. <https://doi.org/10.1111/raq.12208>
Available at: <https://doi.org/10.1111/raq.12208>

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Attraction and repulsion of mobile wild organisms to finfish and shellfish aquaculture: a review

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Received 12 September 2016; accepted 11 July 2017.

Abstract

Knowledge of aquaculture–environment interactions is essential for the development of a sustainable aquaculture industry and efficient marine spatial planning. The effects of fish and shellfish farming on sessile wild populations, particularly infauna, have been studied intensively. Mobile fauna, including crustaceans, fish, birds and marine mammals, also interact with aquaculture operations, but the interactions are more complex and these animals may be attracted to (attraction) or show an aversion to (repulsion) farm operations with various degrees of effects. This review outlines the main mechanisms and effects of attraction and repulsion of wild animals to/from marine finfish cage and bivalve aquaculture, with a focus on effects on fisheries-related species. Effects considered in this review include those related to the provision of physical structure (farm infrastructure acting as fish aggregating devices (FADs) or artificial reefs (ARs), the provision of food (e.g. farmed animals, waste feed and faeces, fouling organisms associated with farm structures) and some farm activities (e.g. boating, cleaning). The reviews show that the distribution of mobile organisms associated with farming structures varies over various spatial (vertical and horizontal) and temporal scales (season, feeding time, day/night period). Attraction/repulsion mechanisms have a variety of direct and indirect effects on wild organisms at the level of individuals and populations and may have implication for the management of fisheries species and the ecosystem in the context of marine spatial planning. This review revealed considerable uncertainties regarding the long-term and ecosystem-wide consequences of these interactions. The use of modelling may help better understand consequences, but long-term studies are necessary to better elucidate effects.

Key words: aquaculture, artificial reefs, attraction, farm waste, fish aggregating devices, repulsion, wild population.

Introduction

Knowledge of aquaculture–environment interactions is essential for the development of a sustainable aquaculture industry and for efficient marine spatial planning. Numerous studies (e.g. Karakassis *et al.* 2000; Buschmann *et al.* 2006, Kutti *et al.* 2008, Hargrave 2010) have evaluated the impact of fish and shellfish farming on wild populations, but most of these have focused on sessile organisms or those with low mobility, particularly infauna. This is logical as these organisms integrate effects on benthic sediments over time and are thus commonly used as indicators of farm environmental performance. More mobile fauna also interact with aquaculture operations, but the interactions are more complex and animals, including crustaceans, fish, birds and marine mammals, may react positively (attraction) or negatively (repulsion) to farm operations. The International Council for the Exploration of the Sea (ICES) Working Group on Aquaculture (WGAQUA) was tasked with reviewing available scientific information on attraction and repulsion of organisms due to aquaculture operations. Here, we (members of WGAQUA) provide an overview of the main mechanisms and effects of attraction and repulsion of wild animals to/from marine finfish cage and bivalve aquaculture, with a focus on effects, at the individual and population levels, on fisheries-related species. Mechanisms considered in this review include those related to the provision of physical structure (e.g. farm infrastructure acting as Fish aggregating devices (FADs) and artificial reefs (ARs), farms acting as sources of food (e.g. farmed animals, waste feed from finfish cage culture, farmed animal wastes, fouling organisms on farm structures) and some farm-related effects (e.g. noise, light). It does not cover disease/pathogen transfer and genetic and toxicological effects as these have been previously reviewed (including Weir & Grant 2005). This review is divided into sections on finfish cage culture and bivalve aquaculture.

Interactions between finfish farms and wild populations

Marine fish farms may influence populations of mobile wild organisms in many ways. For example, fish farms may attract wild fish (e.g. Dempster *et al.* 2010; Holmer 2010), invertebrates (Machias *et al.* 2004), marine mammals (Bonizzoni *et al.* 2013) and birds (Buschmann *et al.* 2009a, b). In large part, this is due to the addition of food (uneaten feed pellets and farmed fish) and physical structure to the environment. The former attracts animals by providing them a direct trophic supplement. The latter creates conditions that are indirectly attractive to animals as farm structures provide habitat for organisms that, in turn, may attract other species. Husbandry activities (e.g. noise and

lights) may also attract wild organisms. At the same time, husbandry operations and the addition of feed, wastes and structure may repel some species through various mechanisms. In this section, we provide an overview of the attraction and repulsive mechanisms (summarized in Fig. 1) and effects of finfish cage culture on wild populations (Table 1), with an emphasis on fisheries-related species, particularly fish. We also discuss various consequences of these behaviours on the species that are most affected by finfish cage aquaculture.

Status of knowledge on attraction of wild fish to fish farms

A vast literature shows that wild fish are attracted to finfish farms throughout the world (Table 1). For example, Carss (1990) found increased numbers of saithe (*Pollachius virens*) around rainbow trout (*Oncorhynchus mykiss*) farms in Scottish lochs. Dempster *et al.* (2002) studied nine fish farms in south-west Spain and found consistently greater abundance, biomass and species richness of fish communities in areas directly adjacent to farm sites than in control areas. Likewise, Dempster *et al.* (2009) compared the abundance of wild fish at nine Atlantic salmon (*Salmo salar*) cage sites to paired reference sites in Norway and found wild fish abundance to be 1–3 orders of magnitude greater at farm sites. Subsequently, Dempster *et al.* (2010) observed that the total abundance of wild fish was 20 times greater directly adjacent to four full-scale coastal Atlantic salmon farms in Norway than at a distance of 200 m from them. In a review of the importance of coastal fish farms as FADs, Sanchez-Jerez *et al.* (2011) reported that ca. 160 species of fish have been reported in close proximity to fish farms, although a causal relationship was only reported for 20 species.

Spatial variation

The influence of fish farms may occur at several spatial scales (Table 1). Vertically, the distribution of attracted fish may vary considerably among farm sites. For example, Dempster *et al.* (2005) found that the abundance and biomass of wild fish were consistently greatest in the depth strata adjacent to cages at Mediterranean farm sites but were variably greatest near the bottom or the surface at Canary Islands farms. In Norway, overall fish abundance was consistently greatest at the surface and depths adjacent to salmon farms (Dempster *et al.* 2009). However, the effect in Norway was also species-specific, such that fish richness and the abundance of some species were greatest closer to the bottom. In Indonesia, attracted fish were most abundant in the depth strata adjacent to sea cages for groupers (*Epinephelus fuscoguttatus* and *Cromileptes altivelis*) and rabbitfish (*Siganus* spp.) (Sudirman *et al.* 2009). Bacher *et al.* (2012) concluded that the spatial distribution

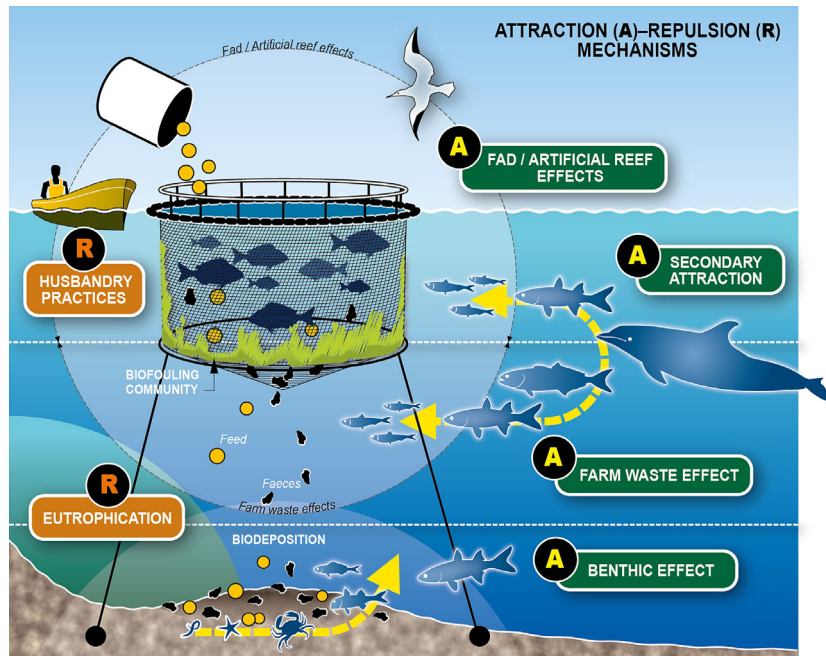


Figure 1 Attraction (A) and repulsion (R) mechanisms of mobile wild populations by fish farming cages. Attraction mechanisms (in green) include: (i) Fish aggregating device (FAD) – and artificial reef (AR) effects (i.e. biofouling communities, refuge, shelter for wild population, light and noise), (ii) Farm waste effect (related to feed waste and faeces, settling of fouling organisms), (iii) Benthic effect (related to the enhancement of organic matter, abundance of benthic invertebrates attracting deposit feeders, etc.) and (iv) Secondary attraction effect (i.e. Predators). Repulsion mechanisms (in orange) include: (i) Husbandry practices (noise, light related to boating, cleaning) (ii) Eutrophication. Yellow dashed arrows illustrate trophic pathways. (Graphic P. Lopez, Ifremer, UMR MARBEC).

of fish around fish farms is a function of both farm and bottom type. The attractive effect of fish farms may also vary over various horizontal spatial scales. Bacher *et al.* (2012) found that cage site attractiveness differed between locations directly under cages from those at the edge of cage arrays, relative to locations more distant from cages, showing that the attraction effect was largely limited to locations within cage arrays. Dempster *et al.* (2010) observed that the dominant wild fish species found near four salmon farms was saithe, which they suggested was consuming waste feed near the farms. Similar patterns were not found for other studied species. The distribution of both Atlantic cod (*Gadus morhua*) and poor cod (*Trisopterus minutus*) varied among farms, with either highest abundances near the farm or a more even distribution of abundance across the distances sampled. No specific pattern of aggregation was evident for the bottom-dwelling haddock (*Melanogrammus aeglefinus*). At a larger spatial scale, work done at a series of three fish farms in the Aegean Sea (Machias *et al.* 2005) found that the abundance of wild fish may be increased even at a considerable distance (2–3 miles) from the farms relative to control sites at >20 miles distant. Likewise, Arechavala-Lopez *et al.* (2011) showed that aggregated bogues (*Boops boops*) around fish farms fed

on waste feed pellets and accounted for a significant part of the artisanal Spanish Mediterranean fishery catch, which operates several kilometres from the fish farms, but did not contribute to the trawl fishery of this species, which operates further away. Arechavala-Lopez *et al.* (2010) used hydroacoustic tagging methods show that grey mullets (*Liza aurata* and *Chelon labrosus*) aggregating around finfish farms may also contribute to commercial fisheries some kilometres from the farm sites. At a bay scale, Goodbrand *et al.* (2013) used hydroacoustic survey methods to evaluate how sea cage aquaculture affects the distribution of wild fish. They concluded that a point source, predictable resource patch, such as a salmon cage farm, within a naturally stochastic environment may enhance biological activity across large spatial scales, increasing the abundance of fish in bays with salmon culture relative to bays without salmon culture. Also using hydroacoustic methods, Gianoulaki *et al.* (2005) showed that fish farms may alter the spatial structure of fish populations over 34–82 km².

Temporal variation

The distribution of fish associated with finfish farming structures (e.g. cages) varies over various temporal scales (Table 1). Many studies have shown that the aggregative

Table 1 Spatial and temporal variability of fish assemblages

References/study area	Farmed species/method	Temporal (daily, seasonal, annual) and spatial effects (horizontal, vertical)
Arechavala-Lopez <i>et al.</i> (2010) Mediterranean Sea	<i>D. labrax</i> , <i>S. aurata</i> VCS	<i>Daily</i> . Grey mullets stay for long period in vicinity of farm. Depth not related to time of day. Except <i>C. labrosus</i> : in deeper water (–15 m) during feeding period. <i>Horizontal</i> . Grey mullet moved to other farm (km away) and nearby commercial fishing area
Arechavala-Lopez <i>et al.</i> (2011) Mediterranean Sea	<i>D. labrax</i> , <i>S. aurata</i> , <i>A. regius</i> /VCS	<i>Horizontal</i> . <i>B. boops</i> , <i>L. aurata</i> , <i>C. labrosus</i> fed around fish farms, may contribute to fisheries some km from the cages
Arechavala-Lopez <i>et al.</i> (2015a) Mediterranean Sea	<i>T. thynnus</i> , <i>S. aurata</i> , <i>D. labrax</i> , <i>A. regius</i> sea/questionnaire surveys	<i>Seasonal</i> . <i>T. thynnus</i> observed throughout the year, except during harvesting time (January to February) and during the spawning period (June) <i>Daily</i> . <i>T. thynnus</i> observed on whole 24 h day period but especially during morning when farm operational activities higher
Arechavala-Lopez <i>et al.</i> (2015b) Mediterranean Sea	<i>D. labrax</i> , <i>S. aurata</i> TM (23 tags)	<i>Seasonal</i> . <i>P. saltatrix</i> . Aggregation in spring and early summer but absent in autumn when seawater temperature dropped (migrating to coastal and estuarine areas for reproduction) <i>Daily × vertical</i> . <i>P. saltatrix</i> significant circadian rhythm regarding swimming depth. Present at deeper waters during feeding periods
Bacher <i>et al.</i> (2012) Mediterranean Sea	<i>T. thynnus</i> , <i>S. aurata</i> VCS; Tt: 0, 30, 200 m; Sa: 0, 100, 200 m	<i>Horizontal</i> . At <i>S. aurata</i> and <i>T. thynnus</i> farms, highest diversity at cage stations <i>Seasonal</i> . No seasonal variation in abundance at <i>S. aurata</i> farm (permanent habitat). At <i>T. thynnus</i> farm, presence of <i>T. thynnus</i> in summer and spring, absence in autumn–winter (related to spawning season and migratory pattern) <i>Vertical</i> . Higher diversity at bottom (35 reef sp.) than in water column (6 sp.)
Bacher <i>et al.</i> (2015) Mediterranean sea	<i>S. aurata</i> VCF; Depth, Feeding intensity, substrate type	<i>Daily</i> . Strong effect of feeding period but species-specific pattern. Most species recorded throughout the day. <i>D. sargus</i> and mugilids strongly affected by feeding vessel proximity; <i>O. melanura</i> and <i>S. salpa</i> dominate surface during feeding period; <i>P. saltatrix</i> (shoals of hundreds of ind) present after feeding period possibly to avoid farm activities, attracted to wild aggregation <i>Vertical × substrate</i> . Abundance and biomass significantly higher at stations over rocky-sandy substrates than sandy substrates stations, especially at bottom. Abundance did not differ by depth at sandy stations
Ballester-Moltó <i>et al.</i> (2015) Mediterranean Sea	<i>S. aurata</i> , <i>D. labrax</i> VCS 4 factors: year, season, day, feeding intensity	<i>Seasonal</i> . Dominant species <i>B. boops</i> , <i>O. melanura</i> and <i>S. aurata</i> showed a strong seasonal pattern related to reproductive stage (maximum abundance occurs during the warmest seasons), whereas <i>L. ramada</i> and <i>S. salpa</i> resident species, no temporal shifts <i>Daily</i> . <i>S. aurata</i> , <i>O. melanura</i> and <i>B. boops</i> dominated during feeding periods. Abundance of <i>L. ramada</i> and <i>S. salpa</i> low early in the morning and increased as the abundance of the dominant species decreased
Bjordal and Johnstone (1993) Norway	<i>S. salar</i> , <i>G. morhua</i> TM (9 tags)	<i>Daily</i> . Local movement of <i>P. virens</i> in relation to fish farms. Active at night. Variability among groups. The fish either had a home range with the cages as the core area, or had a core area in deeper water and visited the farm on a daily basis
Carss (1990) Western Scotland	<i>O. mykiss</i> , <i>S. salar</i> Beach-seine netting, Farm vs Ref. (300 m)	<i>Horizontal</i> . Abundance and biomass beside Farm cages > Ref.
Dempster <i>et al.</i> (2002) Mediterranean Sea	<i>S. aurata</i> , <i>D. labrax</i> + <i>T. thynnus</i> VCS; Farm vs Ref. (200 m)	<i>Horizontal</i> . Abundance, biomass and number of species at Farms > Refs <i>Interfarm</i> . abundance, biomass and number of spp. greater at farms close to shore (proximity to rocky habitat and meadows)
Dempster <i>et al.</i> (2005) Mediterranean Sea, Atlantic (Canary)	<i>S. aurata</i> , <i>D. labrax</i> Farm vs Ref. (50–100 m), Depth	<i>Vertical</i> . Med: consistent vertical structures. Abundances 5.7–162× and biomasses 42–1728× at cage depth > bottom. Canary: Opposite patterns at the 2 farms, highest abundance and biomass at the surface at one farm and on the bottom beneath the other

Table 1 (continued)

References/study area	Farmed species/method	Temporal (daily, seasonal, annual) and spatial effects (horizontal, vertical)
Dempster <i>et al.</i> (2009) Norway	<i>S. salar</i> Farm vs Ref. (1–2 km), Depth	<i>Horizontal.</i> <i>P. virens</i> , <i>G. morhua</i> , <i>M. aeglefinus</i> , 1–3 × greater abundance at Farm > Ref. <i>Vertical.</i> <i>G. morhua</i> and <i>M. aeglefinus</i> more abundant at the bottom
Dempster <i>et al.</i> (2010) Norway	<i>S. salar</i> Video; 0, 25, 50, 100, 200 m	<i>Horizontal.</i> Total abundance 20× time at Farm > Ref. <i>P. virens</i> consistently more abundant at Farm (tightly aggregate to cages). <i>G. morhua</i> and <i>T. minutus</i> either more abundant at Farm site or even distribution across distance. <i>M. aeglefinus</i> : no specific pattern
Fernandez-Jover <i>et al.</i> (2008) Mediterranean Sea	<i>S. aurata</i> , <i>D. labrax</i> VCS Season, Year, Farm and day	<i>Seasonal.</i> Large assemblages of <i>S. aurata</i> and <i>T. mediterraneus</i> at farms during warmer periods (summer). Mugilids and <i>B. boops</i> were dominant in winter <i>Interfarm.</i> High variation among farms (related to environmental conditions and farm characteristics)
Goodbrand <i>et al.</i> (2013) Newfoundland, Canada	<i>S. salar</i> Acoustic surveys Farm bays vs Ref. bays	<i>Horizontal.</i> Bay scale. Abundance in Bays with Farm > Bays without Farm. No effect of cage number on abundance of wild fish
Giannoulaki <i>et al.</i> (2005) Mediterranean Sea	<i>S. aurata</i> , <i>D. labrax</i> Acoustic surveys at night Farm vs Ref. (37 km) Season	<i>Spatial.</i> Effect on the orientation of the spatial structure of wild fish population (directionality) over large spatial scale (34–82 km ²)
Otterå and Skilbrei (2014) Norway	TM (62 tags) + 1837 external T-bar	<i>Horizontal.</i> <i>P. virens</i> maintain connection with salmon farms (part of population does not migrate at all) but long-distance migrations also occur
Özgül and Angel (2013) Red sea	<i>S. aurata</i> VCS	<i>Horizontal.</i> abundance, biomass and diversity: Farm > Ref. 29 species observed only at Farm, 4 at both Farm and Ref., 5 species only at Ref.
Sudirman <i>et al.</i> (2009) South Sulawesi, Indonesia	<i>E. fuscoguttatus</i> , <i>C. altivelis</i> and <i>Siganus</i> spp. VCS, Depth, Times	<i>Daily × vertical.</i> More abundant and highest biomass at surface (0–3 m) around the margins of the cages in the morning (related to feeding period) <i>Horizontal.</i> Total biomass of wild fish outside the cages exceeded the biomass of cultured fish
Šegvić Bubić <i>et al.</i> (2011) Adriatic sea	<i>T. thynnus</i> VCS, Farm vs Ref. (200 m) Season	<i>Horizontal.</i> Abundance and nb. of sp. Farm (17–20 sp.) > Ref. (7 sp.) <i>Seasonal.</i> Highest abundance in summer, lowest biomass in winter <i>Interfarms.</i> Most abundant species: <i>B. boops</i> and <i>B. belone</i> in Farm1; <i>B. belone</i> and <i>O. melanura</i> in Farm2
Uglem <i>et al.</i> (2009) Norway	<i>S. salar</i> Video + 24 tags	<i>Horizontal.</i> Resident <i>P. virens</i> spent 8–10 h day ⁻¹ close to cages. Rapid and frequent movements to adjacent farms (1.6–4.7 km) <i>Daily.</i> Movement pattern strongly related with feeding times. <i>Vertical.</i> Farm1: <i>P. virens</i> more abundant in the upper (5–20 m) part than deeper part (40–60 m). FARM2. evenly distributed across all depth strata
Valle <i>et al.</i> (2007) Mediterranean Sea	<i>S. aurata</i> , <i>D. labrax</i> VCS, Farm vs Ref. (200 m), Season	<i>Vertical.</i> Higher number of species at Farm (12 sp.) > Ref. (4 sp.). Greater abundance, diversity and biomass Farm > Ref. <i>Seasonal.</i> <i>T. mediterraneus</i> dominant in spring, <i>O. melanura</i> dominant in summer and <i>B. boops</i> dominant in winter. Related to recruitment periods for juveniles (ex. <i>O. melanura</i>) and specific preference for warm (<i>T. mediterraneus</i>) or cold (<i>B. boops</i>) water periods

Farmed species: *Dicentrarchus labrax* (European seabass), *Sparus aurata* (gilthead seabream), *Oncorhynchus mykiss* (rainbow trout), *Salmo salar* (Atlantic salmon), *Argyrosomus regius* (meagre), *Thunnus thynnus* (Atlantic bluefin tuna), *Epinephelus fuscoguttatus* (grouper), *Cromileptes altivelis* (grouper), *Siganus* spp (rabbitfish). Aggregated species: *Belone belone* (garfish), *Boops boops* (bogue), *Chelon labrosus* (grey mullet), *Diplodus sargus* (sargo, white seabream), *Gadus morhua* (Atlantic cod), *Liza aurata* (grey mullet), *Melanogrammus aeglefinus* (bottom-dwelling haddock), *Oblada melanura* (oblade), *Pollachius virens* (saithe), *Pomatomus saltatrix* (bluefish), *Sardinella aurata* (round sardinella), *Sardinella maderensis* (Madeiran sardinella), *Sarpa salpa* (salema), *Thunnus thynnus* (Atlantic bluefin tuna), *Trachurus mediterraneus* (horse mackerel), *Trisopterus minutus* (poor cod). Methods used: Visual counts Scuba (VCS), Visual count free diving (VCF), Telemetry (TM), Video survey (Video).

effect of fish farms varies seasonally and may only be present at certain times of the year (Valle *et al.* 2007; Fernandez-Jover *et al.* 2008; Dempster *et al.* 2009; Šegvić Bubić *et al.* 2011; Bacher *et al.* 2012; Özgül & Angel 2013).

Using traditional tagging methods, Bjordal and Skar (1992) found increased numbers of saithe over extended periods (months) around a fish farm in Norway. Subsequent hydroacoustic telemetry work in the same area

showed that saithe at the farm either spent most of their time at the farm or elsewhere but visited cages daily (Bjorndal & Johnstone 1993). Sudirman *et al.* (2009) suggested that variation in fish cage farm attractiveness in Indonesia corresponded to farm feeding times. Other work has shown that feeding operations-related spatial distribution of fish are species-specific such that some species aggregate around feeding times, but other species do not (Uglem *et al.* 2009; Arechavala-Lopez *et al.* 2010; Bacher *et al.* 2015). Bacher *et al.* (2015) showed that fish aggregations around a seabream (*Sparus aurata*) farm generally increased at feeding times. This effect on community distribution was a function of position in the water column (i.e., observed primarily in the mid- and surface waters), whereas species community distribution closer to the seabed was influenced to a greater degree by substrate type. Arechavala-Lopez *et al.* (2015b) observed variation in the abundance of bluefish (*Pomatomus saltatrix*) around Mediterranean seabream/sea bass (*Dicentrarchus labrax*) fish farms at a number of temporal scales. Fish were attracted by farmed fish and telemetry work found that bluefish stayed close to fish farms during the spring and early summer but were absent during the autumn. The fish were typically in deeper waters during the day but moved closer to the surface at night. Both these behaviours reflect movements of bluefish in natural areas. Given that feed input and thus benthic effects (Kutti *et al.* 2007; Valdemarsen *et al.* 2015) vary along the production cycle, it is also logical that the attraction of fish and other animals to farm sites also varies over this time scale. Tuya *et al.* (2006) found that the abundance of most Canary Islands net cage-associated fish species decreased greatly following the cessation of feeding activities. Likewise, work in Norway suggests that the number of saithe present around farm sites decreases following the cessation of salmon feeding (Otterå & Skilbrei 2014). Ballester-Moltó *et al.* (2015) observed that the greatest variation in fish assemblage structure around a Spanish Mediterranean fish farm was related to interseasonal variation, followed by within-season daily variation, and yearly variation between seasons. The abundance of several species was best explained by seasonal effects with their abundances increasing with the onset of reproductive periods. Total abundance was best correlated to feed supply, whereas fish community structure was best explained by the combination of feed supply and photoperiod.

Mechanisms of attraction of wild fish to fish farms

Fish farms may aggregate fish through various mechanisms: a direct trophic link (i.e. a heightened availability of food in the form of waste feed and farmed fish) and FAD/AR effects related to the cage structure,

associated fouling community and secondary attraction of predators (Fig. 1). These mechanisms occur synergistically to attract fish (and other taxa) and are difficult to separate.

Feed waste effects

Uglem *et al.* (2014) reviewed of the impacts of Norwegian salmon farms and suggest that waste aquafeeds are the main attractant of wild fish to fish farms. This was subsequently supported by the study by Ballester-Moltó *et al.* (2015), who found a statistical relationship between total associated fish abundance and feed supply. Feed waste consists of uneaten pellets, feed 'fines' that result from pellet breakage and dust formation during transport, and undigested constituents in cultured fish faeces. Studies on feed wastes around fish farms indicate large variations in their concentration over space and time (Pridmore & Rutherford 1992; Buschmann *et al.* 1996; Lander *et al.* 2014; Brager *et al.* 2015, 2016). Uglem *et al.* (2014) list 17 species that have been shown to feed on waste feed at Norwegian fish farms. This is supported by the large number of studies that have found waste feed in the stomachs of wild-caught fish around net pen sites (e.g. Cars 1990; Fernandez-Jover *et al.* 2007, 2008, 2011b; Dempster *et al.* 2010).

FAD/AR effects

Many studies (see reviews in Rountree 1989; Nelson 2003; Dagorn *et al.* 2013) have found that physical structures in the water column tend to aggregate fish around them and many others have shown the importance of fish cage aquaculture structures as FADs (see reviews in Johannes 2006; but also Boyra *et al.* 2004; Tuya *et al.* 2006; Valle *et al.* 2007; Fernandez-Jover *et al.* 2008; Dempster *et al.* 2009; Oakes & Pondella 2009; Sudirman *et al.* 2009; Dempster *et al.* 2010; Sanchez-Jerez *et al.* 2011). Beveridge (1984) listed a number of features that explain how fish cage aquaculture sites act as FADs (see Table 2). Likewise, Sanchez-Jerez *et al.* (2011) discussed how fish farms may act as ARs by the presence of additional food, increased feeding efficiency, and the presence of shelter to reduce predation and enhance recruitment. They further suggest that fish farms may be of even greater quality than traditional ARs because of the availability of high-quality feed that may be used by wild fish and stimulate the growth of fouling communities. Studies have shown that fouling communities on pens can receive a nutritional boost from the added fish feed (Lojen *et al.* 2005; Callier *et al.* 2013). Likewise, the associated fouling and related communities, including amphipods, small fish, gastropods, may also provide additional trophic resources to aggregated fish which may then be transferred to higher trophic levels (Dolenec *et al.* 2007; Fernandez-Gonzalez *et al.* 2014).

Table 2 Mechanisms proposed to explain floating and stationary Fish aggregating devices (FADs), and their applicability to inland water cage and pen structures (from Beveridge 1984)

Mechanism	Applicability
Use as cleaning stations where external parasites of pelagic fish can be removed by other fish	–
Shade	*
Creates shadow areas in which zooplankton become more visible	*
Provides substrate for egg laying	–
Drifting object serves as schooling companion	–
Provides spatial reference around which fish could orient in an otherwise unstructured environment	*
Provides shelter from predators for small fish	**
Attracts larger fish because of presence of smaller fish	**
Acts as substrate for plant and animal growth, thus attracting grazing fish	**

Note that only water column effects are considered; benthic effects (including feed pellet and other organic loading, benthic community modifications) are not considered. –, * and ** indicate the mechanism has little, some and considerable probable importance.

Biofouling communities. Rich and abundant fouling communities may develop on fish cage nets (see review in Braithwaite & McEvoy 2004; Dürr & Watson 2010; Table 3). Common fouling organisms in marine finfish culture include ascidians, algae, molluscs and cnidarians (Dürr & Watson 2010; Fitridge *et al.* 2012). Spatial and temporal variations in biofouling diversity and biomass may be driven by planktonic events, light availability, water depth and flow, etc.; fouling community biomass will typically decrease with depth (Fitridge *et al.* 2012). In Australia, Cronin *et al.* (1999) found that biofouling on tuna farms added up to an additional 4–5 kg m⁻² net or a total fouling community of 6.5 tonnes per cage. Hodson *et al.* (2000) tested different net types in an Australian salmon farm and reported a biofouling biomass of 1.9 kg ww m⁻² on silicon-coated netting and up to 8.5 kg ww m⁻² (mostly ascidians and the green macroalga *Ulva rigida*) on black uncoated netting. Zongguo *et al.* (1999) examined the fouling communities associated with five Hong Kong fish farms and found between 33 and 55 fouling species per site with a biomass between ca. 4.9 and 11.0 kg m⁻². They also reported an effect of mesh sizes; intermediate mesh sizes of 4 and 6 mm were most heavily fouled, reaching up to ca. 1.4 kg m⁻² after only 21 days in the water. A study on the seasonal (monthly) succession at an offshore cage site in Maine, eastern USA, showed that net fouling biomass reached up to 30 kg m⁻², most of which was mussels (*Mytilus edulis*) (Greene & Grizzle 2007). Although aquaculture cages constitute a good substrate for various sessile marine organisms, it is not fully clear if the nutrients from

the cages (e.g. faeces and waste feed) may cause biofoulers to grow faster, denser or heavier than they would on comparable structures distant from farms. However, although fouling organisms on cage structures may assimilate such wastes (e.g. Redmond *et al.* 2010; Gonzalez-Silvera *et al.* 2015), few studies have attempted to separate structural and nutritional effects. Madin *et al.* (2010) measured the fouling of mesh panels after 8 weeks of immersion in a fish cage culture site in Malaysia and report that sessile organism biomass reached 2.3 kg ww m⁻² in net cages stocked with fed fish as compared to 1.7 kg ww m⁻² on net cages without fish and feed, suggesting that farm wastes stimulate growth of biofouling organisms associated with cage structures.

Studies have shown that these fouling organisms likely impact the associated fish assemblages. Oakes and Pondella (2009) observed increased fish abundance and diversity associated with cage structures in California, noting that the trophic structure of those fish assemblages differed from those from nearby kelp beds. In short, there was a shift towards crushers and pickers at cage sites, suggesting the importance of the fouling community on the cage structures in shifting fish community composition and abundance. This suggests that the physical structure attracts a certain suite of fish. To separate the effect of feed waste and structure on the associated biota, Tuya *et al.* (2006) multiple surveys prior to and following the removal of fish and feeding (but leaving the cage structure in place) at a Canary Islands fish farm. The abundance of most species declined markedly following post-fish removal but that of several groups remained the same (herbivores, benthic macro- and mesocarnivores), including one (benthic macrocarnivores) that remained in greater abundances than in control locations, suggesting that they were present because of the physical farm structure and associated biofouling. Clearly, the level of fouling on nets, and thus net maintenance, will influence the communities of fish and other mobile organisms associated with farms.

Secondary attraction of predators

Fernandez-Jover *et al.* (2016) reported that plankton accumulates around fish farms and that this may aggregate wild fish that feed on this resource. Wild fish may also be attracted by the presence of fish within the cages or by the aggregated fish around them (Arechavala-Lopez *et al.* 2015b). Attraction due to feeding opportunities related to forage fish aggregations and waste feed may occur simultaneously and may be a function of the ecology (species, size, trophic level and feeding strategy) of the wild fish (Bayle-Sempere *et al.* 2013). For example, Bagdonas *et al.* (2012) observed dense aggregations of saithe and small cod beneath salmon cages that were attracted by waste feed, whereas larger cod were attracted by the saithe as prey.

Table 3 Artificial reef effects: dominant species and biomass of fouling communities developing on finfish netcages and shellfish farm

Finfish farm	Dominant fouling organism	Biomass of biofouling on cages (kg ww m ⁻²)	Reference
Atlantic salmon	Marine plants and invertebrates	3.5	Hargrave <i>et al.</i> (2003)
Atlantic salmon	<i>Mytilus edulis</i>	30 (max)	Greene and Grizzle (2007)
Atlantic salmon	Solitary ascidians <i>Asterocarpa humilis</i> and <i>Molgula ficus</i> Green algae <i>Ulva rigida</i>	1.9–8.5	Hodson <i>et al.</i> (2000)
Southern blue-fin tuna	Bivalve and green algae <i>Ulva</i> sp.	≈4	Cronin <i>et al.</i> (1999)
Giant sea perch, Golden snapper Red snapper	Barnacles and <i>Polysiphonia</i> algae	2.3	Madin <i>et al.</i> (2010) (after 8 weeks)
Shellfish farm	Dominant fouling organism	Biomass of biofouling (ww, except mentioned)	Reference
<i>Mytilus edulis</i>	Sedentary: Ascidians, Bivalves, Echinoderms, Polychaetes Errant: Crustaceans, polychaetes	Sedentary: 0.02–36.8 Errant: 0.07–1.44 (g AFDW m ⁻¹)	Jansen <i>et al.</i> (2011)
<i>Euvola ziczac</i>	Barnacles and oysters	>1	Lodeiros and Himmelman (2000)
<i>Placopecten magellanicus</i>	<i>Hiattella artica</i> and <i>Mytilus edulis</i>	0–8	Claereboudt <i>et al.</i> (1994)
<i>Mytilus edulis</i>	Tunicates (<i>Ciona intestinalis</i>)	up to 4 kg m ⁻¹	McKindsey <i>et al.</i> (2009)
<i>Perna canaliculus</i>	brown seaweed <i>Undaria pinnatifida</i> calcareous tube worm <i>Pomatoceros</i> sp.	120 g m ⁻²	Watts <i>et al.</i> (2016)
<i>Mytilus galloprovincialis</i>	green alga <i>Ulva rigida</i> and the calcareous sponge <i>Leucosolenia</i> sp.	Only relative data	Antoniadou <i>et al.</i> (2013)
<i>Clinocardium nuttallii</i>	barnacles, sponges, tube worms sand bryozoans	Expressed in %	Dunham and Marshall (2012)
<i>Pinctada margaritifera</i>	Bivalvia, Ascidiacea, Calcareo and Demospongia and Polychaeta	1798 g net ⁻¹	Lacoste <i>et al.</i> (2014)
<i>Pinctada fucata</i>	Ascidian <i>Didemnum</i>	0.16 g g ⁻¹ oyster	Kripa <i>et al.</i> (2012)
<i>Crassostrea gigas</i>	Ascidians, bryozoans	75% shell surfaces	Rodriguez and Ibarra-Obando (2008)
<i>Perna perna</i>	Algae <i>Polysiphonia subtilissima</i> and <i>Ulva rigida</i> , the bryozoa <i>Bugula neritina</i> and spat of <i>Perna perna</i>	4357 g m ⁻¹ rope	de Sa <i>et al.</i> (2007)

Biofouling may represent a source of food for wild population aggregating around aquaculture farms.

Likewise, Arechavala-Lopez *et al.* (2014, 2015a) observed large predatory fish (tuna *Thunnus thynnus* and swordfish *Xiphias gladius*) to aggregate around Mediterranean fish farms and Papastamatiou *et al.* (2010) used hydroacoustic tags to document site fidelity and aggregations of sharks around Hawaii fish farms, underlining the importance of fish farms in aggregating these top predators. A number of other studies have also described the attraction of several shark species to fish cages in a number of sites worldwide (see Price *et al.* 2017). These top piscivorous fish do not seem to change their feeding behaviour around farms (Sanchez-Jerez *et al.* 2008; Arechavala-Lopez *et al.* 2014), likely indicating that they are using farms as hunting areas (Izquierdo-Gomez *et al.* 2014).

Benthic effect

There is a wealth of information on how fish farm-related organic loading may modify benthic conditions (i.e. infaunal communities, macro-epifaunal

communities, sediment biogeochemistry) (e.g. Black 2001; Holmer *et al.* 2008). This and the addition of physical structure (e.g. anchors) may also impact various seagrasses and algae that may underlay netpen structures (Holmer *et al.* 2003; Vandermeulen 2005). In general, benthic impacts are typically greatest directly below farms and there may also be a stimulatory effect on benthic infaunal biomass and diversity at intermediate distances (Kutti *et al.* 2007; Callier *et al.* 2013), as may also occur for algae and epifauna. Although not the subject of this review, toxicity of hydrogen sulphide in sediments and sulphide outgassing from anoxic areas under and around fish cages should not be ignored. These by-products are known to have a great effect on infaunal communities and are thus used as indicators of stress in monitoring programs (e.g. Hargrave *et al.* 2008; Hargrave 2010). Although the effects of sulphide *per se* and related geochemical processes are well studied for wild populations of macro-epifaunal animals in the field,

there is a vast literature showing the importance of these products to farmed species. For example, Xu *et al.* (2014) found that sulphide had a variety of negative effects on the swimming crab *Charybdis japonica* and Black *et al.* (1996) observed that sulphide levels were negatively and positively correlated with farmed Atlantic salmon growth and mortality, respectively, at farms in Scotland and Ireland, suggesting that sulphide may have similar effects on wild macro-epifaunal species. The necrobenthic fauna, with their greater mobility and home ranges, may be attracted both directly by the increased sedimentation of organic wastes below and in the vicinity of the fish farms and indirectly by the increased biomass of primary producers, infauna and fouling organisms (Vizzini & Mazzola 2006). Modification of these communities and sediment geochemical conditions may attract or repel fish and other organisms, depending on a given species' ecology. These effects have not been well examined, but Dempster *et al.* (2011) suggested that differences in diet (other than the presence of fish feed) in saithe and cod between farm and reference locations was likely due to shifts in benthic macrofaunal and fish communities brought on by salmon farming. Likewise, Fernandez-Jover and Sanchez-Jerez (2015) found that non-aquafeed stomach contents differed between sea bream/sea bass farm locations and nearby reference locations for newly recruited sand smelt (*Atherina boyeri*), saddled seabream (*Oblada melanura*), and salema (*Sarpa salpa*), perhaps also reflecting differences in benthic assemblages due to farm effects.

Husbandry practices

Artificial lights are used to light work areas at night and to stimulate or suppress sexual maturation of farmed fish to stimulate somatic growth, to maintain fish flesh quality, or to affect swimming behaviour, fish density and welfare (Juell & Fosseidengen 2004; Oppedal *et al.* 2011). Lights may be deployed above or below the water surface (Trippel 2010) and may be moved vertically in the water column over various time scales (Wright *et al.* 2015). Although little information is available on the impact of such lighting on the attractiveness of fish farms to wild fish and other organisms, using lights to fish at night for various fish and squid is a well-known practice and thus likely also occurs for fish cage-related lighting over some spatial scale (see review in Marchesan *et al.* 2005; Trippel 2010). Indeed, McConnell *et al.* (2010) showed that various fish species were attracted to a light typically used in salmon aquaculture in British Columbia. This effect may be due to attracted zooplankton attracting fish predators (Otterå & Skilbrei 2014) and affect both the horizontal and vertical positions of fish around cages (Skilbrei & Otterå 2016). Likewise, lights may also affect the distribution of marine

birds, with many nocturnal ones being attracted to light sources (Montevecchi 2006), and mammals, but little evidence was found for this in the literature specifically as it relates to finfish aquaculture.

As outlined by Olesiuk *et al.* (2010), noise related to aquaculture activities may have a variety of attraction and repulsive effects on invertebrates, fish, birds and marine mammals. Noise includes that made by normal farm operations (e.g. farm machinery, operational vessels), that produced occasionally (e.g. construction and demolition) and that specifically used to ward off predators, particularly pinnipeds (e.g. Acoustic Harassment Devices – AHDs, cracker shells). Noise is well propagated in the marine environment and may displace animals from their habitat, interrupt normal movement or migration patterns, affect foraging and reproductive behaviour and increase the risk to predation (Richardson *et al.* 2013). AHDs to deter pinniped attacks at salmon farms may have a variety of far-field effects on non-target cetaceans, including porpoises and killer whales, displacing these marine mammals large distances from farms protected in this manner (Mate & Harvey 1987; Strong *et al.* 1995; Taylor *et al.* 1997; Johnston & Woodley 1998; Morton 2000; Gordon & Northridge 2002; Johnston 2002; Morton & Symonds 2002). In contrast, pinnipeds may habituate to these devices and may eventually experience related hearing loss (Götz & Janik 2015). Furthermore, Nelson *et al.* (2006) questioned the effectiveness of AHDs and the Aquaculture Stewardship Council (2012) discourage the use of AHDs and recommend other management strategies. Careful stock management (density control and regular removal of mortalities from cages), use of seal blinds and appropriate net tensioning are all considered suitable methods to minimize interactions between some marine mammals and finfish culture. Effects on fish and invertebrates have not been documented (Olesiuk *et al.* 2010), although some work has shown that recruitment of some invertebrates may be stimulated by farm-related (e.g. generators and engines) noises (Stanley *et al.* 2012; Wilkens *et al.* 2012; McDonald *et al.* 2014).

Effects of fish farms upon wild fish fitness and population effects

Biomass

Aggregations of wild fish around fish farms may have a variety of population-level effects on wild fish. As outlined by Uglem *et al.* (2014), given that 1.3% of the 1.6 M t of feed used for the salmon farming industry has been assumed to be consumed by wild saithe, this suggests that the biomass of this fish may have increased by ca. 21 000 t since the onset of farming. How this estimated increase in biomass impacts the population of this species and the fitness of individuals is unclear. Likewise, estimates of lost

feed and faeces to the environment in British Columbia, Canada, amount to greater than 6500 tonnes per year (Brown *et al.* 2011). If a fraction of this is taken up by fished species, then their total biomass should be likewise increased.

Condition

As discussed above, many fish that aggregate around fish farms likely do so for the waste feed, the consumption of which modifies lipid signatures. For example, Fernandez-Jover *et al.* (2007) showed that Mediterranean horse mackerel feeding around sea bass and seabream farms off the Spanish Mediterranean coast had significantly higher body fat content than fish from a more distant location and that the fatty acid composition also differed between fish from these two locations. Saithe, particularly abundant around salmon cages in northern Europe (Dempster *et al.* 2010), may obtain a significant proportion of their diet from waste feed (Uglem *et al.* 2014). This has been suggested to increase body and liver condition of gadoids around fish farms in Norway, including increasing the concentration of terrestrial-derived fatty acids and decreasing the concentration of docosahexaenoic acid (DHA) in the flesh and liver of these fish (Fernandez-Jover *et al.* 2011b). These authors and others (e.g. Ramírez *et al.* 2013) have thus suggested that fatty acid composition could serve as a biomarker to infer the influence of fish farms on local fish communities, which help to better understand the environmental consequences of fish farming. Izquierdo-Gomez *et al.* (2014) examined four species of fish around Mediterranean fish farms and found total lipid content and fatty acid profiles from fish from up to around 10 km distant from farms to differ from those of fish caught further from farms. Effects are not limited to fish. Northern shrimp (*Pandalus borealis*) fatty acid signatures were altered close to salmon farms in Norway relative to those caught away from farms (Olsen *et al.* 2012). Izquierdo-Gomez *et al.* (2015) showed that caramote prawn (*Melicertus kerathurus*) were larger and heavier close to farms than distant from them and isotopic evidence suggested that prawns close to the farm had been feeding on farm wastes. Feeding on aquafeeds has been shown experimentally to impact saithe skin and muscle colour, pH, fatty acid composition and sensory parameters relative to wild-caught fish (Skog *et al.* 2003; Otterå *et al.* 2009).

Growth and reproductive success

The implication of these modifications of fish populations and communities in terms of health status and reproductive potential is poorly understood (Fernandez-Jover *et al.* 2011a). Fernandez-Jover and Sanchez-Jerez (2015) found that a number of morphological traits for a number of fish species (*A. boyeri*, *O. melanura* and *S. salpa*) differed

between natural rocky reefs and farm (seabream/seabass) sites in south-east Spain. Fish in farm sites were, on average, smaller than those in reference areas, which was reflected in lower growth rates, as detected by otolith measurements in salemma (*S. salpa*). Abaad *et al.* (2016) also found that otolith size varied for salemma between seabream/seabass farm cage sites and natural sites on Gran Canaria (Canary Islands) but that fish size-corrected otoliths were larger in fish close to farms than in those from reference sites; the size of bogue otoliths did not differ between treatment areas.

Measures of fish condition, including condition indices and hepatosomatic indices, are typically correlated with spawning success and are often greater in fish that aggregate around fish farms (Fernandez-Jover *et al.* 2011a). However, Fernandez-Jover *et al.* (2011a) point out that modified fatty acid composition may impact reproductive success, potentially reducing growth, egg quality, fecundity and larval survival. The implication of this on fish populations is poorly understood (Fernandez-Jover *et al.* 2011a). Although Jørstad *et al.* (2008) and van der Meeren *et al.* (2012) have found that cod offspring from adults reared in netpens may survive and become a *de facto* part of the wild population, Uglem *et al.* (2012) have shown that they also have reduced reproductive viability relative to cod fed on natural feed and suggested that this is due to nutritional deficiencies.

Migration patterns

Evidence suggests that fish farms may alter the movement and migration patterns of fish aggregated around them. Although early studies on the movement of saithe found that salmon farming has not influenced seasonal migration patterns (Bjordal & Skar 1992), more recent work has found conflicting results. Otterå and Skilbrei (2014) did a combined hydroacoustic and T-bar tagging study to examine the movement of saithe around salmon farms in Norway and found that while many finfish continue to undertake normal migration patterns, many others do not migrate offshore and remain in the farm area for much of the year, although they may move often between farm sites, as was also noted by Uglem *et al.* (2009). Likewise, Arechavala-Lopez *et al.* (2010), also using hydroacoustic tagging methods, showed that grey mullet aggregating around seabream and sea bass farms also move rapidly among farm sites and are similarly connected to populations on fishing grounds in the western Mediterranean Sea. Ballester-Moltó *et al.* (2015) suggest that Atlantic bluefin tuna (*T. thynnus thynnus*) modify their migration patterns due to the attractiveness of a Mediterranean fish farm. Özgül and Angel (2013) showed that the suite of species associated with Red Sea fish farms were usually associated with coral reefs, including those >4 km distant from cage sites, suggesting that the

farms modified the distribution of these species. Anecdotal evidence from fishers in Norway suggests that migrating cod have changed their spawning migratory behaviour since the establishment of salmon farms in some areas. Likewise, fishers in the Bay of Fundy, eastern Canada, have suggested that herring and gravid female lobster avoid areas where salmon aquaculture has established (Wiber *et al.* 2012).

Fisheries consequences

As discussed above, many fish tend to aggregate around fish farms at various temporal and spatial scales. These fish are often, to some extent, protected from fishing pressure through legal instruments (i.e. laws to prevent fishing close to farms) or simply practical issues (e.g. to avoid entanglement in farm infrastructure) (Dempster *et al.* 2010). In other locations, fish may be at greater risk of capture as they are concentrated in smaller areas. Indeed, Bacher and Gordo (2016) suggested that artisanal fishing within farm areas and commercial fishing may impact fish abundances, even though the latter occurs some distance from farms. Likewise, Izquierdo-Gomez *et al.* (2014) found that fish caught directly around farm sites by small-scale artisanal fishers had lipid signatures of fish that had fed on aquafeeds, whereas fish caught by trawl fisheries away from farms did not. Arechavala-Lopez *et al.* (2010) used hydroacoustic tags to demonstrate that farms and local fishing grounds in the western Mediterranean Sea are connected through wild fish movements, concluding that these farms probably cause ecological changes to large numbers of commercially important fish species, directly around and up to several kilometres away from farms. Similar patterns have been observed elsewhere (e.g. Giannoulaki *et al.* 2005; Arechavala-Lopez *et al.* 2011; Goodbrand *et al.* 2013).

Machias *et al.* (2006) suggested that increased abundances due to the trophic subsidy provided by finfish net culture increases fisheries landings. Fish may be caught in some sort of ecological trap whereby short-term gains in fitness due to trophic benefits from waste feed or associated prey species may be greatly offset by increased susceptibility to capture by commercial or recreational fishing (Fernandez-Jover *et al.* 2008). For example, Sanchez-Jerez *et al.* (2011) suggested that commercial and recreational fishing has increased around fish farms in the Mediterranean part of Spain. In addition, many fish species having isotopic signatures that suggest they are trophically connected to fish farms have been observed in fisheries catches (Arechavala-Lopez *et al.* 2011; Izquierdo-Gomez *et al.* 2014). Dempster *et al.* (2011) suggested that fish farms may act as reproductive sources for wild fish populations, provided the fish are protected from fishing while resident near farms to allow increased condition to result in greater reproductive output. Thus, a number of authors have suggested that fish

farms be managed somewhat like marine protected areas (MPAs) to ensure that they contribute to wild stocks through increased biomass and related parameters (e.g. Dempster *et al.* 2002, 2005; Dempster & Sanchez-Jerez 2008; Özgül & Angel 2013; Arechavala-Lopez *et al.* 2014).

Interactions with birds and marine mammals

Marine mammals and birds may also be attracted to sea cages. For example, a series of studies by Díaz López *et al.* (2005, 2008), Díaz López (2006, 2009), Díaz López and Bernal Shirai (2007) has shown that bottlenose dolphins (*Tursiops truncatus*) are attracted to fish cages in Italy because of the large number of fish, on which they feed, that are attracted to the net structures. They have also shown that the dolphins have changed their social structure, modifying hunting tactics to respond to increased prey densities around fish farms. Piroddi *et al.* (2011) suggest that this same species has also increased in abundance in Greek fish farm areas because the farms facilitate prey capture. Elsewhere, Ribeiro *et al.* (2007) suggested that the spatial distribution and habitat use by Chilean Dolphins (*Cephalorhynchus eutropia*) are not influenced by the presence of salmon cage farms in Chiloé Island, Chile. Likewise, Haarr *et al.* (2009) suggested that harbour porpoise (*Phocoena phocoena*) fed around and were not displaced by an Atlantic salmon farm in the Bay of Fundy, eastern Canada, except for short periods when high levels of disturbance, such as feed delivery or cleaning, were present. Seals and sea lions are also attracted to fish farms and have been recorded to be more abundant around them than similar areas without fish farms (Sepúlveda & Oliva 2005; Nelson *et al.* 2006; Robinson *et al.* 2008; Sanchez-Jerez *et al.* 2011; Northridge *et al.* 2013). Indeed, Quick *et al.* (2004) suggested that pinnipeds are the group of greatest concern for predation or control on Scottish salmon farms. In contrast, Jacobs and Terhune (2000) suggest that harbour seals in New Brunswick, eastern Canada, are not attracted to areas with salmon farms. Although mustelids, such as otters and mink, may also be attracted to fish culture sites as sources of food (Quick *et al.* 2004; Sales-Luis *et al.* 2013), this review found only anecdotal evidence of the importance of this attraction.

Birds may be attracted to the physical structure provided by netpens as they create novel roosting areas (Forrest *et al.* 2007), to lights used in farming operations (Sagar 2013), or to waste feed (Christopher W. McKindsey, pers. obs., 2016, 2017). Birds may also be attracted to farmed and associated fish. For example, a study in Chile found that the abundances of omnivorous diving and carrion-feeding marine birds were two and five times, respectively, as abundant in areas with salmon farms than in nearby reference areas (Buschmann *et al.* 2009a,b). On the other hand, fish farms

may also displace seabird colonies or feeding areas, either directly by occupying space or indirectly by altering benthic conditions to make them less attractive to birds that feed on benthos or due to farm activities (e.g. noise, light) (Sagar 2013). At times, top predatory birds, such as bald eagles *Haliaeetus leucocephalus*, may roost on salmon net pens, consuming salmon that have jumped onto protective netting (Christopher W. McKindsey, pers. obs., 2016, 2017). Elsewhere, osprey *Pandion haliaetus* and other predatory birds may prey on juvenile farmed fish and may cause significant damage to farm operations (Bechard & Márquez-Reyes 2003).

Trapping in anti-predator netting and other causes of mortality

A variety of methods are used to reduce the impacts of predators that are attracted by farmed and associated fish, with the most efficient means appearing to be anti-predator netting. Such nets and related hardware pose a risk of potential entanglement to seals and other marine mammals, birds and sharks (Kemper & Gibbs 2001; Tlusty *et al.* 2001; Würsig & Gailey 2002; Forrest *et al.* 2007; Ribeiro *et al.* 2007), although there are few verified reports of marine mammals being entangled by aquaculture gear (Price *et al.* 2017). Data on rates of entanglement are rarely quantitative, and the extent of the problem is poorly known. In a 15-month survey in Italy, Díaz López and Bernal Shirai (2007) observed an average entanglement rate of one dolphin per month for cages with loose anti-predator netting and zero for those with taut anti-predator netting. As visits by dolphins to fish cage sites in the study area seem to be increasing with the number of farms (Bearzi *et al.* 2009), such encounters may become more common. Minimum estimates (i.e. from self-reporting) of harbour seal entanglements in Washington, western USA, from 1997 through 2001 declined from 15 in 1997, to five in 1998, and to zero thereafter (Carretta *et al.* 2009). Likewise, seabirds may also become entangled in anti-predator netting or otherwise killed from various practices associated with finfish net cage aquaculture, as has been reported from Scotland (Carss 1993, 1994). Many farms cover cages to keep piscivorous birds away from juvenile fish, and Carss (1994) reported that many types of birds (e.g. shags, cormorants, and herons) were killed both intentionally (i.e. shot, drowned or poisoned) and unintentionally (entanglement while foraging within cages on farmed fish or around cages on associated organisms) during net cage operations in Scotland. A more recent study in Scotland (Quick *et al.* 2004) also found managers use top nets and shooting to control bird problems and suggested that gulls may currently cause greater problems than they had in the past.

Losses to the aquaculture industry due to direct predation by pinnipeds or by them damaging netting, which

may lead to escapes, may be substantial (e.g. Jamieson & Olesiuk 2001). Thus, lethal deterrents are permitted in several jurisdictions and may impact pinnipeds directly. For example, Fisheries and Oceans Canada (2016) report that licensed pinniped killings at British Columbia marine fish farms dropped from a high of almost 750 animals in 1999 to a couple of hundred by 2011, and then down to only a few per year thereafter once license conditions (i.e. killing only animals trying to breach the system or causing harm to infrastructure) were better enforced and public online reporting of mammal kills was initiated (Fig. 2). Prior to this, deaths of Stellar sea lions dropped to zero once it was designated by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) as a Species of Special Concern in 2003. Accidental deaths (e.g. from entanglement) have remained fairly stable at an average of about 12 per year since 2008. Likewise, the number of pinnipeds killed to protect farms in Scotland have also decreased from a maximum total of 459 in 2011 to 69 in the first three quarters of 2016 (Scottish Government 2017). Price *et al.* (2017) suggest that interactions between pinnipeds and fish farms in some regions have decreased with improved net tensioning, farm husbandry and siting practices, and enhanced vigilance and enforcement of license conditions. While this is the case in British Columbia, Kerra Shaw (pers. comm., 2017) suggests that the main driver of decreased mortalities is a recent reticence of the industry to kill nuisance animals, even while pinniped populations and non-lethal interactions are increasing.

Interaction between shellfish farms and wild populations

There are two main general mechanisms by which bivalve aquaculture activities attract and repel wild populations of mobile species. The first is the addition of physical structure to the environment. This includes the farm infrastructure as well as the bivalves that are being grown, both of which provide hard substrate for a variety of sessile and mobile organisms. Second, the farmed bivalves, the organisms growing on or otherwise associated with the farm infrastructure and product, and those organisms impacted by organic loading related to farming, may be important food resources in an area. Farm husbandry activities may also influence the degree to which various organisms are attracted or may display aversion to farm sites.

Attraction of wild fish populations by shellfish farm structure

Shellfish aquaculture introduces considerable hard physical structure into an environment (bottom and water column)

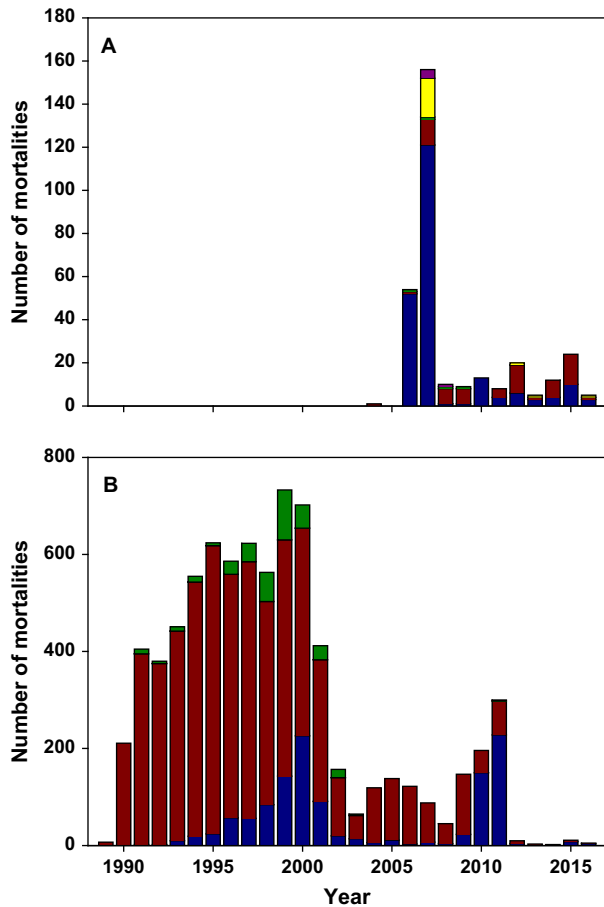


Figure 2 Marine mammal fatalities at marine finfish aquaculture facilities in British Columbia, Canada, 1989–2016. (A) Accidental deaths (entanglements, etc.) (■) California sea lion; (■) Harbour seal; (■) Stellar sea lion; (■) Unidentified pinniped; (■) Harbour porpoise; (■) Humpback whale. (B) Intentional deaths (i.e. animals killed intentionally for predator management). Note that data on accidental deaths prior to about 2007 is incomplete. (Data from Aquaculture Management Directorate, Pacific Region, Fisheries and Oceans Canada.) [Colour figure can be viewed at wileyonlinelibrary.com]

where such structure may largely be absent (Moroney & Walker 1999; Carman *et al.* 2010; McKindsey *et al.* 2011). The physical farm infrastructure (buoys, ropes, anchors, cages, nets, etc.) provides substrate for organisms from a wide range of taxa, including macroalgae, bryozoans, other molluscs and tunicates (Willemssen 2005). The shells of farmed bivalves add additional hard substrate to the environment. These farmed, fouling and associated organisms thus form the biological components of artificial reef-like structures which may attract fish and invertebrates (Costa-Pierce & Bridger 2002). Often, the extent to which these animals are attracted to the structure itself (e.g., as a refuge from predators) or to the prey associated with the structure is unclear (Würsig & Gailey 2002).

Water column

Fouling is the bane of the aquaculture industry (Dürr & Watson 2010; Fitridge *et al.* 2012) and there is abundant literature on that associated with bivalve culture (Table 3), including its ecological effects (see reviews in Dumbauld *et al.* 2009; Forrest *et al.* 2009; McKindsey 2011; Lacoste & Gaertner-Mazouni 2015). In summary, addition of physical structure in the water column allows for the development of substantial and diverse communities in the water column that have a structure similar to that of natural reefs. The physical structure, associated organisms and organic matter that settle within these structures may then attract fish and other large organisms. For example, Brooks (2000) and Carbones (1993) describe a diversity of fish that are attracted to farm sites as they feed on the mussel line-associated communities. Brehmer *et al.* (2003) examined the distribution of fish and fish schools in a French Mediterranean longline mussel growing area and found a greater number, but smaller size, of fish schools within mussel culture sites than outside of the sites. Šegvić-Bubić *et al.* (2011) reported that some fish that frequent mussel sites in Croatia were present because they hunted other fish that were attracted to the farm. Dealeris *et al.* (2004) found a greater abundance and diversity of fish and mobile invertebrates associated with rack and bag oyster culture than with either seagrass or sand areas in Rhode Island, eastern USA, and attributed this to the former having the greatest habitat value for these organisms. Also working on rack and bag oyster culture in Rhode Island, Tallman and Forrester (2007) found that some species of fish were more abundant in culture sites than either natural reefs or ARs, suggesting that this habitat was attractive for these species. Similar results were found in Delaware for rack and bag oyster culture (Erbland & Ozbay 2008) and for floating oyster bag culture (Marenghi *et al.* 2010). In France, an experimental study determined that sole (*Solea solea*) use rack oyster-rearing structures as resting sites during daytime (Laffargue *et al.* 2006).

Bottom

Fixed benthic structures include bags used for oyster or clam culture, on-bottom anti-predator netting used for infaunal clams, PVC tubes for outplanting large individual clams and anchoring systems. Although there is limited information on how bivalve aquaculture-related benthic physical structure attracts or repels wild fish and invertebrates, there is considerable information on the importance of artificial structures used as reefs to enhance fisheries species (e.g. Jensen *et al.* 2000; Seaman 2000; Brickhill *et al.* 2005). Similar conclusions may be inferred on the importance of benthic structure in aquaculture. In general, benthic structures provide considerable surface area for sessile and other hard substrate-associated organisms that are not

normally found on soft sediment bottoms, as is often the case in coastal embayments where bivalve aquaculture is practised. An experimental study showed that American lobster (*Homarus americanus*) were attracted to the presence of cement anchor blocks used in mussel farms in eastern Canada rather than to mussel fall-off *per se* (Drouin *et al.* 2015). In Washington, the abundance of transient fish and macroinvertebrates in geoduck (*Panopea generosa*) sites with outplanting structures was twice that observed in reference areas, suggesting that some groups were attracted to the physical structure provided, or to the organisms associated with it (Washington Sea Grant 2013). Powers *et al.* (2007) suggested that the increased abundance of structural species (macroalgae and some erect epifauna) growing on quahog (*Mercenaria mercenaria*) grow-out bags in North Carolina increased the abundance and diversity of associated macrofauna (fish and macroinvertebrates) from baseline levels observed in sandy habitats to levels at least as great as those found in nearby seagrass beds.

The accumulation of biogenic structure (i.e. shells and shell hash) on the bottom and on nearby shores within bivalve farm sites from fall-off and other processes may be considerable and add physical structure to the benthic environment (Cole 2002). In Canada, Léonard (2004) showed that an average of 130 g m⁻² of material fell daily to the bottom under mussel lines in îles de la Madeleine, Fréchet (2012) suggested that 59% of the total benthic organic loading from mussel culture is from fall-off, and Comeau *et al.* (2015) estimated that 89% of the spat seeded on mussel lines in Prince Edward Island is lost through fall-off prior to harvesting. In Denmark, Nielsen *et al.* (2016) reported that 95% of the stocked mussels were lost during the production cycle. In Scotland, shell hash from fallen mussels can dominate sediments (Wilding & Nickell 2013). Kaspar *et al.* (1985), de Jong (1994), and Inglis and Gust (2003) reported the build-up of live mussels and shell material under mussel farms in New Zealand. Iglesias (1981) and Freire and González-Gurriarán (1995) also noted an abundance of mussels and shell, and shell fragments in the Ría de Arosa, Spain. Given the importance of bivalves in general in creating conditions that attract a great diversity of organisms (Gutiérrez *et al.* 2003; Sousa *et al.* 2009), such accumulations on the bottom should also logically attract a variety of associated species. A number of studies on mussel farm effects mention that rich communities may be associated with these shell reefs but little work has quantified the attractiveness of these habitats to fish and other groups.

For bivalves cultured on the bottom, such as oysters, the physical structure added also includes the shells of the live farmed organisms, which may serve as biogenic habitat for benthic invertebrates, fish and mobile crustaceans in areas where this may be limiting (National Research Council 2010). There is a large literature on natural oyster reefs as

habitat and ecosystem services provided (see review by Peterson *et al.* 2003). For example, Trianni (1995) examined epifauna and infauna in habitat types in California and found that diversity was greater in sites with on-bottom oyster culture relative to one with a muddy bottom because of the increased abundance of epifauna associated with oyster valves. Studies have also shown greater diversities and abundances of fish associated with on-bottom oyster sites relative to areas without structure and/or similar to those with some type of natural structure. Mussel beds are areas of high secondary production, but also sites where hard substrate species are able to find an attachment surface and other species may find a refuge within the mussel bed matrix. However, the density of associated species was lower for culture plots compared with natural mussel beds, particularly for soft sediment species but, given the high number of culture plots, the total pool of associated infaunal species at the ecosystem scale was estimated to be greatest in culture plots (Drent & Dekker 2013).

Attraction of wild populations by farmed shellfish

Many organisms are attracted to bivalve farms because the farmed animals themselves are an attractive potential food source. In addition to the bivalves on culture structures, many mussels and associated organisms may also fall off from culture structures and thus become available to benthic predators. The fall-off of dry tissue mass at a Danish mussel farm totalled 0.5 kg m⁻² during the approximately 1-year production cycle with a mean daily loss of 3 g m⁻² (calculated from data in Nielsen *et al.* 2016). Early studies found increased abundances of crabs and fish within mussel farms relative to adjacent areas (Tenore & González 1976; Chesney & Iglesias 1979; Romero *et al.* 1982) and subsequent work in the same area (Freire *et al.* 1990; Freire & González-Gurriarán 1995) found that crab diets in farms had shifted to contain a greater proportion of mussels, suggesting that the animals move to the mussel farming areas to obtain a trophic advantage.

Other predatory animals, such as starfish and gastropods, are also commonly more abundant within mussel farms relative to adjacent areas (Olaso Toca 1979, 1982; Inglis & Gust 2003; D'Amours *et al.* 2008). However, multiple factors may account for this observation. For example, Drouin *et al.* (2015) used observational and manipulative studies to describe spatial variation in the abundance of American lobster in and around a mussel farm in Canada. Spatial variation was attributed to lobster being attracted to anchor blocks that serve as refuges and to increased prey abundance, including both fallen mussels and crabs that feed on the mussels. Gerlotto *et al.* (2001) reported that the abundance of fish, particularly seabream, increased following the introduction of suspended mussel culture and attributed

this to increased prey availability at the farm site as they observed fish feeding on farmed mussels. Likewise, Šegvić-Bubić *et al.* (2011) suggested that a variety of fish are attracted to mussel longline sites in Croatia and are responsible for significant losses from mussel socks. This effect was also observed in Spanish rias (Filgueira *et al.* 2007; Peteiro *et al.* 2010) and in New Zealand (see references in Schiel 2004). Similarly, bottom culture of bivalves attracts a variety of predatory species, at times changing the structure of benthic communities. For example, Kluger *et al.* (2016a, b, 2017) modelled community changes due to on-bottom culture of Peruvian bay scallop *Argopecten purpuratus* based on field data and report that the abundance of benthic predators increased markedly with the expansion of the industry and would continue to do so as the activity expands.

Interactions with birds, marine mammals and other non-fisheries species

A number of sea birds are attracted to suspended bivalve culture sites because of the increased availability of food (Meire 1993). For example, birds such as ducks and cormorants are known to hunt in and around farms (Dumbauld *et al.* 2009). There are two major feeding modes for birds on bivalves: the waders (plovers, oyster catchers and the like) and divers (scaup, scoters, etc.). The first group of birds may feed at low tide on bivalves growing in intertidal beach culture, whereas the second group may consume subtidal bivalves (bottom and suspended culture). Bivalves in culture may provide a direct food source to many types of birds (Dankers & Zuidema 1995). Mussels grown in suspended culture have traits (i.e. high meat content and thin shells) that make them particularly appealing to diving ducks (Dunthorn 1971; Davenport *et al.* 2003; Kirk *et al.* 2007). Indeed, Bustnes (1998) showed that eiders discriminate and select mussels with these same characteristics and Cervencel *et al.* (2015) have shown that large- and medium-sized mussels from culture plots provide a significant food source for foraging Eider ducks in the Dutch Wadden Sea. Farmed mussels are targeted by a number of diving ducks and are a serious challenge for the mussel culture industry in some locations (Varenes *et al.* 2013).

Habitat changes associated with bivalve culture may also impact associated communities, potentially increasing (or decreasing) the abundance of food for certain birds. For example, Caldwell *et al.* (2003) experimentally manipulated the density of mussels in an intertidal mudflat and monitored the abundance of birds in the area. None of the species monitored dropped in abundance and some increased, especially in areas where the availability of one of their preferred prey items, the amphipod *Corophium volutator*, was greatest. Organic loading from mussel faeces also attracts

some benthic infauna in the direct proximity of mussel beds (effluence area). For example, Christianen *et al.* (2015) suggested that organic loading intertidal mussel beds was responsible for a greater than threefold increase (relative to soft sediment reference areas) in the abundance of foraging birds – such as oyster catchers, curlew and bar-tailed godwit. As intertidal areas are not commonly used for mussel cultivation, the net attraction of foraging birds by aquaculture in intertidal areas is likely insignificant at a larger scale. The effects of effluence areas for sublittoral mussel plots are unknown.

Suspended bivalve culture structures are used as resting places for a variety of sea birds (Butler 2003). In an observational study, Roycroft *et al.* (2004) reported a greater number of species and abundance of birds in suspended mussel culture sites in Ireland than in a series of control sites, suggesting that this was mainly attributable to the provision of perching areas (buoys, platforms, etc.) and to the diverse communities of organisms growing on the farm-associated gear offering an attractive food source for a variety of species. A subsequent study in the same area (Roycroft *et al.* 2007) found that the activity budgets of a number of bird species differed between farm and reference sites, concluding that the impact of mussel culture on those birds was either neutral or positive.

Infaunal clam culture may also attract birds that may feed easily on large concentrations of these bivalves. This includes birds that feed at high tide (e.g. scoters) and at low tide (e.g. oyster catchers) (Hilgerloh & Siemoneit 1999; Godet *et al.* 2009; Žydelis *et al.* 2009). In some areas, this has led to vast expanses of beaches being covered with anti-predator netting (Spencer *et al.* 1996; Cigarria & Fernández 2000; Carswell *et al.* 2006; Toupoint *et al.* 2008; Bendell & Wan 2010) and Godet *et al.* (2009) have suggested that this may reduce the abundance of oystercatchers locally.

Oyster aquaculture also seems to influence bird populations. For example, Kelly *et al.* (1996) examined the distribution of shorebirds in California relative to oyster culture sites and found some species to be attracted to, some repulsed by, and others were not affected by the presence of oyster leases. Overall, the authors suggested that oyster aquaculture led to a net decrease in the abundance of shorebirds in the area studied. Species- and site-specific variation in the abundance of shorebirds between oyster trestle and reference areas have also been observed in Ireland (Hilgerloh *et al.* 2001; Gittings & O'Donoghue 2012).

Marine mammals may also be attracted to bivalve farms. Although Würsig and Gailey (2002) suggested that the bivalve aquaculture industry suffers 'significant losses from river and sea otters, Nash *et al.* (2000) suggested that the risk of large crop losses is small. Seals and other pinnipeds may also be attracted to mussel farms as they occasionally consume mussels as well as the benthic organisms that are

typically associated with mussel farms, including crabs and fish (Roycroft *et al.* 2004). It appears possible that large, swimming animals, such as marine mammals and possibly sea turtles, may avoid shellfish suspension-culture arrays because the lines may interfere with swimming (Mann & Janik 1999), thereby minimizing entanglement risks detailed below. The extensive nature of suspended bivalve culture may, however, displace marine mammals from habitat they otherwise would use. Markowitz *et al.* (2004) and Duprey (2007) found that Dusky Dolphins (*Lagenorhynchus obscurus*) avoided areas occupied by mussel culture longlines in the Marlborough Sounds, New Zealand, concluding that further expansion of the activity would limit dolphin's access to foraging areas. Similarly in the Marlborough Sounds, Pearson (2009) found that dolphins modified their behaviour to avoid travelling within areas with suspended mussel culture. Würsig and Gailey (2002) suggested that this may be due to the suspended structure inhibiting the dolphin's ability to aggregate fish prey. Although Heinrich (2006) reported that Chilean *C. eutropia* and Peale's *Lagenorhynchus australis* dolphins avoided farm sites in southern Chile, the former were frequently observed to feed on schooling fish shoreward of farms, in open spaces between densely placed longlines, and to pass under longlines. In Australia, bottlenose dolphins (*Tursiops* sp.) were reported to be excluded from parts of their home range by oyster culture longlines (Watson-Capps & Mann 2005). Ribeiro *et al.* (2007) studied the distribution of Chilean dolphins in a bay in Chile and found that suspended mussel culture influenced dolphin habitat use such that the mammals spent less time than would be predicted (based upon surface area and habitat type) in areas with the greatest density of suspended mussel culture but were not less prevalent in areas with lower concentrations of mussel culture. Both area types were associated with foraging activities and not socializing or resting, suggesting that suspended bivalve culture modified dolphin habitat use within the area. In contrast, Díaz López and Methion (2017) suggest that bottlenose dolphins are attracted by mussel rafts in Galicia, suggesting that this is due to the large aggregations of fish species around the mussel rafts that provide high concentrations of high-quality food for the dolphins.

The physical structure added to the water column in suspended bivalve culture may be a hazard to marine mammals, sea turtles and sea birds because of entanglement risk (Young 2015; Price *et al.* 2017). Lloyd (2003) suggested that the risk of entanglement probably is greatest for thin ropes and those that are not under tension, and that baleen whales, which cannot echolocate, may be particularly susceptible to such entanglement. Thus, more offshore areas used for spat collection may also create hazards for whales. Lloyd (2003) discussed how Bryde's whales (*Balaenoptera brydei*) died after becoming entangled in mussel spat

collectors in New Zealand. Other examples may be found in Price *et al.* (2017). There are no verifiable data on these potential effects, and it is not clear whether entanglement is a consequence of mammals being attracted or oblivious to shellfish-farming gear. The physical structure associated with bivalve farms may displace some species of sea birds, including diving duck and grebes, and anti-predator netting may trap birds (Pillay 2004; Varennes *et al.* 2013).

Effects of shellfish farm husbandry practices

Activities associated with shellfish farm maintenance and operation include fouling control (Enright 1993; Adams *et al.* 2011), grading and thinning, and harvesting. Such activities can disturb the environment with human and machine activity such as noise and release of materials associated with the gear and the shellfish (fouling, biodeposits, dead shells, etc.). The release of fouling organisms and some farmed organisms into the environment typically attracts a variety of scavenging organisms, such as crabs and other crustaceans, fish and birds (D'Amours *et al.* 2008) in a similar way as described in 2.1 and 2.2 for fall-off. This attraction helps to recycle materials and energy into the ecosystem's trophic pathways. Although there is much anecdotal evidence of a variety of organisms being attracted by this fall-off, there have been very little quantitative data published on the subject.

Dredge harvest of bottom-cultured northern quahogs represents a disturbance of the benthic habitat, but consequences to sediment composition (resuspension and washout of fine organic particles and re-oxygenation) may improve habitat quality on medium time scales (Goldberg *et al.* 2014; Meseck *et al.* 2014). Benthic meiofauna are displaced, but this biological displacement is short-lived and less extensive spatially and temporally than repeated dredging of common-resource clam beds (Goldberg *et al.* 2012).

The relative attractiveness of a site for birds varies over time with respect to seasonal variation and husbandry practices. For example, Ferns *et al.* (2000) noted that bird feeding activity increased following mechanical harvesting for cockles in Wales, with gulls and waders consuming the invertebrates that were made available by harvesting. Thereafter, bird activity declined relative to that in reference areas.

Human activity, including motion, noise and release of waste materials (engine exhaust, other emissions), stimulates alarm responses in many organisms, especially vertebrates that avoid potentially harmful humans. Accordingly, some marine mammals (Becker *et al.* 2011 – but see <http://www.ptreyeslight.com/article/seal-study-debunked-scientists>) and birds (Varennes *et al.* 2013) may be repulsed by farm operation activities, including devices deployed to this end. The main evidence for this is the effectiveness (to varying degrees) of sounds to repel predators on farmed

shellfish. Conversely, there is evidence of acclimatization to such human activities by birds and marine mammals following repeated exposure. Research has also shown that some predators, such as crabs, may be averted and have their foraging activities impacted by vessel noise (Wale *et al.* 2013) and thus normal husbandry operations may impact the distribution of these organisms through this mechanism. In contrast to the attraction effects of harvesting discussed above, a number of studies have suggested that harvesting bivalves may have a repulsive effect on bird populations. For example, Spencer *et al.* (1998) suggested that Manila clam harvest will impact infaunal communities with consequent effects on the distribution of bird populations. Recently, it has become apparent that various noises associated with farm husbandry (e.g. generators and engines) may induce a variety of sessile organisms to settle on hard substrates (e.g. Wilkens *et al.* 2012; McDonald *et al.* 2014; Stanley *et al.* 2014). This may encourage the development of fouling communities associated with mussel infrastructure and have consequent impacts on bivalve culture–environment interactions. This review found no evidence of other organisms displaying an aversion to farmed shellfish themselves.

Conclusions

Both finfish and shellfish farms have clearly been shown to attract and repel a wide variety of species under a variety of conditions. However, considerable uncertainty remains regarding the long-term and ecosystem-wide consequences of these interactions. The use of modelling may help us to understand these consequences, as shown for fish aggravated around fish farms (Bayle-Sempere *et al.* 2013) and organisms impacted by Peruvian scallop farming (Kluger *et al.* 2017). Recent advances have also directly incorporated attractive effects into foodweb models for bivalve aquaculture through the use of mediation functions (Ferriss *et al.* 2016). Alternatively, qualitative network models have been developed to better understand trophic links and their impacts on ecosystem functioning using only qualitative data, which is useful in coastal systems as they are commonly data-limited (Reum *et al.* 2015). Results from these types of studies may help identify priorities for additional empirical research on aquaculture–environment relations. In addition, inclusion of such interactions in management decisions with respect to fisheries, for example, will promote a more sustainable use of coastal resources.

Acknowledgements

The core of this paper was developed during the International Council for the Exploration of the Sea (ICES) Working Group on Aquaculture (WGAQUA) workshops that

were held in Vigo, Spain, in April 2014, Rhode Island, USA, in March 2015, and Yerseke, The Netherlands, in April 2016. Thanks go to the WGAQUA. This paper has also been improved during a workshop held in Palavas in February 2016. MC and CWM would like to thank the GDRI RECHAGLO (International Research Group in the field of fisheries and aquaculture ‘Responses to the global population change and fisheries and aquaculture communities and their habitats, 2015–2019’) for financial support.

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