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The Ecology and Distribution of European Bass (Dicentrarchus labrax) in inshore and coastal waters of the U.K.

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The Ecology and Distribution of European Bass (*Dicentrarchus labrax*) in inshore and coastal waters of the U.K.

By

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A thesis submitted to the University of Plymouth in partial fulfilment for the degree of

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Author’s Declaration

At no time during the registration for the degree of Doctor of Philosophy has the author been registered for any other University award without prior agreement of the Doctoral College Quality Sub-Committee.

Work submitted for this research degree at the University of Plymouth has not formed part of any other degree either at the University of Plymouth or at another establishment.

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Abstract

European bass (*Dicentrarchus labrax*) is a commercially and recreationally important finfish native to the Northeast Atlantic and Mediterranean Sea. The species is targeted throughout its range and represents a significant commercial and recreational fishery, which in the UK are estimated to have a value of £5-6million at first sale, and £100-200 million per year respectively. In 2010, the International Council for Exploration of the Seas (ICES) reported a dramatic decline in the Northeast Atlantic stock (ICES divisions 4.b–c, 7.a, and 7.d–h), which in 2016 declined below “safe biological limits”. In 2019 ICES reported that the Northeast Atlantic stock increased above B_{lim}, however relative to historic levels the population remains in a highly impoverished state and is still below maximum sustainable yield thresholds.

Due to the local economic and social significance of European bass fisheries, the Devon and Severn Inshore Fisheries and Conservation Authority (D&S IFCA) co-funded and co-supervised the current PhD with the University of Plymouth to investigate; the feasibility of localised management/conservation policies to improve local European bass populations. Due to the localized/restricted movement characteristics and estuarine dependence of this species, the PhD project was focussed on identifying; movement, feeding and growth within estuarine habitats, with a particular emphasis on measuring the effectiveness of designated Bass Nursery Areas within the D&S IFCA’s district.

The results from this thesis demonstrate that estuaries and coastal embayments have been subjected to substantial alteration as a result of human activities. This has resulted in an estimated net loss of 2, 482.9km^2 of intertidal habitat historically, with this loss estimated to continue at a rate of 0.2% per year. European bass specifically are thought to utilize

intertidal habitats e.g. saltmarsh, as a primary feeding habitat within the first year. Analysis of growth variability from three coastal nursery sites, indicated that factors influencing growth within the first year may have important implications for latter growth and corresponding recruitment. It was therefore recommended that the habitat requirements of European bass should be integrated within management policies.

Using acoustic telemetry, European bass were also recorded displaying spatially restricted movement characteristics, and were estimated to occupy an area of <4.7km^2 for 42.9-75.5% of the year (depending on tagging location). These results, combined with the wider literature, suggest that a regionalized fisheries management approach may be appropriate for this species.

Presence/absence of European bass within coastal sites in response to environmental variables also demonstrated that site characteristics can fundamentally influence local fish residency characteristics. Notably, within sites with limited freshwater input e.g. coastal rias and/or natural harbours, European bass may maintain residency throughout winter. Therefore seasonal protection/management within designated nursery sites may not be relevant to the behaviour of local European bass populations.

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Chapter 1: General Introduction

1.1 Introduction

European bass (*Dicentrarchus labrax*) is a commercially and recreationally important demersal finfish, commonly found in estuaries and coastal waters throughout the Northeast Atlantic and Mediterranean Sea (core range between 30-54°N) (Pickett & Pawson, 1994; Garcia *et al.,* 1997; Vinagre et al., 2012). Across their geographic range, this species is thought to occur primarily within inshore coastal and estuarine water within the summer, and deeper offshore water within the winter (Pickett & Pawson, 1994). Coastal embayments and estuaries are also known to be important nursery habitats (Pickett & Pawson, 1994).

European bass is targeted by commercial and recreational fisheries throughout its geographic range. In the UK specifically, the commercial and recreational fisheries have an estimated value of £5-6million at first sale (MMO, 2020), and £100-200 million per year respectively (B.A.S.S, 2004 from Ares*,* 2016; Carroll*,* 2014; MRAG, 2014). Since 2010, the International Council for Exploration of the Seas (ICES) reported a dramatic decline in the Northeast Atlantic stock (central and southern North Sea, Irish Sea, English Channel, Bristol Channel, and Celtic Sea). Which in 2016 declined below “safe biological limits”, a threshold known as B_{lim}. In 2019, ICES reported that the Northeast Atlantic stock increased above B_{lim}, however relative to historic levels the population remains in a highly impoverished state and is still below maximum sustainable yield thresholds (ICES, 2019).

Due to little evidence for genetically distinct populations, European bass from across the Northeast Atlantic are considered a single functional stock. However, despite limited genetic evidence, tagging and stable isotope studies report the tendency of this species to maintain high residency and site fidelity to defined coastal areas during a variety of life stages (Pickett

& Pawson, 1994; Green *et al.,* 2012; Cambiè *et al.,* 2016; Doyle *et al.,* 2017; O'Neill, 2017; Pontual *et al.,* 2019). This supports the theory of spatial structuring and sub-populations across the Northeast Atlantic, which may exist at a finer spatial resolution than current management units.

Within England, the Inshore Fisheries and Conservation Authorities (IFCAs) have fisheries management jurisdiction within a defined “district” to a limit of 6nm from the coastline (Figure 1.6). Within the Devon and Severn IFCA (D&S IFCA) district, European bass represent the most economically valuable fin fishery. In particular, this species has a high economic value for vessels under 10m (commonly referred to as the inshore fleet), and has an estimated landed value of £700-800k per year (at first sale) across the district (MMO, 2020). Due to the potential localized movement characteristics of European bass across a variety of life stages, combined with the diminished stock across the Northeast Atlantic, the D&S IFCA collaboratively funded and supervised the current PhD.

The D&S IFCA district hosts many estuarine and coastal sites which are designated as protected Bass Nursery Areas (MAFF, 1990). Prior research has highlighted; the importance of these sites as key nursery areas which may increase local recruitment rates (Pickett & Pawson, 1994; Pickett *et al.,* 2004), but also as potential feeding sites for mature fish (Cambiè *et al.,* 2016). There however remains uncertainty on how this species interacts with estuarine and coastal habitats. Therefore, the PhD project was focussed on identifying; movement, feeding and growth within estuarine habitats, with a particular emphasis on measuring the effectiveness of designated Bass Nursery Areas within the D&S IFCA’s district.

The remainder of this introductory chapter summarises the relevant available literature on European bass life history and the relevance of the research contained within this thesis to the commercial & recreational fisheries.

1.2 Life history

European bass form spawning aggregations within offshore locations from early February (Pickett & Pawson, 1994) to June (Jennings & Pawson, 1992). The timing of which is thought to be temperature dependent, occurring mainly within a temperature range of 8.5-11°C (Thompson & Harrop, 1987) and may follow the 9°C isotherm within early spring (Pawson *et al.,* 1987).

Planktonic eggs are broadcast spawned into the water column and hatch within 6-9 days (Pickett & Pawson, 1994). The yolk sac is absorbed within 9-25 days, following which they persist as pelagic larvae (Pickett & Pawson, 1994). From approximately May-June juvenile fish actively migrate into defined coastal nursery habitats, which in the UK largely take the form of estuaries on the east, south and west coast (Pawson *et al.,* 1987; Kelley, 1988; Pawson *et al*., 2007). Individuals are then thought to maintain residency or dependency to a specific nursery area for the first two-four years (Pawson *et al.,* 2007).

Using mark-recapture techniques Pawson *et al.* (1987) reported juvenile European bass (<32cm total length) generally remained within 16km of their host nursery area. Adolescent fish (32-42cm total length) are, however, thought to disperse more widely. Greater dispersion from the host nursery site during "adolescence" has been reported by other authors (Kelley, 1988; Pickett & Pawson, 1994), who have suggested that individuals are seeking coastal or estuarine feeding locations to which they maintain residency during proceeding summer months (Pawson *et al.,* 1987; Cambiè *et al.,* 2016; Doyle *et al.,* 2017).

European bass display sexual dimorphism with females achieving sexual maturity at a greater size and later age (39-42cm total length) than males (32-35cm – total length) (Kennedy & Fitzmaurice, 1972; Carroll, 2014; Cambiè *et al.* 2016). From early winter, sexually mature individuals will begin migrating to offshore spawning locations which in the UK are thought to occur in the English Channel and Celtic Sea (Pickett & Pawson, 1994).

Following spawning, adults migrate inshore and display high inter-annual site fidelity/residency to specific coastal or estuarine feeding locations (Cambiè *et al.,* 2016; Doyle *et al.,* 2017), however are thought to migrate offshore to spawn each successive winter (Pickett & Pawson, 1994).

1.3 North Atlantic stock identity and status

A variety of genetic studies have assessed stock differentiation throughout the geographic range of European bass (Child, 1992; Castilho & McAndrew, 1998; Patarnello *et al.,* 1993; Garcia *et al.,* 1997). While Mediterranean populations appear to be genetically separated into several sub-basins, it is thought there is high gene flow across the Northeast Atlantic (Fritsch *et al.,* 2007). Despite tagging and stable isotope approaches which provide evidence for geographically/regionally distinct movement and feeding groups (Fritsch *et al.,* 2007; Cambiè *et al.,* 2016; Doyle *et al.,* 2017; Pontual *et al.,* 2019), little evidence has been found for genetically distinct populations of European bass in the Northeast Atlantic (Fritsch *et al.,* 2007). Due to a lack of evidence from genetic studies, at the Interbench Protocol meeting 2012 (ICES, 2012) it was agreed by the European Commission that European bass in the North Sea, Irish Sea, Channel and Celtic Sea (ICES divisions; 4b & c, 7.a, 7.d-h) would be treated as one functional stock.

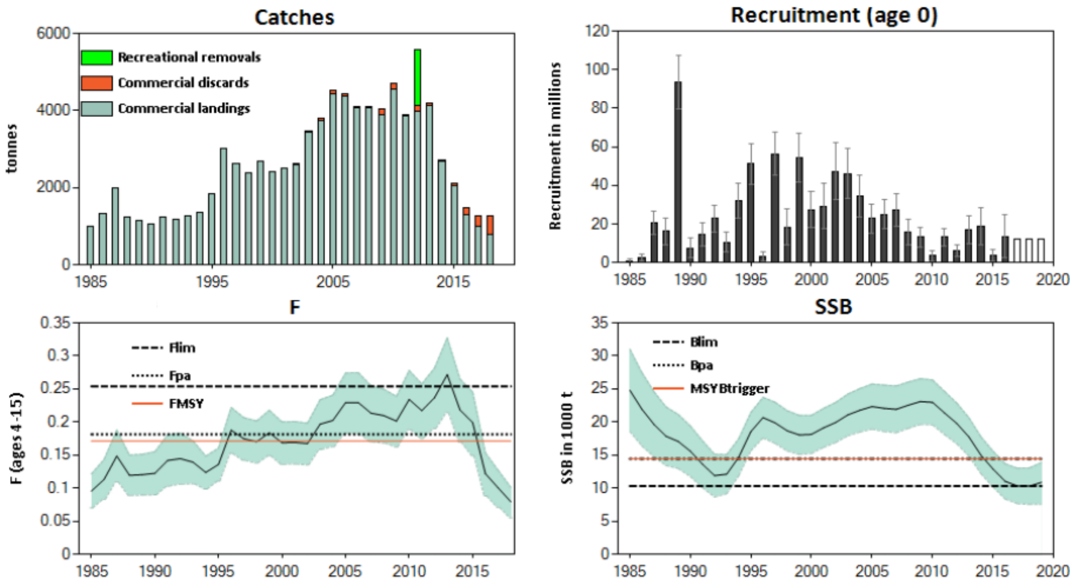


Figure 1. 1 - Seabass in ICES statistical rectangles 4.b-c, 7.a, and 7.d-h. Summary of stock assessment (weight in thousand tonnes). Total landings (commercial landing and estimated recreational removals, available for 2012 and 2016, taking mortality or released fish into account). Fish mortality is shown for the combined commercial and recreational fisheries. Predicted recruitment vales are not shaded. Recruitment, F, and SSB are shown with 95% confidence intervals (Image source: ICES, 2019)

Since 2010, ICES reported a dramatic decline in the Northeast Atlantic European Bass stock (Figure 1.1). This is measured by recording the number of sexually mature individuals within the population, otherwise known as the Spawning Stock Biomass (SSB). In 2018, the SSB was approximately 64% lower than pre decline levels in 2010 (2010 – 18215 tonnes; 2018 – 6414 tonnes; ICES, 2019). In 2018, the population fell below what is termed “safe biological limits”, a threshold called “B_{lim}” (Figure 1.1 – bottom right) (ICES, 2019). Below B_{lim}, reproduction and hence recruitment is at significant risk of being impaired (ICES, 2019) and the ability of the stock to recover is in serious jeopardy (Williams *et al.,* 2018). In 2019, the Northeast Atlantic stock increased above B_{lim}, however relative to historic levels the population remains in a highly impoverished state and is still below maximum sustainable yield thresholds (Figure 1.1).

1.4 Commercial fisheries

In the UK, European bass is landed into ports along the Southeast, South and Southwest coast of England and Wales (Figure 1.2). From 2014-2017, the 5 most significant UK ports in regard to the average first sale value of UK registered vessels landings were; 1) Weymouth; 2) Eastbourne; 3) Brixham; 4) Portsmouth; 5) Plymouth. From 2014-2017, the value of landed European seabass was worth an average of £5.5 million per year to UK registered vessels. Following re-sale the fishery is however worth an estimated £35million per year to the UK economy (Barclay, 2011 from Carroll, 2014).

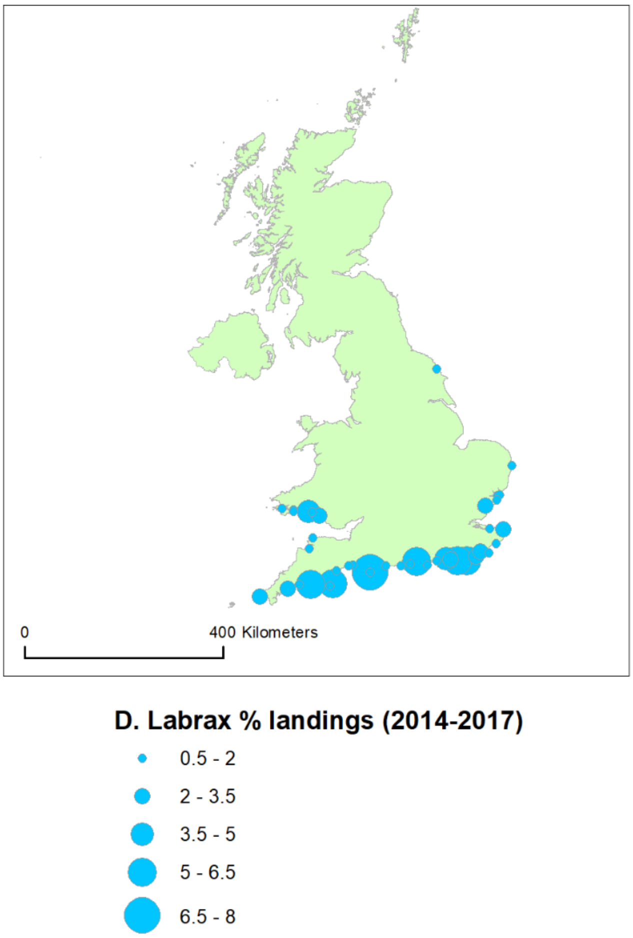
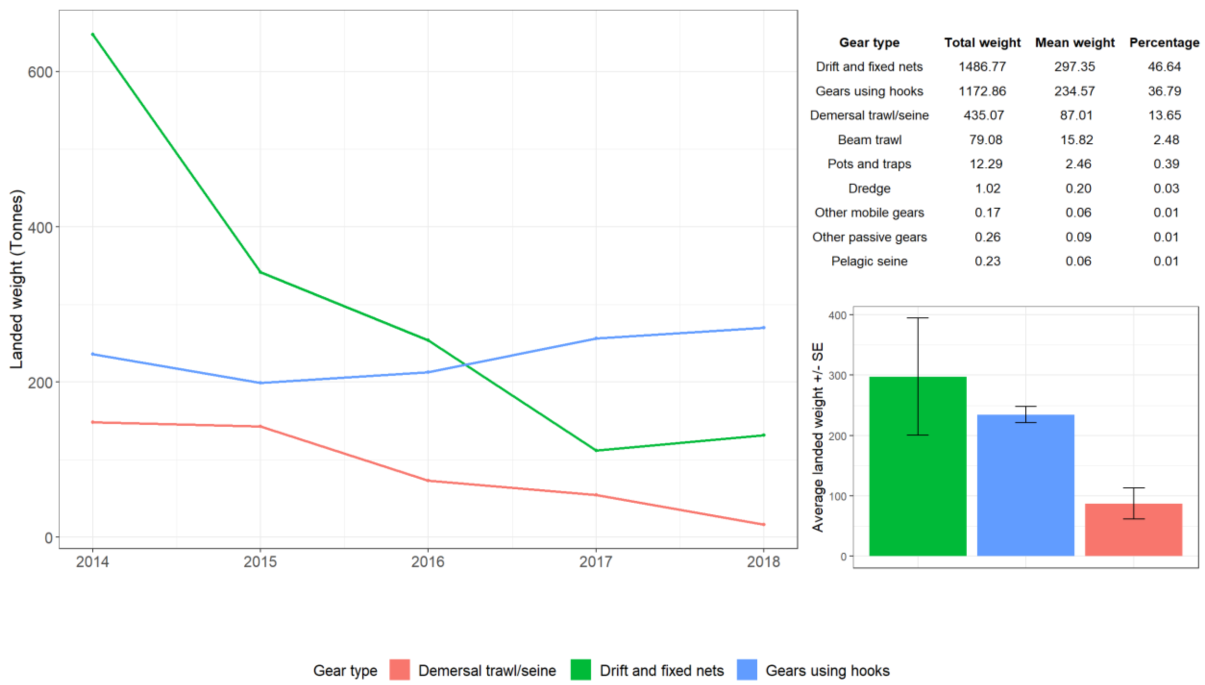


Figure 1. 2 - Commercial landings of European bass (*D. labrax*) by UK registered vessels within UK ports. The size of each circle is proportional to the amount of catch landed within each port (Data source: MMO, 2020)

European bass is particularly significant for the inshore fleet (vessels under 10m), which from 2014-2017 landed an average of 83.6% of the total landed European bass in the UK. In regard to value, this particular species accounts for an average 22% of the landed value for inshore fin-fisheries by UK registered vessels (MMO, 2020).

Typically the commercial fishery is seasonal, with the majority of landings occurring in summer and autumn (Carroll, 2014), however, some fishing fleets from; UK, France, Spain and Portugal are active all year (Carroll, 2014; Williams *et al.,* 2018). European bass is landed via a number of fishing techniques (Figure 1.3), the relative importance of which is variable across the UK. In terms of total landings from UK registered vessels the most significant methods are defined by the Marine Management Organisation (MMO) as; 1) Drift and fixed nets; 2) Gear using hooks; 3) Demersal trawl/seine (MMO, 2020).



Gear type	Total weight	Mean weight	Percentage
Drift and fixed nets	1486.77	297.35	46.64
Gears using hooks	1172.86	234.57	36.79
Demersal trawl/seine	435.07	87.01	13.65
Beam trawl	79.08	15.82	2.48
Pots and traps	12.29	2.46	0.39
Dredge	1.02	0.20	0.03
Other mobile gears	0.17	0.06	0.01
Other passive gears	0.26	0.09	0.01
Pelagic seine	0.23	0.06	0.01

Figure 1. 3 - European bass landings by weight (tonnes), total for each year 2014-2017 (left), and, average for all years combined (right bottom). Table (right top) shows cumulative total, mean and percentage landings by gear type from 2014-2017. Data sourced from Marine Management Organisation (MMO) landing statistics. Data is for UK registered vessels- England; Guernsey; Isle of Man; Jersey; Northern Ireland; Scotland; Wales. (Data source: MMO, 2020)

1.5 Recreational fisheries

European bass is also a highly prized recreational sport fish, famed for its "fighting prowess". In 2012, there were an estimated 884,000 sea anglers in the UK which spent an estimated £831 million that year on direct expenses incurred whilst angling e.g. petrol, accommodation and subsistence (Armstrong *et al.,* 2013; Ares, 2016). More specifically, the recreational sport fishery for European bass has been estimated to be worth £100 - £200 million per year to coastal economies of the UK (B.A.S.S, 2004 from Ares, 2016; Carroll, 2014; MRAG, 2014).

In 2012, the UK government launched the Sea Angling review (Armstrong *et al.*, 2013) which estimated the number of recreational sea angler in the UK, and assessed their impact on marine fish populations. Armstrong *et al.* (2013) reported that in 2012 recreational sea anglers were landing/keeping an estimated 230-440tonnes of European bass in England. When compared to commercial landings into UK ports from the same time period (897tonnes), recreational sea anglers were estimated to remove approximately 25-49% of the total UK commercial catch (Table 1.1). Armstrong *et al.* (2013) did emphasize that the estimated recreational catch represented the extreme values from several different analysis techniques, and that the values should be interpreted with caution.

Table 1.1 – Estimated European Seabass removal from recreational angling in England, France & the Netherlands compared to commercial landings in 2012 (Armstrong *et al.,* 2013)

Country	Recreational fishery: annual kept catch 2012 (tonnes)	Commercial fishery landings 2012 (tonnes)	Percentage of recreational removal to commercial
England	230-440	897 (UK total)	25-49%
France	940	2,492	37%
Netherlands	128	372	34%
Total	1,300-1,510	4,060 (all countries)	32-37%

The estimates produced by Armstrong *et al.* (2013) have been widely disputed by a number of recreational sea angling enthusiast groups (e.g. Angling Trust, Bass Angling Sports fishing Society). However, the recreational European bass fishery is now regulated by Technical Conservation Measures (TCMs) introduced in 2015 by the European Commission. From 2016 – 2018 a similar project called the Sea Angling Diary was launched by the Centre for Environment, Fisheries, Aquaculture Science (CEFAS). Within the Sea Angling Diary Project, recreational sea anglers are encouraged to record their catch data on an online portal, as well as extra information which estimates the value of recreational fishing to local economies. The results from the Sea Angling Diary have however not yet been made publicly accessible.

1.6 Management of the Northeast Atlantic European bass stock

ICES provides marine policy and fisheries management advice to regulating bodies across the Northeast Atlantic, Mediterranean sea and Black Sea. For the purposes of simplifying management advice, ICES split regions into "Statistical rectangles". These statistical rectangles are then often incorporated into the management measures imposed by regulators such as the European Commission.

In regard to the Northeast Atlantic stock, this refers to European bass which are captured within ICES divisions: 4.b–c, 7.a, and 7.d–h (Figure 1.4).

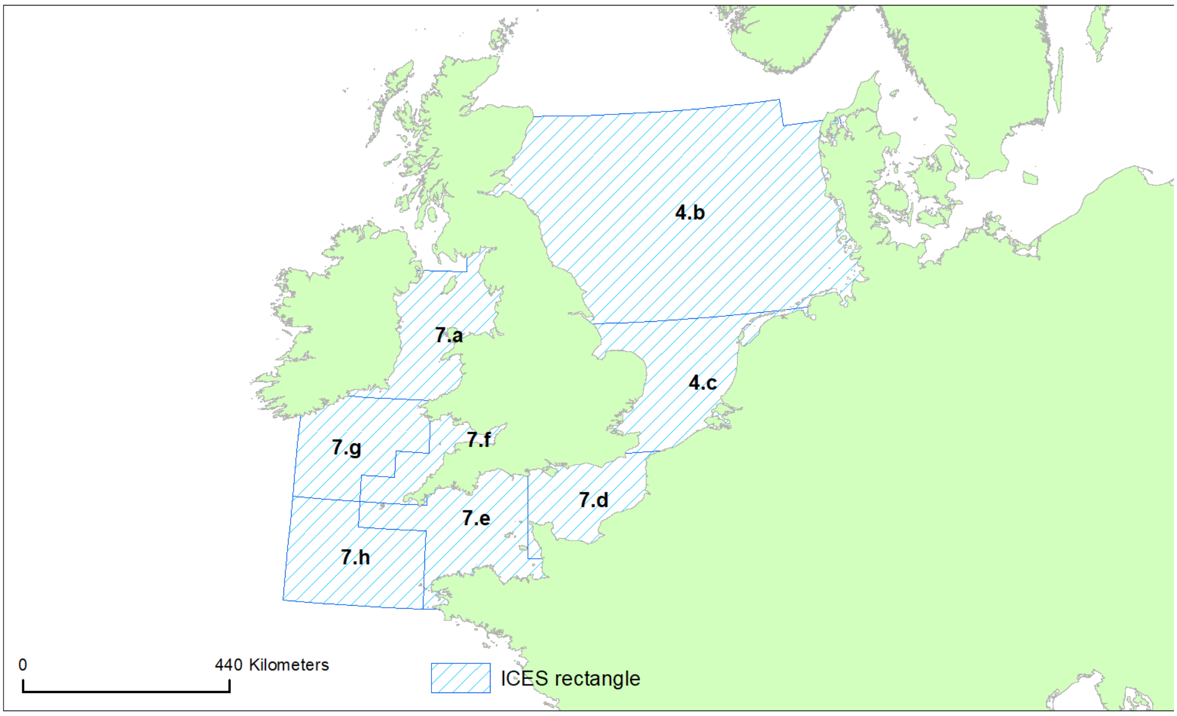


Figure 1. 4 – Distribution of ICES statistical rectangles relevant to management of North Atlantic European bass stock

1.6.1 European Commission – Emergency Technical Conservation Measures

Unlike many other fisheries within the territorial waters of the European Union, there is currently no fisheries management plan for the Northeast Atlantic European bass stock (Ares, 2016). Commercial and Recreational fisheries are instead largely regulated by emergency Technical Conservation Measures (TCM), introduced by the European Commission in 2015. These TCMs are annually reviewed in relation to advice from ICES and the requirements of each member state's commercial and recreational fishing operations. At the time of writing no TCMs have been published for the 2020 fishery, however the 2019 measures are listed within Table 1.2.

1- Closure of targeted commercial fishing during spawning periods

In 2015, the European Commission imposed a ban on pelagic trawl fishing which targeted spawning aggregations of European bass within February-March. This was a major targeted winter fishery in offshore areas in the western Channel and approaches, including off North Devon and Cornwall (UK) (Pickett & Pawson, 1994). There is evidence that European bass spawning follows the 9^{o}C isotherm, and therefore may occur later into spring (April-May) in northern latitudes (e.g. Wales – Picket & Pawson, 1994). This however, is not accounted for within the European bass TCMs.

Current conservation measures have extended this protection, to impose a ban on all targeted commercial fishing for European bass during February-March.

2- Increase in minimum landing size from 36cm to 42cm – Introduced in 2015

In 2015, the minimum landing size or "minimum conservation reference size" was increased from 36cm to 42cm (total length) to allow females the opportunity to reach sexual maturity and spawn prior to harvesting (Ares, 2016). Accompanying the increase in minimum landing size were complimentary increases in the minimum mesh sizes to 90mm for gill, tangle drift, trammel and any other enmeshing nets (Ares, 2016).

3- Area closure – Introduced for Irish vessels from 1990 but extended to all EU vessels in 2015

In 1990, a closed area was designated from which Irish vessels were prohibited to land European bass from the area of the Celtic Sea, Irish Sea, south of Ireland and west of Ireland (ICES areas 7a, b, c, g, j, k outside the UK 12 mile zone) (ICES, 2019). In 2015, the European Commission introduced further measures which prohibited any European Union vessel from landing European bass from within this area.

4- Restrictions on commercial and recreational landings

The MMO issue authorisations to allow commercial fishermen to land European bass. 2019 authorisations have the following restrictions:

Table 1.2– 2019 Catch restrictions for commercial European bass fishermen within the UK

	Demersal Trawls	**Demersal Seines**	**Gears using Hooks**	**Fixed Gillnets**	**All other gears (including drift nets)**	**Commercial shore fisheries**
Fishery restrictions	Closed February and March	Closed February and March	Closed February and March	Closed February and March	All bass catches prohibited	All bass catches prohibited
Maximum catch limits	Maximum 1% by weight of all marine organisms per day. Unavoidable by-catch of 400kg per two consecutive calendar months	Maximum 1% by weight of all marine organisms per day. Unavoidable by-catch of 210kg per month	5.5 tonnes per year	Unavoidable by-catch of 1.4 tonnes per year	All bass catches prohibited	All bass catches prohibited

Recreational fishermen are limited to catch and release from 1st February – 31st March and 1st November – 31st December. From 1st April - 31st October 2019, one fish may be retained per angler per day.

1.6.2 UK Legislation – Designated Bass Nursery Areas

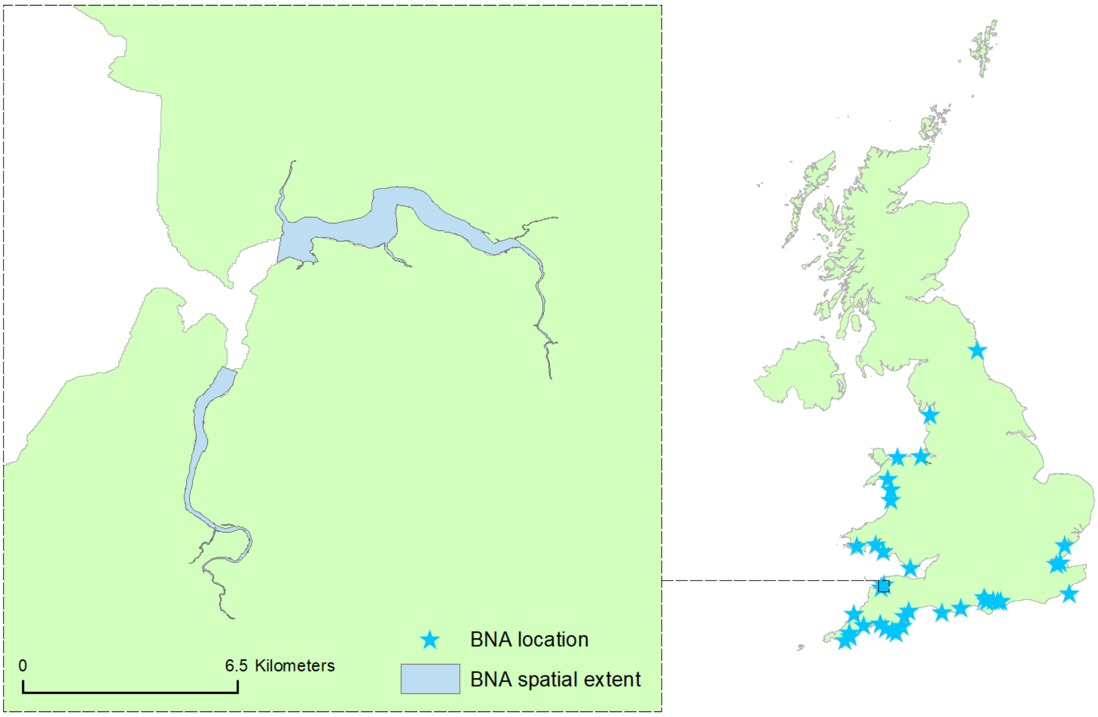


Figure 1. 5- Designated Bass Nursery Areas (BNAs) in England and Wales (Right). Example of designated Bass Nursery Area (Taw/Torridge estuaries) boundaries (Left)

In 1990, the Ministry of Agriculture, Fisheries and Food (MAFF) introduced legislation in England and Wales to protect juvenile European bass from commercial fishing. Through the *Bass (Specified Areas) (Prohibition of Fishing) (Variation) Order 1999,* 37 Bass Nursery Areas (BNAs) were designated largely in estuaries on the east, south and southwest coast of England and Wales (Figure 1.5). Within BNAs; fishing for any sea fish species using sand-eels is prohibited; and targeted commercial fishing for European bass from a vessel is prohibited for all or part of the year (MAFF, 1990). Management of each BNA is the responsibility of the local Inshore Fisheries Conservation Authority (IFCA), which may also have additional local by-laws which prohibit certain activities within or adjacent to estuaries or BNAs.

1.7 Behavioural and life history traits which increase the vulnerability of European bass to over exploitation

The decline in Northeast Atlantic European bass stock is thought to be a result of several contributory factors, which relate to; increasing fishing effort and a lack of responsive fisheries management. There are however also a number of life history and behavioural traits which increase the vulnerability of European bass to over-exploitation, these primarily include; philopatry/fidelity to feeding grounds; and dependence on estuarine habitats.

1.7.1 Philopatry/fidelity to feeding grounds

Mark-recapture (Pawson *et al.,* 1987) and Data Storage (DS) tagging campaigns conducted by CEFAS (Unpublished data) & IFREMER (Pontual *et al.,* 2019) have shown that during winter sexually mature European bass make large migrations to spawning areas in the Bay of Biscay, English Channel and Celtic Sea (Fritsch *et al.,* 2007). Adolescent fish are also thought to disperse widely from their host nursery area in search of defined coastal feeding locations (Pawson *et al.,* 1987). However, during summer adults are known to display residency to specific summer feeding locations (Pawson *et al.,* 1987; Pickett *et al.,* 2004; Fritsch *et al.,* 2007; Green *et al.,* 2012; Pawson *et al.,* 2007; Pawson et al., 2008; Cambiè *et al.,* 2016; Doyle *et al.,* 2017).

From the 1980s to 2000s mark-recapture studies were published (Pawson *et al.,* 1987; Pickett *et al.,* 2004; Fritsch *et al.,* 2007; Pawson *et al.,* 2007). European bass were captured and a numbered ID tag attached to each individual, a number of these fish were re-captured and movement patterns inferred between tagging and re-capture locations. These studies demonstrated that, whilst regionally variable, in general tagged adult and juvenile European bass were captured within 16km from their respective tagging locations and therefore were not thought to disperse widely from defined nursery grounds (when juvenile), or summer feeding grounds (when mature).

Doyle *et al.* (2017) furthered these observations; acoustic telemetry was used to track 30 individual adult European bass (>42 cm total length) within Cork Harbour, Ireland. All tagged fish were highly resident to both the harbour as a whole (average residence time – 167 days), but also maintained residence at specific locations within the harbour (variable between individual fish). All tagged fish left Cork Harbour for the winter spawning migration, however, of the 30 tagged fish 24 returned to the same area within the harbour that they occupied prior to the winter migration, demonstrating that European bass display inter-annual site fidelity.

Cambiè *et al.* (2016) used the stable isotope ratios (δ13C and δ15N) to assess connectivity and movement of European bass across Wales, UK. The last growing segment of the scales from 189 individual European bass were removed, and their stable isotope (δ13C and δ15N) signatures calculated. The last growth segment of the scales was removed because their isotopic signature will be representative of the region that each fish inhabited in the latest growth season. The results indicated geographic segregation into 2 distinct feeding regions, with individual European bass captured from North and mid wales having distinct isotopic signatures from those captured in south wales.

The high residency and site fidelity displayed by this species may introduce spatial structuring into wider populations (Cambiè *et al.,* 2016), in which localized movement and not genetic separation (O'Neill, 2017) define the underlying biological structure. From a fisheries management perspective, this is an important behavioural trait because it decreases mixing/movement within the population, and therefore increases the vulnerability to local population declines (Ares*,* 2016).

1.7.2 Dependence on estuarine habitats

It is well cited that juvenile European bass are highly dependent on defined coastal nursery areas, which in the UK largely take the form of estuaries on the east, south and west coast (Kelley, 1988). When residing within estuaries, saltmarsh habitats are known to play a key role for both refuge and nutrition (Kelley, 1988; Laffaille *et al.,* 2001; Green *et al.,* 2012; Fonseca *et al.,* 2011). The importance of saltmarsh as feeding habitat for juvenile fish is best illustrated by Laffaille *et al.* (2001) & Fonseca *et al.* (2011), who reported that on average 33-38% of juvenile European bass entering saltmarsh have empty stomachs, whereas when leaving saltmarsh 93-98% of individuals have full stomachs. It was estimated that in the brief 1-2 hour tidal submersion of saltmarsh, the fish were capable of consuming 8% of their total body weight (Laffaille *et al.,* 2001). Furthermore, Laffaille *et al.* (2001) reported that when 0-group European bass were in estuaries but did not have access to intertidal saltmarsh habitat, their diet was dominated by the mysid *Neomysis integer,* which feed predominantly on detritus from saltmarsh and terrestrial sources (Fockedey & Mees, 1999).

Green *et al.* (2012) and Doyle *et al.* (2017) also suggested that not only do specific habitats contribute significantly to European bass nutrition, but that both juveniles and mature (>42cm total length) fish may display high site fidelity to specific locations within estuaries. Green *et al.* (2012) used a stable isotope technique to identify the isotopic signature of 5 saltmarsh sites within the Blackwater-Colne and Stour-Orwell estuary complexes, Essex. Specimens were collected from numerous trophic levels- primary producers and detritus e.g. *Spartina anglica*; secondary consumers e.g. *Carcinus maenus*; and the dominant fish species e.g. 0-group European bass. At each trophic level site-specific isotopic signatures were evident, suggesting that 0-group European bass as well as other estuarine fish species; e.g. Common Goby (*Pomatoschistus microps*) may have highly localized movement within estuaries.

Cambiè *et al.* (2016) also reported that all European bass >50cm total length captured as part of their study, had an estuarine isotopic signature (low $\delta 13$ C). These results indicate that these individual fish may feed within estuaries for an extended period of time, possibly over the entire summer feeding season. Cambiè *et al.* (2016) therefore suggested that if protecting large individuals (e.g. large spawners) was identified as a management target, an effective method to achieve this goal would be to afford estuaries higher protection.

1.8 PhD context & research aims

The Devon & Severn Inshore Fishing Conservation Authority (D&S IFCA) is one of 10 regional inshore fisheries enforcement bodies across England. The IFCAs were created by the Marine and Coastal Access Act (2009) and superseded the prior inshore fisheries authorities known as the Sea Fisheries Committees. The D&S IFCA is the largest of the 10 IFCA districts (4,522km^2), which includes the areas of; Devon, Somerset, Gloucestershire County Councils; Bristol City and Plymouth City Councils; North Somerset and South Gloucestershire Councils and all adjacent waters out to six nautical miles offshore or the median line with Wales (Figure 1.6).

The D&S IFCA is overseen by an “authority” comprised of 30 members drawn from; the relevant local authorities within the IFCA district, general members (appointed by the MMO), and statutory members representing the; MMO, Environment Agency and Natural England. Officers employed by the D&S IFCA work on behalf of the authority.

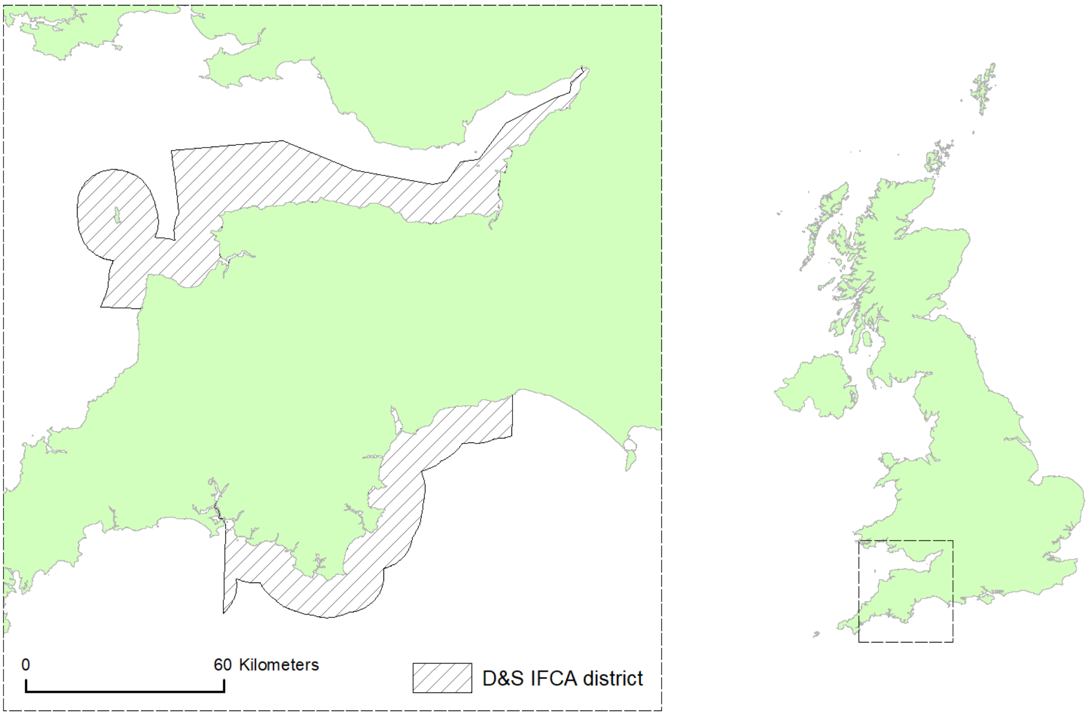


Figure 1. 6 – D&S IFCA district boundary

The D&S IFCA district contains two major fishing ports; Brixham and Plymouth, which in 2018 accounted for approximately 17% of the UK European bass landings (most recent publically available landing figures – MMO, 2020). Across all the ports within the district European bass represent the most economically valuable fin fishery, and has an estimated landed value of £700-800k per year (at first sale) (MMO, 2020).

As a result of the local importance of the European bass fishery within the D&S IFCA district combined with the overarching decline across the Northeast Atlantic, the D&S IFCA co-funded and co-supervised the current PhD with the University of Plymouth to investigate; the feasibility of localised management/conservation policies to improve local European bass populations. Due to the localized/restricted movement characteristics and estuarine dependence of this species, the PhD project was focussed on identifying; movement, feeding and growth within estuarine habitats, with a particular emphasis on measuring the effectiveness of designated Bass Nursery Areas within the D&S IFCA's district.

1.8.1 Chapter structure

The following five chapters are submitted in paper format, therefore information regarding the context of the European bass fishery and requirements for research may be shared between chapters.

Chapter 2: Highlighting large-scale historic anthropogenic disturbance in estuaries and its implications for commercial and recreational fin fisheries in the UK

A literature review to assess the importance of estuarine habitats for multiple commercially and recreationally exploited fin-fish species (including European Bass). Evidence of estuarine use/dependence is contextualized using intertidal habitat loss data provided by the Environment Agency, and stresses the importance for further research and/or management attention to incorporate habitat requirements within fisheries management.

Chapter 3: Assessment of European bass (Dicentrarchus labrax) somatic growth within protected Nursery Areas in the southwest United Kingdom

An assessment of European bass growth variability from three designated Bass Nursery Areas within the D&S IFCA district. Results highlight that growth within the first year may have important implications for subsequent size at age and survival.

Chapter 4: Using feeding rates and diet to assess the suitability of compensatory saltmarsh habitat for multiple estuarine fish species

An assessment of the habitat suitability within estuarine habitat creation schemes (Managed re-alignment schemes) for dependent fish species; European bass (*Dicentrarchus labrax*), Thinlip mullet (*Chelon ramada*) & Common/sand gobies (*Pomatoschistus spp.*). The results highlight that re-aligned sites provide feeding opportunities for local fish populations, however not currently in the same proportions as in surrounding natural saltmarsh.

The remaining chapters focus on the use of acoustic telemetry to monitor movement of European bass within three designated Bass Nursery Areas within the D&S IFCA district. These works were largely funded via a European Maritime and Fisheries Funding application - Immature Bass Acoustic Stock Surveillance (award: ENG1389) - £250k. Considerable in-kind support was also provided by both the D&S IFCA and the University of Plymouth. In order to implement these works, a home office project license was also written and successfully awarded (License ID: P81730EA5).

Chapter 5: Acoustic telemetry highlights localized movement of juvenile European bass (Dicentrarchus labrax) to coastal sites in the Southwest UK

An assessment of European bass residency to three designation Bass Nursery Areas in the D&S IFCA district. The results highlighted restricted movement of tagged fish and support the efficacy of more localized fishery management interventions.

Chapter 6: Environmental drivers and spatial-temporal patterns in European bass (Dicentrarchus labrax) movement within coastal sites in the Southwest UK

An assessment of the influence of environmental drivers for European bass presence/absence within three designation Bass Nursery Areas in the D&S IFCA district. The results highlight that fish may be present throughout the year and localized conditions, notably water temperature, have a strong influence on presence/absence.

Annex 1: Detailed methods statement for acoustic telemetry tag implantation

A methods chapter detailing the tagging method used to tag fish within chapters 5&6. Metadata associated with each individual fish and post-operative tagging survival are provided.

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Chapter 2: Highlighting large-scale historic anthropogenic disturbance in estuaries and its implications for commercial and recreational fin fisheries in the UK

Keywords

Marine fisheries, habitats, holistic management, ecosystem approach

Contributions

All supervisors provided logistical and academic support: Elizabeth West, Tim Robbins, Shaun Plenty, Martin Attrill, Emma Sheehan.

2.1 Abstract

It is widely accepted that estuaries provide important nursery and feeding habitat for numerous commercially and ecologically important fish species. Estuaries have however been historically subject to substantial habitat alteration/degradation via; environmental fluctuations, sea level rise, human activity on intertidal habitats and adjacent land management.

This chapter has summarised estuarine habitat use for numerous economically important fish species. Via a freedom of information request the extent of habitat loss in estuaries has also been summarised. This chapter reveals that approximately 2, 482.9km^2 of intertidal habitat has been historically lost from estuaries in England and Wales, an area approximately the size of Luxembourg. The implications of this large-scale habitat loss and continued anthropogenic disturbance within estuaries for a variety of fish species is discussed.

As a result of the high economic and social value of commercial and recreational fisheries, it is suggested that further research attention should investigate fish-habitat linkages, in particular for vulnerable life stages. Holistic fisheries management policies should also be considered which both sustainably managed fisheries landings but also account for the habitat requirements of the fishery.

2.2 Introduction

Estuaries are defined under the European Commission's Habitats Directive (Council Directive 92/43/EEC) as the downstream part of a river valley, subject to the tide and extending from the limit of brackish water (Davidson *et al.,* 1991). These ecosystems host a complex mosaic of subtidal and intertidal habitats which are closely associated with surrounding terrestrial environment. In Northern Europe, these habitats include but are not limited to; mudflats, sandflats, saltmarshes, seagrass beds, rocky and biogenic reefs.

Estuaries are known to be an important ecosystem for a variety of finfish species at a variety of life stages, such as adult feeding, refuge, nursery grounds and as migration routes (Table 2.1). In particular, a number of species targeted by commercial and recreational fisheries are known to use estuaries as a key nursery habitat, or estuaries are thought to provide a nursery role along with other shallow coastal habitats, e.g. shallow embayments (Pickett & Pawson, 1994; Wennhage *et al.,* 2007; Seitz *et al.,* 2014).

Despite the important role estuaries provide in regard to nursery and feeding habitats for finfish, in Northern Europe they are typically highly impacted by anthropogenic activities (Airoldi *et al.,* 2008). These activities includes: direct removal or adaptation of intertidal habitat (Elliott *et al.,* 1990; Sheehan *et al.,* 2010 a & b), water abstraction (Greenwood, 2008) and the introduction of harmful substances (including sewage effluent, agricultural waste, industrial chemicals, heavy metals and increased levels of suspended solids).

The impact of human disturbance within estuaries on fish populations is largely unknown (Chesney *et al.,* 2000), it has however been argued that anthropogenic activities such as those listed above has reduced the capacity of estuarine ecosystems to support fish populations relative to historic levels (Mclusky *et al.,* 1992; Rochette *et al.,* 2010). This review was written to highlight the scale of estuarine ecosystem change across England and Wales and its relevance to dependent fish populations.

2.3 Summary of commercial and recreational fisheries in the UK

Commercial fisheries in the UK directly employs an average of 12,262 fishermen per year, plus an additional estimated 13,455 Full Time Equivalent (FTE) jobs within processing plants and employment within the associated supply chain (Curtis *et al.,* 2018). 297k tonnes of finfish are landed by the UK fishing fleet per year (average from 2014-2018). These landings have an estimated value of £322million per year and account for approximately 60% of the total landed value of UK fisheries. The remaining 40% of which is comprised of shellfish such as; Nephrops (*Nephrops norvegicus*), Scallops (*Pecten maximus* and/or *Aequipecten opercularis*), Brown crab (*Cancer pagurus*) or European lobster (*Homarus gammarus*) (MMO, 2020).

In 2018 the UK commercial fishing fleet comprised of 6036 fishing vessels (MMO, 2020), which can broadly be split into those above and below 10m in length (Davies *et al.,* 2018). Those below 10m are typically termed the "inshore fleet" and characteristically fish within 6nm of the coastline, whereas larger vessels (>10m) typically fish in offshore waters (>6nm). The inshore fleet account for an average of 5.9% of the landed catch per year (MMO, 2020), however, accounts for approximately 80% of the number of vessels and 65% of the direct employment (Davies *et al.,* 2018; MMO, 2020).

Marine Recreational Fisheries (MRF) are also an economically and socially important sector in the UK (Armstrong *et al.,* 2013; Hyder *et al.,* 2017), with an estimated 2% of the adult population (1.08 million people) actively participating (Armstrong *et al.,* 2013). While annually variable, recreational sea angling (in isolation) is estimated to contribute £831 million to the UK economy and support 10,400 FTE jobs (estimate for 2012) (Armstrong *et al.,* 2013). Furthermore, the presence of specialist forums and fishing clubs, in particular for iconic species like European bass (*Dicentrarchus labrax*) demonstrate the social importance of MRF to the general public.

2.4 Economically important finfish species for commercial and recreational fisheries

Commercial fisheries in the UK are highly diverse, and landings data provided by the Marine Management Organisation (MMO) report that 182 different fish species are landed. At the time of writing UK landings data was available from 2014-2018. For the purposes of this chapter any species which individually accounted for more than 5% of the total landed value from 2014-2018 was considered economically important for the inshore or offshore fishery.

Mackerel (*Scomber scombrus*), Cod (*Gadus morhua*), Monkfish (*Lophius sp.*), Haddock (*Melanogrammus aeglefinus*), Herring (*Clupea harengus),* Hake (*Merluccius merluccius*) individually accounted for more than 5% of the landed value for the offshore fleet (vessels over 10m) (Figure 2.1). Bass (*Dicentrarchus labrax),* Sole (*Solea solea*), Mackerel (*Scomber scombrus*), Pollack (*Pollachius pollachius*) individually accounted for more than 5% of the landed value for the inshore fleet (vessels less than 10m)(Figure 2.1).

In 2012, the Department for Environment, Food and Rural Affairs (DEFRA) and MMO commissioned the sea angling review (Armstrong *et al.,* 2013). The survey collected catch data from marine recreational sea anglers, to help improve scientific understanding of the diversity of species captured and the economic and social value of recreational sea angling (Ares, 2016). This was achieved using a variety of techniques, including; an "Opinions and Lifestyle survey" conducted by the Office of National Statistics to estimate the number of recreational sea anglers in England and how actively they participated in recreational sea angling. This was combined with an online survey, as well as random shore and boat-based surveys conducted by the Inshore Fisheries and Conservation Authorities (IFCAs). The collected data was used to estimate the diversity of fish species captured by recreational sea anglers and the proportion of fish caught and released (Armstrong *et al.,* 2013).

Armstrong *et al.* (2013) represents the most recent publicly available assessment of fish species caught by recreational sea anglers, however a further assessment is being produced via the Sea Angling Diary (CEFAS & Substance, 2019). MRF covers capture methods such as: netting or sea angling, however information regarding fish species captured via methods other than sea angling are not readily publicly available. However, the UK MRF sector is thought to be dominated by recreational sea angling (Armstrong *et al.,* 2013; Hyder *et al.,* 2017). Therefore, while it is accepted that there will likely be some variability in the diversity of species captured by location, year and capture method, we are using the species list published by Armstrong *et al.* (2013) to be representative of the most targeted or important species for MRF in the UK. From this assessment, Armstrong *et al.* (2013) highlighted 14 species which were commonly captured by recreational sea anglers. While no value is assigned to these species the following individually account for >5% of the overall fish captured within MRF: Mackerel (*Scomber scombrus*), Whiting (*Merlangius merlangus*), Bass (*Dicentrarchus labrax*), Dogfish (*Scyliorhinus sp.*), Dab (*Limanda limanda*), Cod (*Gadus morhua*) (Figure 2.1).

Across the offshore, inshore and recreational fisheries, 12 finfish species have been identified as economically important. Some species are captured across all fisheries, however due to differences in fishing techniques and equipment, and the distribution of targeted fish within inshore or offshore environments, the relative importance of each species varies between the respective fisheries (Figure 2.1).

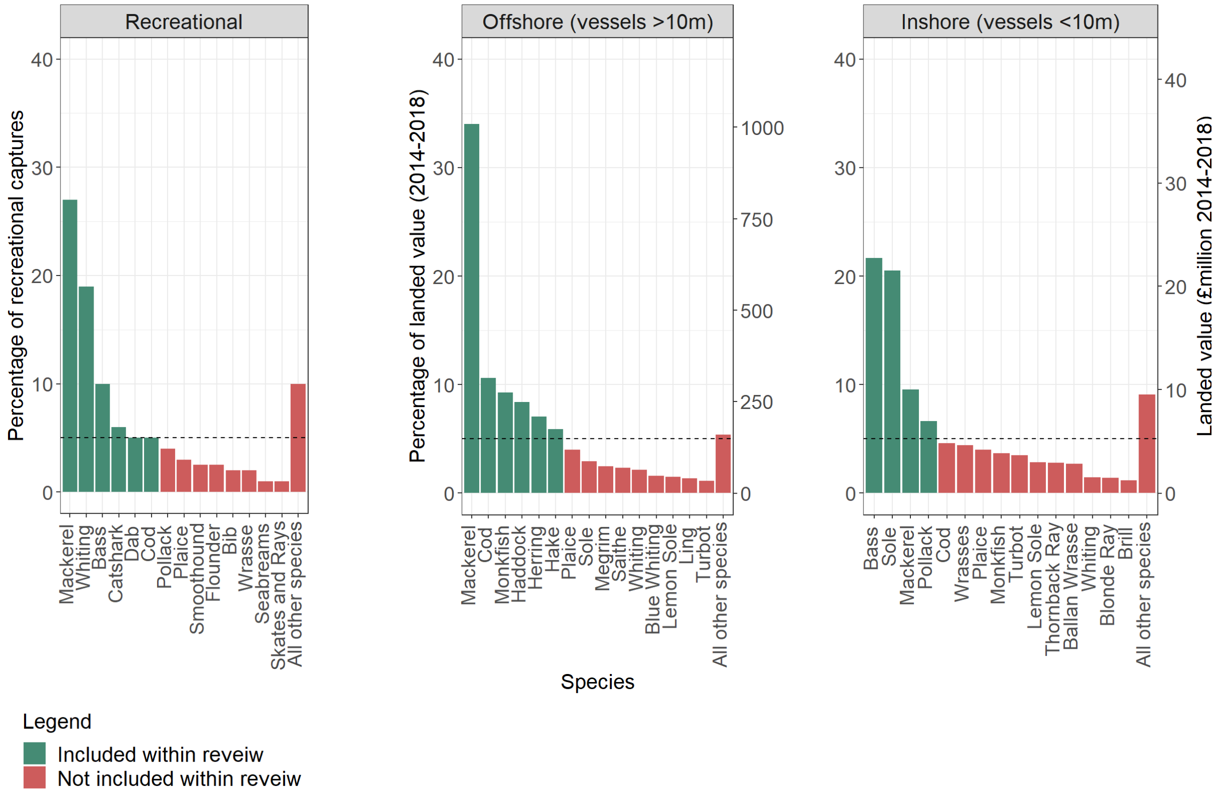

Figure 2. 1 - Economic value of finfish species which account for >=5% of the total landed value within the inshore and offshore commercial fishing fleet 2014-2018, or ≥=5% of captures within the recreational fishery. Black dashed line represents 5% of landings value (commercial fisheries) or 5% of recreational fisheries captures. All species which individually account for ≥=5% of the landings value or recreational captures highlighted green, species <5% highlighted red (Data source: MMO, 2020 & Armstrong, 2013)

2.5 Estuary use by economically valuable species/taxa captured by commercial fisheries and recreational sea angling

For all 12 finfish species highlighted within Figure 2.1, a google scholar search was conducted during December 2018 which included: “Species/taxa name” + “Estuary” + “Nursery”. The relevant literature was summarised and referenced within Table 2.1 and includes studies across each species geographic range.

Of the 12 species/taxa highlighted within Figure 2.1, seven (58%) were identified as using estuaries during their life cycle, usually in combination with other shallow coastal habitats e.g. coastal embayments. Notably however, Bass (*Dicentrarchus labrax*), Sole (*Solea solea*), Whiting (*Merlangius merlangus*), and Herring (*Clupea harengus*) were often identified as being common/dominant components of estuarine fish assemblages, and a significant evidence base suggested that estuaries represent important "nursery habitat" for these species (Table 2.1). With the exception of Herring, evidence from the peer-reviewed literature suggests many of the species captured within the offshore commercial fleet are not regularly recorded within estuaries. Bass, Sole and whiting are however identified as being highly significant for the inshore and recreational fisheries (Figure 2.1), suggesting estuaries may provide a significant role in supporting these fisheries within the UK (Meynecke *et al.,* 2007).

Table 2. 1– Economically important species/taxa identified through UK landings within the inshore and offshore commercial fishing fleet (MMO, 2020), and recreational fisheries captures (Armstrong *et al.,* 2013) listed in descending order of economic importance. Estuary use has been summarised for each species/taxa via peer-reviewed publications. Google scholar search terms include: “Species/taxa name” + “estuary” / “Nursery”. Search completed 25/01/2019. All species/taxa highlighted with * and emboldened text indicates evidence found for significant use of estuarine habitats.

Taxa	Summary of estuary use	Reference list
Mackerel (*Scomber scombrus*)	No significant use of estuaries found in peer reviewed literature	Ware & Lambert, 1985; Jansen & Burns, 2015
Bass (*Dicentrarchus labrax*) *	**Shallow coastal bays and estuaries used as nursery habitat until year 2-4 (Pickett & Pawson, 1994). Estuaries may also provide significant adult feeding habitat (Cambiè *et al.,* 2016)**	**Kelley, 1988; Costa & Bruxelas, 1989; MAFF, 1990; Pickett & Pawson, 1994; Laffaille *et al.,* 2001; Green *et al.,* 2012; Leitão *et al.,* 2006; Martinho *et al.,* 2008; Leakey *et al.,* 2009; Fonseca *et al.,* 2011; Cambiè *et al.,* 2016; Doyle *et al.,* 2017**
Sole (*Solea solea*) *	**Shallow coastal bays and estuaries used as nursery habitat until year 2** **Please note reference list is not exhaustive due to the high volume of research conducted on this species. However, there is consensus across studies**	**Coggan & Dando, 1988; Marchand, 1991; Marshal & Elliot, 1998; Cabral & Costa, 1999; Amara *et al.,* 2000; Cabral, 2000; Pape *et al.,* 2003; Vinagre *et al.,* 2005; Fonseca *et al.,* 2006; Vinagre *et al.,* 2006; Nicolas *et al.,* 2007; Martinho *et al.,* 2008; Vinagre *et al.,* 2008; Leakey *et al.,* 2009; Kostecki *et al.,* 2010; Rochette *et al.,* 2010; Tanner *et al.,* 2012**
Whiting (*Merlangius merlangus*) *	**Larvae found in shallow coastal bays, however 0 group and adults known to form dominant component of the fish assemblages in Thames and Severn estuaries**	**Nagabhushanam, 1964; Arntz & Weber, 1972; Gordon, 1977; Van den Broek, 1979 & 1980; Potter *et al.,* 1988; Henderson & Holmes, 1989; Potter *et al.,* 1988; Elliott *et al.,* 1990; Hamerlynck & Hostens, 1993; Armstrong & Dickey-Collas, 1997; Power *et al.,* 2002; Gerritsen *et al.,* 2003; Leakey *et al.,* 2009; Henderson & Bird, 2010; Bastrikin *et al.,* 2014**
Cod (*Gadus morhua) **	**Larvae/juveniles found in shallow coastal bays (Tupper et al., 1995), however, may also use estuaries as nursery area. Some adult presence/use recorded within estuaries**	**Cohen *et al.,* 1991; Elliott *et al.,* 1990; Gotceitas *et al.,* 1998; Lazzari, 2013; Bastrikin *et al.,* 2014**
Monkfish (*Lophius sp.*) – UK species include: *Lophius piscatorius*	Significant information on stock structure, behaviour or spawning biology of monkfish is scarce (Solmundsson *et al.,* 2009)	Solmundsson *et al.,* 2009; Colmenero *et al.,* 2013; Hernández *et al.,* 2015; Ofstad *et al.,* 2017

Lophius budegassa	No significant use of estuaries found in peer reviewed literature	
Pollack (*Pollachius pollachius*) *	**Juveniles spend 2-3 years in coastal areas, typically found in the following habitats; rocky areas, kelp beds, sandy shores and estuaries (Cohen *et al.,* 1991)**	**Costa & Bruxelas, 1989; Cohen *et al.,* 1991**
Haddock (*Melanogrammus aeglefinus*)	Literature regarding Haddock life history is scarce. No significant use of estuaries found in peer reviewed literature	Olsen *et al.,* 2010; Wright *et al.,* 2010; Castaño-Primo *et al.,* 2014;
Herring (*Clupea harengus*) *	**Several herring stocks spawn in inshore waters and estuaries (Fox *et al.,* 1999). Juvenile herring (Year 1) are amongst one of the most abundant fish within UK estuaries (Henderson, 1989), where they are known to feed within habitats such as saltmarsh (Green *et al.,* 2012).**	**Chenoweth, 1971; Chenoweth, 1971; Dempsey & Bamber, 1983; Henderson *et al.,* 1984; Henri *et al.*, 1985; Claridge *et al.,* 1986; Henderson, 1989; Elliot *et al.,* 1990; Lazzari *et al.,* 1993; Fox *et al.,* 1999; Maes & Ollevier, 2000; Power *et al.,* 2000; Lacoste *et al.*, 2001; Thiel & Potter, 2001; Maes *et al.,* 2005; Maes *et al.*, 2005; Henderson & Bird, 2010; Green *et al.,* 2012**
Catshark (*Scyliorhinus sp.*)	No significant use of estuaries found in peer reviewed literature	Ellis & Shackley, 1997;
Hake (*Merluccius bilinearis*)	No significant use of estuaries found in peer reviewed literature	Fahay, 1974; Steves & Cowen, 2000; Lock & Packer, 2004
Dab (*Limanda limanda*) *	**Larvae/juveniles found in open coastal bays (Bolle *et al.,* 1994), however estuaries may also be used as nursery habitat for short periods: 1-3 months; (Forth estuary: Elliott *et al.,* 1990)**	**Elliot *et al.,* 1990; Bolle *et al.,* 1994**

2.6 Intertidal and estuarine habitat loss

Estuaries are highly dynamic environments, which experience a wide range of environmental and anthropogenic stressors (Attrill *et al.,* 1999; Ladd *et al.,* 2006). Fluctuations in; sediment supply (Ladd *et al.,* 2006), hydrology (Cui *et al.,* 2016), and sea level rise (Nicholls *et al.,* 1999; Adam, 2002; Hay *et al.,* 2015, Lawrence *et al.,* 2018) can influence the extent of intertidal and subtidal habitats e.g. saltmarsh or biogenic reefs. Introduction of alien and/or harmful substances (Kelly, 1988; Jennings, 1990; Ogburn *et al.,* 2007) or human activities such as; construction of "hard" sea defences (Dixon *et al.,* 1998; Morris et al., 2004; Lawrence *et al.,* 2018), and farming on intertidal habitats (Laffaille *et al.,* 2000) can also negatively affect estuarine water quality and habitat extent. The cumulative influence of this complex mosaic of both naturally occurring and anthropogenic induced environmental instability, on estuarine dependent fish populations is however not well-understood (Chesney *et al.,* 2000).

Another major issue cited within the peer-reviewed literature is historic land-claim, which is the process of humans converting intertidal habitat into terrestrial habitat, typically for agricultural or industrial purposes (Lotze *et al.,* 2006). It is estimated that as much as 85% of estuaries in the UK have been impacted by historic land claim (Davidson, 2016). Whilst locally variable, this has resulted in substantial intertidal habitat loss across UK estuaries, for example within the Forth and Thames estuaries it is estimated that 50% (Mclusky *et al.,* 1992) & 64% (Attrill *et al.,* 1999) of the intertidal habitat has been lost respectively.

The full scale of intertidal habitat loss is hard to quantify, as limited historical records exist to show pristine estuarine environments prior to human development. However, as part of the Water Framework Directive: 2000/60/EC (WFD) Transitional and Coastal Waters angiosperm: Saltmarsh assessment, historic intertidal habitat extent is estimated using Light Detection And Ranging (LiDAR). Areas of historic intertidal habitat are identified, by detecting coastal land which is below the highest astronomical tide but located behind an artificial flood defence (full methods: Best, 2007 & WFD UKTAG, 2014).

The results from the most recent publically accessible intertidal habitat loss assessment have been summarised within this chapter (Assessment conducted by Environment Agency. FOI: NR73435). To highlight spatial variability across the UK and aide visualisation at a national scale, ESRI shapefiles of the estimated intertidal habitats loss across England and Wales (provided by the Environment Agency) were converted to 100km2 grid cells. The area of estimated habitat loss per 100km^2 grid cell is then displayed in figure 2.2-A. To highlight broad scale regional differences, the total estimated habitat loss across coastal NUTS regions in England and Wales has been calculated and displayed in figure 2.2–B.

The results of the WFD assessment indicate widespread historic intertidal habitat loss across England and Wales. Loss of intertidal habitat was however spatially variable, with 1728km^2 (67%) occurring within NUTS regions along the east coast of England, notably: East England, East Midlands, Yorkshire and the Humber. Within the remaining NUTS regions (London, Wales and South east, South west and North west England) a total of 755km2 (33%) of intertidal habitat is estimated to have been historically lost. When combined it is estimated that 2,483 km^2 of intertidal habitat has been historically lost from across England and Wales. When put into context this is an area larger than modern day London (1,572 km^2) or roughly approximate to the area of Luxembourg (2,586km^2).

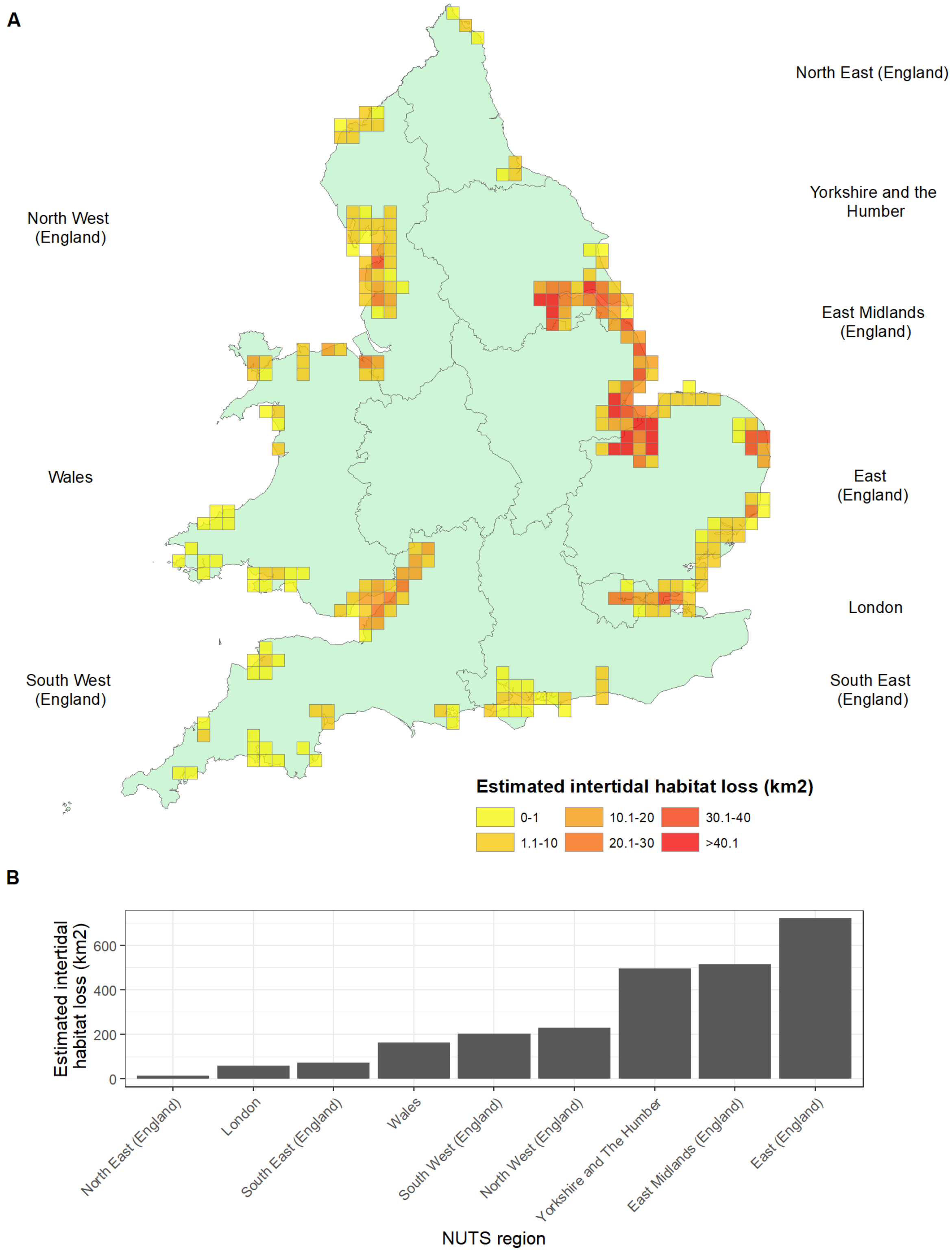

Figure 2. 2 – Estimated intertidal habitat loss per 100km2 grid cell (A), and by coastal NUTS region across England and Wales (B). Data source: Best (2007) & WFD UKTAG (2014)

2.6.1 Historic saltmarsh habitat loss

It is uncertain which specific intertidal habitats have been historically degraded or lost from England and Wales e.g. saltmarsh, mudflat or reef, however as part of the WFD historic intertidal habitat loss assessment, the historic extent of saltmarsh across England and Wales was also estimated. The Environment Agency digitised “first epoch” Ordinance Survey (OS) maps (1843-1893); areas identified as “Saltmarsh”, “Saltings” or “Grazing marsh” were then spatially defined as “Historic saltmarsh”.

When comparing the total current extent of saltmarsh (405 km^2 – Environment Agency, 2020) to the estimated historic extent of saltmarsh (1123km^2), it is estimated that 708km^2 of saltmarsh habitat has been cumulatively lost within England and Wales. Figure 2.3 represent the worst affected estuaries and embayments, from which the estimated historic saltmarsh habitat loss is: 24km^2 (the wash, plus associated estuaries), 45km^2 (The Blackwater and Colne estuaries), 133km^2 (The Thames estuary), 147km^2 (The Medway estuary). These four sites account for 349km^2 (31%) of the historical saltmarsh habitat loss across the England and Wales. The remaining 774km^2 (69%) of historic saltmarsh habitat loss is distributed widely across the coastline of England and Wales.

There is considerable uncertainty surrounding the WFD intertidal habitat loss estimates presented within this chapter. For example, Ladd *et al.* (2019) argue that saltmarsh habitat extent can vary both temporally and spatially and in some regions of the UK, saltmarsh habitat extent has increased by 158% since 1846. Furthermore, a lack of historical records detailing intertidal habitat (prior to the commencement of ordinance surveys - 1843) mean that land claim estimates derived from LiDAR data cannot be validated (WFD-UKTAG, 2014). Despite these caveats it is likely that substantial loss of historic intertidal habitat has cumulatively occurred across England Wales.

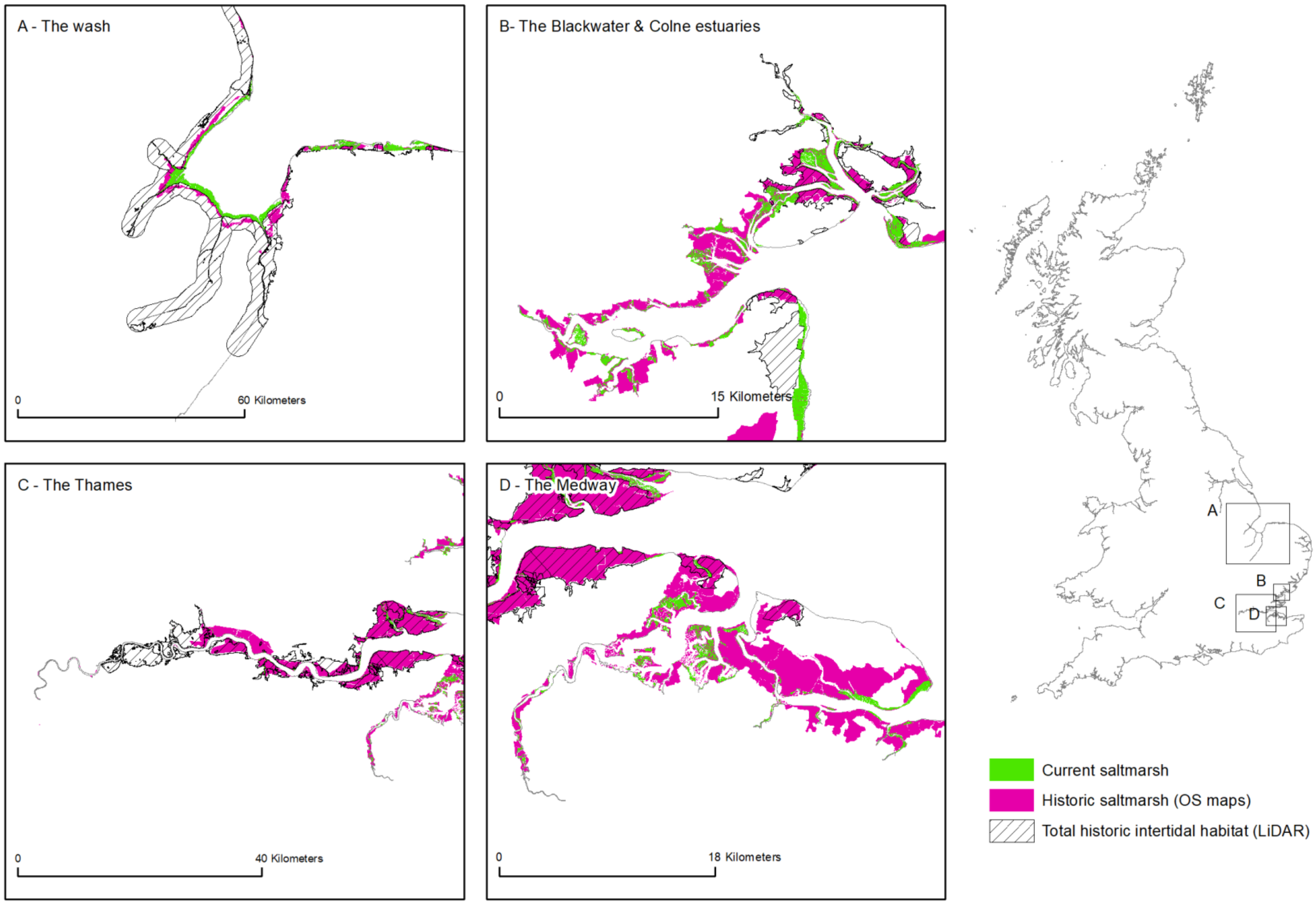

Figure 2. 3 – Estimated estuarine intertidal habitat loss and historic saltmarsh extent compared to current extent of saltmarsh within four locations in England and Wales, UK. Data provided by Environment Agency, UK, through Freedom of Information Request: NR73435 and an Open Government License. UK high water boundary shapefile sourced from Edina Digimap (Ordinance survey, 2005)

2.7 Implications for fisheries management

As mentioned previously, the cumulative impacts of the variety of natural and anthropogenic stressors on estuarine ecosystems, plus the associated fish communities is not currently well understood (Chesney *et al.,* 2000). There are however numerous studies which highlight the importance of estuaries for fish, notably juveniles may use shallow vegetated habitats (e.g. saltmarsh) to seek refuge from predation (Kelley, 1988; Paterson & Whitfield, 2000) or for feeding (Hampel & Cattrijsse, 2004; Kelley, 1988; Laffaille *et al.,* 2001 & 2002; Green *et al.,* 2012; Fonseca *et al.,* 2011; Cambiè *et al.,* 2016). Other studies have also demonstrated a correlation between estuarine habitat extent to local fish production (Mclusky *et al.,* 1992; Rochette *et al.,* 2010; Sunbald *et al.,* 2014). Linking large-scale fisheries landings with juvenile habitat availability has however proven difficult, with limited examples in the peer reviewed literature showing a direct correlation (Chesney *et al.,* 2000). Chesney *et al.* (2000) argued that this may be a result of the extreme complexity of this topic, and is likely to be confounded by intra and interspecific differences as well as several environmental and anthropogenic factors occurring concomitantly.

Assessment of fish-habitat associations within estuaries is however logistically and technologically challenging, as well as financially expensive (Mullin, 1995). As a result, for many commercially and recreationally important fish species while there is evidence that estuaries are utilized, information on how they interact with, or are dependent on, estuarine or wider coastal habitats is often lacking (Vasconcelos *et al.,* 2007; Seitz *et al.,* 2014). This is particularly problematic as it is estimated that 85% of coastline across Europe is at high or moderate risk for unsustainable coastal construction and development (Seitz *et al.,* 2014).

It is possible that some fish species will be unaffected by coastal development, for example Chesney *et al.* (2000) highlighted the stability of fisheries landings within Louisiana, USA despite an estimated loss of 80-117km^2 or intertidal marsh per year. However, without a better understanding of how commercially and recreationally important fish species move within and exploit estuarine habitats, there could be unknown negative consequences on the these fisheries because of continued anthropogenic pressure on these ecosystems. Furthermore, since many important fish species may have quite specific habitat preferences (Fodrie & Levin, 2008; Seitz *et al.,* 2014) or localized movement behavior (Green *et al.,* 2012), decreased habitat availability (in particular for juvenile life stages) may introduce population bottlenecks (Sundblad *et al.,* 2014; Seitz *et al.,* 2014).

Furthermore, estuarine fish populations are also exposed to several other anthropogenic threats which may impact on survival, feeding and growth (Vasconcelos *et al.,* 2007). Anthropogenic threats to estuarine fish populations may include but are not limited to;

- Continued habitat loss,
- Channel adaptation (e.g. channelization or dredging) (Reise, 2005)
- Industrial water abstraction (Greenwood, 2008),
- Sewage effluent (Kelley, 1988),
- Uptake of persistent contaminants (Hardisty *et al.,* 1974; Dallinger *et al.,* 1987; Elliott *et al.,* 1990)

It is therefore suggested that further research attention, investigates fish-habitat linkages within inshore and estuarine locations. If necessary, holistic fisheries management policies could also be employed that both sustainably manage fisheries landings, but also account for the habitat requirements of the fishery. A relevant case study includes the USA Atlantic

Striped Bass (*Morone saxatilis*) fishery, where a key management action is identification, protection and monitoring of; spawning; nursery and wintering habitat, as well as migratory corridors (Hill *et al.,* 1989; ASMFC, 2020).

2.8 Concluding remarks

This chapter has published evidence of substantial habitat alteration throughout estuaries in England and Wales (WFD-UKTAG, 2014). Whilst estuarine habitat degradation and decline is widely cited in the peer reviewed literature (Kennesh, 2002; Lotze *et al*., 2006; Airoldi & Beck, 2007; Vasconcelos *et al.,* 2007), this review has highlighted the linkage between intertidal habitats and economically important fish species in the UK.

Incorporation of habitat management within fisheries is not a novel concept, for example since 1996 Essential Fish Habitat (EFH) has been incorporated into USA fisheries management through an amendment to the Magnuson–Stevens Fishery Conservation and Management Act (Chesney *et al.,* 2000). This amendment is based on the premise that some fish species are dependent on specific habitats during their life cycles, and therefore fisheries managers should widen their remit to ensure fishery-dependent habitats remain "healthy" and be able to support sustainable fisheries (Rosenberg *et al.,* 2000).

Within the European Union, the requirement to protect essential habitats utilized by fisheries is also specified though high level strategic policies aimed at implementing or supporting Ecosystem Based Fisheries Management (EBFM), notably, the Marine Strategy Framework Directive (MSFD), Common Fisheries Policy (CFP), Marine Spatial Planning Directive (MSPD) and Habitats Directive (HD). Specifically, under Article 8 of the reformed Common Fisheries Policy (enacted in 2014) it was proposed that EU member states establish a network of marine reserves known as "Fish Stock Recovery Areas". These areas are proposed to protect habitats, which provide essential ecosystem services to commercially and recreationally important fish and shellfish species, with particular reference to the protection of spawning and nursery grounds (Roberts & Hawkins, 2012). Post Britain's exit from the European Union it is uncertain what fisheries policies will be implemented within the UK, however, via the Conservation of Habitats and Species Regulations 2017 equivalent protection will be afforded to habitats and species identified through the habitats directive. Furthermore, Marine Spatial Planning via the Marine and Coastal Access Act (2009) and the UK fisheries Bill (2020) specifically mention identification of Essential Fish Habitat and an Ecosystem Based Approach to Fisheries Management.

Despite these legislative drivers providing a legal framework at both a EU and UK level since 2014, little political attention or progress has been made to implement protection for fishery-dependent habitats across Europe (Oceana, 2019). While some relevant habitats (e.g. Saltmarsh) are currently legally protected by European and UK national legislation (e.g. Habitat's directive: Council Directive 92/43/EEC; or as Sites of Special Scientific interest), these site designations do not often incorporate dependent fish species or assemblages within management plans (Vasconcelos *et al.,* 2007). Therefore, due to the high economic and social value of commercially and recreationally exploited fisheries, it is imperative that further research and management attention is given to identifying the habitat requirements for fisheries which provide an important ecological and/or economic role. Specifically to; identify, protect and/or restore habitats upon which fisheries are dependent, in particular for those species which have known associations with estuarine habitats (Chesney *et al.,* 2000; Seitz *et al.,* 2014).

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Chapter 3: Assessment of European bass (*Dicentrarchus labrax*) somatic growth within protected Nursery Areas in the Southwest United Kingdom

Keywords

European bass, fisheries, growth, scales

Contributions

All supervisors provided logistical and academic support: Elizabeth West, Tim Robbins, Shaun Plenty, Martin Attrill, Emma Sheehan.

Additional academic support provided by Ben Ciotti

3.1 Abstract

European bass (*Dicentrarchus labrax*) is a commercial and recreationally important fin fish native to the Mediterranean Sea and Northeast Atlantic. In 2010, ICES reported a dramatic decline in the Northeast Atlantic stock, which in 2015 fell below "safe biological limits". Following this decline, increasing recruitment was identified as a critical recovery pathway. Growth in wild fish populations is a widely-used metric to assess fish habitat suitability, and is an important driver in survival and recruitment. In the context of the diminished population across the Northeast Atlantic, the aim of the study was to quantify differences in growth across a range of nursery sites in the UK in order to better define mechanisms to boost recruitment.

Scales were collected from 147 European bass across three designated bass nursery areas in the Southwest UK; The Dart estuary, Salcombe Harbour and the Taw/Torridge estuaries. Using a back-calculation method the length of each fish at years 0-4 were estimated. A linear mixed effect model was then used to estimate, and compare growth rates between nursery sites. Growth rates were similar between nursery sites, but substantial differences in the size achieved at age 0-1 were detected.

Further work is required to validate results however, the results suggest that growth in years 0-1 may have important consequences for latter size at age. Management and/or research attention should therefore focus on processes which are important regulators of growth at this stage of development e.g. density-dependent regulation of growth and/or habitat access and suitability.

3.1 Introduction

European bass (*Dicentrarchus labrax*) is a commercially and recreationally important finfish commonly found in estuaries and coastal seas throughout the Northeast Atlantic and Mediterranean Sea (Pickett & Pawson, 1994; B.A.S.S, 2004 from Ares*,* 2016; Carroll, 2014; MRAG, 2014). In 2010 the International Council for Exploration of the Seas (ICES) reported a dramatic decline in the Northeast Atlantic stock (ICES divisions 4.b–c, 7.a, and 7.d–h), which in 2016 declined below "safe biological limits", a threshold known as B_{lim}. In response to ICES advice the European Commission implemented a number of strict emergency "Technical Conservation Measures" which have imposed restrictions such as; banning targeted pelagic trawling during spawning periods, restrictions on commercial and recreational landings, and increasing the minimum landing size to 42cm total length (Ares, 2016). In 2019 ICES reported that the North Atlantic stock increased above B_{lim}, however relative to historic levels the population remains in a highly impoverished state and is still below maximum sustainable yield thresholds (Figure 3.1).

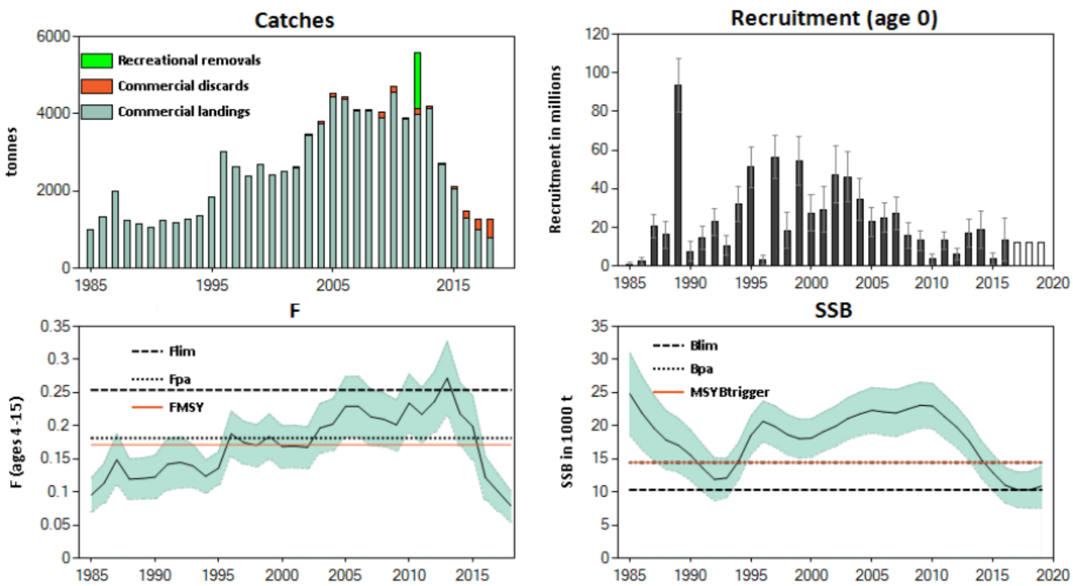


Figure 3. 1- Sea bass in ICES divisions' 4.b–c, 7.a, and 7.d–h. Summary of the stock assessment. Catches - Total landings (commercial landings and estimated recreational removals, available for 2012 only [green bar], taking mortality of released fish into account). F - Fishing mortality is shown for the combined commercial and recreational fisheries. Discard estimates are available from 2009. Recruitment (age 0) - Assumed recruitment values are not shaded. SSB – Spawning stock biomass. Recruitment, F, and SSB are shown with 95% confidence intervals (Image source: ICES (2019)

The decline in Northeast Atlantic European bass stock is thought to be a result of several contributory factors, which relate to; increasing fishing effort, a lack of responsive fisheries management, life history characteristics and variable recruitment (ICES, 2019). Notably, the commercial fishery dramatically increased from the 1970-1990s (Pawson *et al.,* 2007). With few catch restrictions imposed on the fishery, commercial landings across the region increased to their maximum of 4562 tonnes in 2010, which combined with the Spawning Stock Biomass (SSB) rapidly declined each consecutive year following. Furthermore, over a similar period recruitment was defined as "low" and fluctuating without trend (ICES, 2019). It is therefore thought that an unsustainable increase in fishing effort and fishing mortality, combined with poor recruitment are thought to be the primary cause for the decline in the Northeast Atlantic stock (Williams *et al.,* 2018).

In regard to recruitment, European bass are thought to be highly dependent on defined shallow coastal habitats e.g. embayments and estuaries, as nursery habitat for the first four years of life (Pawson *et al.,* 1987; Kelley, 1988; Pawson *et al*., 2007). These nursery habitats therefore provide a crucial recruitment pathway to replenish the diminished commercially fished stock (Pickett *et al.,* 2004). However, whilst inhabiting nursery habitats juvenile populations are thought to be vulnerable to damaging anthropogenic activities and environmental fluctuations, which may increase mortality and therefore affect recruitment success (Pawson, 1992; Pickett & Pawson, 1994).

In 1990, through the *Bass (Specified Areas) (Prohibition of Fishing) (Variation) Order 1999,* 37 coastal sites in the UK were designated as protected Bass Nursery Areas (BNAs). These sites were designated largely within estuaries on the east, south and west coast of England and Wales, and designed to protect juvenile bass from commercial fishing pressure (Pickett *et al.*, 2004). However, while BNAs provide protection for the direct removal of under-sized/immature European bass from commercial fishing activity, this legislation does not provide corresponding protection of habitats which support juvenile European bass populations. While a number of estuarine habitats which are utilized by European bass are protected through the European Commission's Habitats Directive (Council Directive 92/43/EEC) e.g. saltmarsh (Fonseca *et al.,* 2011; Green *et al.,* 2012), monitoring/assessments do not often take account of dependent fish populations.

A number of authors have reported the tendency of European bass to display high residency and fidelity to specific nursery sites for the first four years of life (Kelley, 1988; Pawson *et al.,* 1987; Pickett & Pawson, 1994; Green *et al.,* 2012; Cambiè *et al.,* 2016; Doyle *et al.,* 2017). Whilst occupying nursery sites; growth, survival, and ultimately successful recruitment, is likely to be intrinsically related to local environmental conditions and/or food resources (Pickett & Pawson, 1994; Burrows *et al.,* 2004; Ciotti *et al.,* 2013). Quantification of growth variability in juvenile fishes has been used as a measure of habitat quality, with higher growth being achieved in habitats of higher "quality" (Able, 1999; Ciotti *et al.,* 2013). Therefore, as a result of their tendency to maintain residency to specific nursery sites for their first four years, measurements of growth variability in European bass captured from a variety of estuarine nursery habitats may provide an important assessment of the nursery habitat "quality".

Growth in juvenile European bass is however known to be affected by wide variety of factors. Commercial aquaculture has demonstrated feed availability and diet (Kaushik , 2002; Peres & Oliva, 2007), plus environmental conditions such as salinity and oxygen availability (Dendrinos & Thorpe, 1985; Thetmeyer *et al.,* 1999) are important determinants of growth. In wild populations water temperature has also been linked to mortality of over-wintering 0-group bass (Pawson, 1992), and anecdotally reported to dictate the distribution of 0-group bass in autumn and early winter (Pickett & Pawson, 1994). It is also thought that habitat suitability and prey availability may be a secondary factor regulating growth in wild populations, however this has not been widely tested (Kelley, 1988 & 1986).

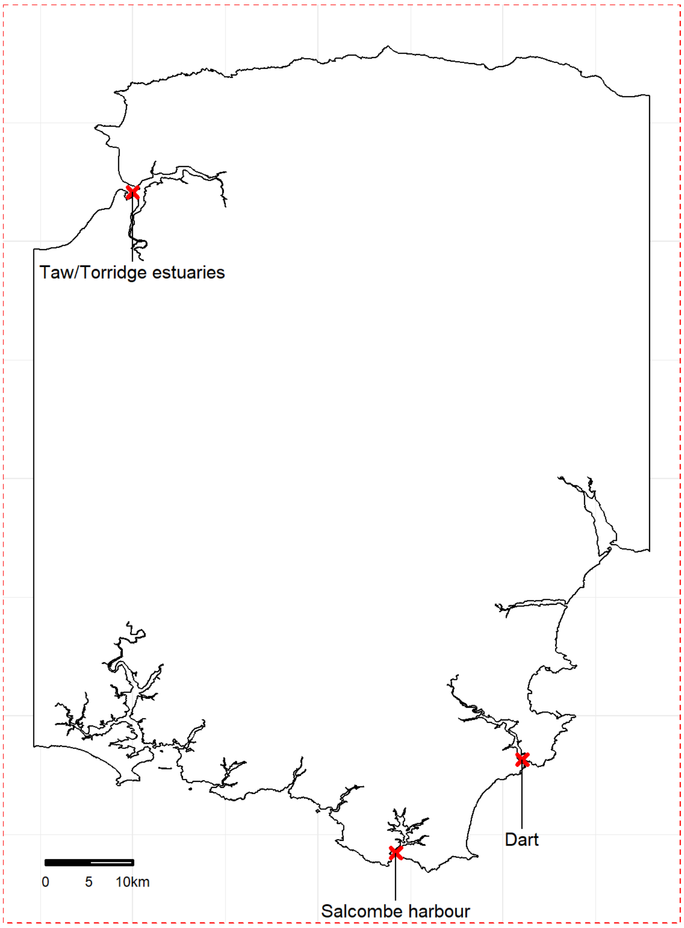
Scales and calcified structures (e.g. otoliths, opercular bones) have been used to assess growth in fishes (Cassleman, 1990). Typically concentric rings are laid annually at the start of the growth season, which in European bass begins from May (Pickett & Pawson, 1994) (Figure 3.3). The number of rings in each scale can be used to estimate age (years), and the width between each ring used to measure the relative growth rate within each corresponding year (Pickett & Paswon, 1994). Using back-calculation methods, the relative change in fish size between years can be estimated and compared between nursery sites (Francis, 1990, Lea, 1910).

The aim of this study is to use scales collected from European bass, to assess differences in growth rates at three nursery sites in the southwest UK and identify significant development stages for these fish.

3.2 Methods

In order to determine growth rates, scales were collected from European bass captured within three nursery sites in the southwest UK: The Dart estuary, Salcombe Harbour, Taw/Torridge estuaries. From each scale, measurements of annual increments were conducted and a back-calculation method used to measure the growth rates at each nursery site. All data analysis was conducted using R version 3.6.0 (R Core Team, 2019).

All three nursery sites are designated Bass Nursery Areas: The Dart estuary (capture dates: 10-19/08/2018), Salcombe Harbour (capture dates: 27-28/06/2018, 31/07/2018 & 01/08/2018) and the Taw/Torridge estuaries (capture dates: 16-20/07/2018) (Figure 3.2). Salcombe harbour is a Ria system, which is the remnants of a now extinct river valley and therefore no longer has any major fresh water sources. The Dart and Taw/Torridge are however major estuaries within the region. In regard to latitude, The Taw/Torridge estuary is located approximately 0.8^{o} latitude further North than Salcombe harbour and Dart estuaries (Figure 3.2).



Capture location	lat	lon
Dart	50.34473	-3.568823
Salcombe harbour	50.22648	-3.773907
Taw/Torridge estuaries	51.06184	-4.200472

Figure 3. 2 - Nursery sites where European bass were captured to assess variability in growth

3.2.1 - Water temperature

As a result of differences in site hydrology and latitude, water temperature may vary between the nursery sites and have a resultant impact in the growth of resident fish populations. Water temperature was therefore selected as the key environmental variable to compare to the estimated growth rates.

As part of the UK's statutory duties under the Water Framework Directive (WFD), water temperature records are collected from estuarine (referred to as transitional waters) and coastal sites. These are typically collected as spot measurements on a monthly basis, however sampling can be sporadic.

Due to poor monthly replication in each of the nursery sites included within the study, WFD water temperature records were binned into the following seasons: Winter (December-February), Spring (March-May), Summer (June-August), Autumn (September-November).

Seasonal differences in water temperature were compared between the nursery sites using a linear mixed effect model (lme4 package; Bates *et al.,* 2015), with the following notation:

Water temperature (^{o}C) ~ Season * Nursery site + (1|month)

Initially the most complex model was fit, then sequentially each term and interaction removed. The corresponding models were scored using Akaike Information Criterion (AIC). The model with the lowest AIC score was selected as the best fitting model. If model AIC scores were <2 then the model with the fewest terms and/or interaction terms was selected (Zuur *et al.,* 2013). To account for temporal autocorrelation within model residuals, month was used as a random variable. Temporal autocorrelation within model residuals was assessed via visual inspection of an AutoCorrelation Function (ACF) plot, none was visually apparent.

The Tukey pairwise comparison (lsmeans package; Lenth *et al.,* 2020) was used to assess at which levels (season * nursery site) water temperature significantly differed.

3.2.2 – Scale collection

A total of 147 individual European bass were captured via hook and line from Salcombe harbour, the Dart and Taw/Torridge estuaries. Under home office license: P81730EA all fish were anaesthetized via immersion within Tricaine Methanesulfonate (80mg/litre MS222) (ASPA, 1986). Once anaesthetized to a surgical plane (Annex 1), 3-5 scales were retained from each fish which were sourced from above the lateral line adjacent to the operculum

(Figure 3.3). Scales from each fish were stored within individual scale packets, which were labelled with; the fork length, capture location and capture date. All fish were subsequently released at the site of capture once the effects of anaesthesia were no longer visually evident (recovery stage 1 - Annex 1).

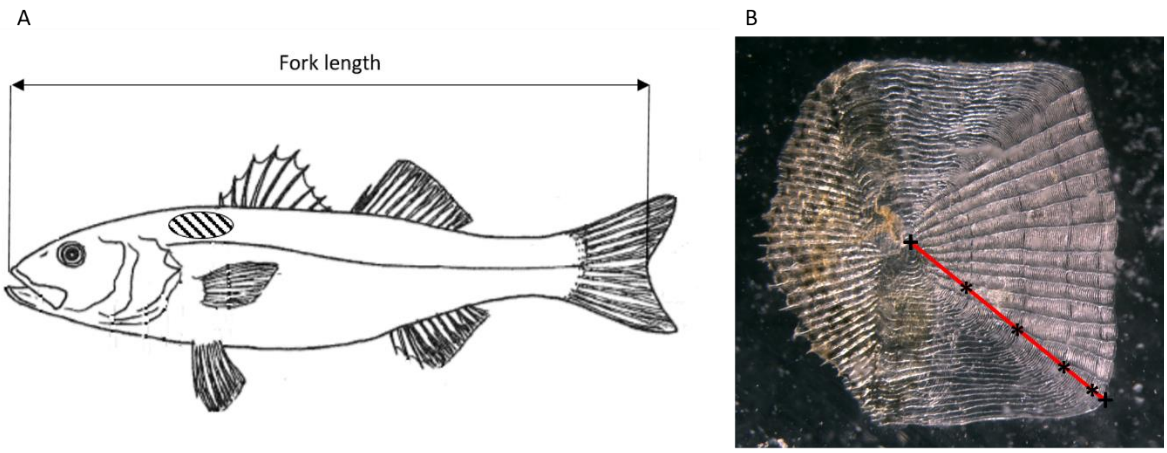


Figure 3. 3 - A: Scale removal site from European bass included within the study, figure adapted from Pickett & Pawson (1994). B: Annotated example image of age 4+ European bass scale. Red line = reading axis, + = Scale nucleus and margin, * = annual check/annuli (Image A adapted from Pickett & Pawson, 1994)

3.2.3 – Scale preparation and selection

A single scale from each fish was photographed using a camera mounted Leica M205C microscope. Scales were sandwiched between two transparent microscope slides, and photographed at an appropriate magnification to ensure the whole scale was in focus and in view.

All images were imported into ImageJ with ObjectJ plugin where the scale nucleus, each annuli and scale margin, were marked along a standardized reading axis (Figure 3.3). From each image; the scale radius width and width from the nucleus to each visible annuli was measured. All images were scaled with a photographed graticule taken at the same magnification which provided a precision of 0.1mm.

All images were assigned a confidence score of 1 or 2; where 1 represents a high confidence in age determination, with highly visible annuli present; 2 represents a low confidence score in age determination, where annuli were not easily identified. All replacement scales (Figure 3.4) were assigned a score of 2. Replacement scales occur when a scale is lost at some point during the fish's life, and a new scale is grown rapidly to replace the lost scale. These replacement scales will lack any growth annuli up to the point of it's formation (Pickett & Pawson, 1994). If scales were assigned a confidence score of 2 they were excluded from the study (Nolan & Britton 2019).

Figure 3. 4 - Representative image of replacement scale, within which annuli are not easily identified

3.2.4 – Growth estimates

Dahl-Lea back calculated size at Year^n

The Dahl-Lea back calculation (Lea, 1910) was used to estimate fish length at each annuli. This method has previously been used by Kelley (1988) & Pickett & Pawson (1994), and is reported to generate appropriate back calculated length for European bass. The Dahl-Lea back calculation is defined as:

$$Ln = \frac{Rn}{R} * L$$

Where: *Ln* is the fork length of the fish at age[n]; *Rn* is the scale radius at age[n]; *R* is the total scale radius; *L* is the fork length at capture.

This back calculation method assumes a linear relationship between radius width ~ fork length, and does not account for the size of the fish when the scale was first formed (25-31mm Kennedy & Fitzmaurice, 1972; Barnabé, 1976). Multiple regression (Stats package; R core team, 2019) was conducted to validate the assumption of a linear relationship between scale radius ~ fork length, and assess if this relationship varied between nursery sites. Model simplification using AIC scores was conducted following the same protocol for analysis of water temperature records. To account for growth which occurred prior to the formation of the first annuli, 25mm was added to all size estimates derived from Dahl-Lea method.

Please note that during fish capture, fish which ranged in ages were captured. All fish captured were used to validate the Dahl-Lea method however only fish which were aged 4 years were used to assess variability in growth rates between nursery sites (Page 99 & 101).

Back calculated growth rate

Evidence within the peer reviewed literature suggest that European bass are highly resident to their defined nursery site during years 0-4 (Kelley, 1988; Pawson *et al.,* 1987; Pickett & Pawson,). Therefore, using the back calculated length at year 0-4, growth rates were estimated and compared between nursery sites with a Linear Mixed Effects model (lme4 package; Bates *et al.,* 2015) with the following notation:

$$\textbf{Length in year}^{n} \sim \textbf{year}^{n} * \textbf{nursery site} + \textbf{(1|fish ID)}$$

The back calculated length at year^{n} was included as the dependent variable. Year^{n}, nursery site and their interaction were used as fixed effects. To account for non-independence of samples due to repeated observations from each individual fish, fish ID was included as a random effect. Model simplification using AIC scores was conducted following the same protocol for analysis of water temperature records. The Tukey pairwise comparison (lsmeans package; Lenth *et al.,* 2020) was used to assess in which nursery site growth rates varied.

To account for inter-annual variability in water temperature, which could influence growth rates (Pickett & Pawson, 1994), only fish from the same cohort were included to quantify growth rates and assess variability between nursery sites.

3.3. Results

3.3.1 Water temperature

Water temperature records were available from 2010-2019, however water temperature records were only collected from each of the nursery site in all seasons from 2010-2013 (901 water temperature records - Table 3.1 & Figure 3.5). Water temperature records from 2010-2013 were therefore used to show the relative differences in water temperature between the nursery sites. Two records were identified as outliers (Figure A2.1 - Annex 2): water temperatures from these records were implausible for the associated season and were therefore excluded from further analysis.

Table 3. 1 – Average seasonal water temperature records collected from Dart estuary, Salcombe harbour and Taw/Torridge estuaries by the Environment Agency as part of Water Framework Directive Transitional and Coastal water surveys from 2010-2013

Season	Nursery site	Mean water temperature (^{o}C)	n	SD	SE
	Dart	8.100	*36*	1.783	0.297
Winter	*Salcombe*	8.955	*32*	1.304	0.231
	Taw and Torridge	7.935	*67*	1.161	0.142
	Dart	11.831	*54*	2.417	0.329
Spring	*Salcombe*	11.483	*51*	1.986	0.278
	Taw and Torridge	11.109	*102*	2.698	0.267
	Dart	16.355	*67*	1.583	0.193
Summer	*Salcombe*	15.866	*107*	1.388	0.134
	Taw and Torridge	16.832	*150*	1.629	0.133
	Dart	14.494	*57*	2.199	0.291
Autumn	*Salcombe*	14.583	*59*	2.218	0.289
	Taw and Torridge	13.459	*117*	2.142	0.198
	Total	*13.400*	13.4	*3.50*	*0.117*

To meet the assumptions of normality and homoscedasticity a square-root transformation was applied to the water temperature data from 2010 - 2013.

Table 3. 2- Candidate linear mixed effect models to assess differences in water temperature from 2010-2013 between The Dart estuary, Salcombe harbour and the Taw/Torridge estuaries. Delta AIC scores are shown to demonstrate the relative difference in model AIC scores

Model ID	Model notation	Δ AIC
1	**Water temperature ~ Season * Nursery site + (1|month)**	0
2	Water temperature ~ Season + Nursery site + (1|month)	38.406
3	Water temperature ~ Season + (1|month)	30.466
4	Water temperature ~ Nursery site + (1|month)	45.78
5	Water temperature ~ 1 + (1|month)	37.788

AIC scores indicated inclusion of an interaction term between season and nursery site improved the model performance, suggesting that water temperature varied seasonally at different rates between the nursery sites (Table 3.2, 3.3 & Figure 3.5).

Table 3. 3 – Fixed and random effects of the linear mixed effect model of seasonal water temperature within each of the nursery sites: Dart estuary, Salcombe harbour, Taw/Torridge estuaries from 2010-2013

Fixed effects	Estimate	Std. Error	t value
Intercept (Dart estuary)	3.758	0.161	23.409
Season - spring	-0.51	0.227	-2.245
season - summer	0.289	0.227	1.276
season - winter	-0.924	0.228	-4.054
Nursery site - Salcombe	-0.025	0.036	-0.68
Nursery site - Taw and Torridge	-0.119	0.031	-3.808
Season - spring: Nursery site - Salcombe	-0.035	0.053	-0.662
Season - summer: Nursery site - Salcombe	-0.044	0.047	-0.924
Season - winter: Nursery site - Salcombe	0.211	0.06	3.525
Season - spring: Nursery site - Taw and Torridge	0.031	0.045	0.682
Season - summer: Nursery site - Taw and Torridge	0.174	0.042	4.108
Season - winter: Nursery site - Taw and Torridge	0.12	0.052	2.303
Random effects			
Month	0.075		
Residual	0.037		

Across all the nursery sites from 2010 – 2013, water temperature was lowest in the winter with an average of 8.2°C (± 0.12), then increased in spring to 11.38°C (± 0.12), was highest within summer 16.41°C (± 0.08) and then declined in autumn to 14.1°C (± 0.14).

In winter, water temperature was not significantly different between the Dart and Taw/Torridge estuaries (Tukey test, p = 0.99), however was on average 0.7°C higher within Salcombe harbour (Tukey test Dart-Salcombe, p = 0.003; Tukey test Taw and Torridge-Salcombe, p = <0.001). In spring, water temperature was higher within the Dart than Taw and Torridge estuaries (Tukey test, p = 0.04). No difference was detected between the Dart estuary and Salcombe harbour (Tukey test, p = 0.18) or Salcombe harbour and the Taw/Torridge estuaries (Tukey test, p = 0.93). In summer, water temperature was highest within the estuarine nursery sites (Tukey test Dart – Taw and Torridge, p = 0.06), and on average 1°C lower in Salcombe harbour (Tukey test Dart-Salcombe, p =0.025; Tukey test Taw and Torridge-Salcombe, p <0.001). In autumn, water temperature was highest within the Dart estuary and Salcombe harbour (Tukey test Dart-Salcombe, *p* =0.759) and on average 1.12 ^{0}C lower in the Taw/Torridge estuaries.

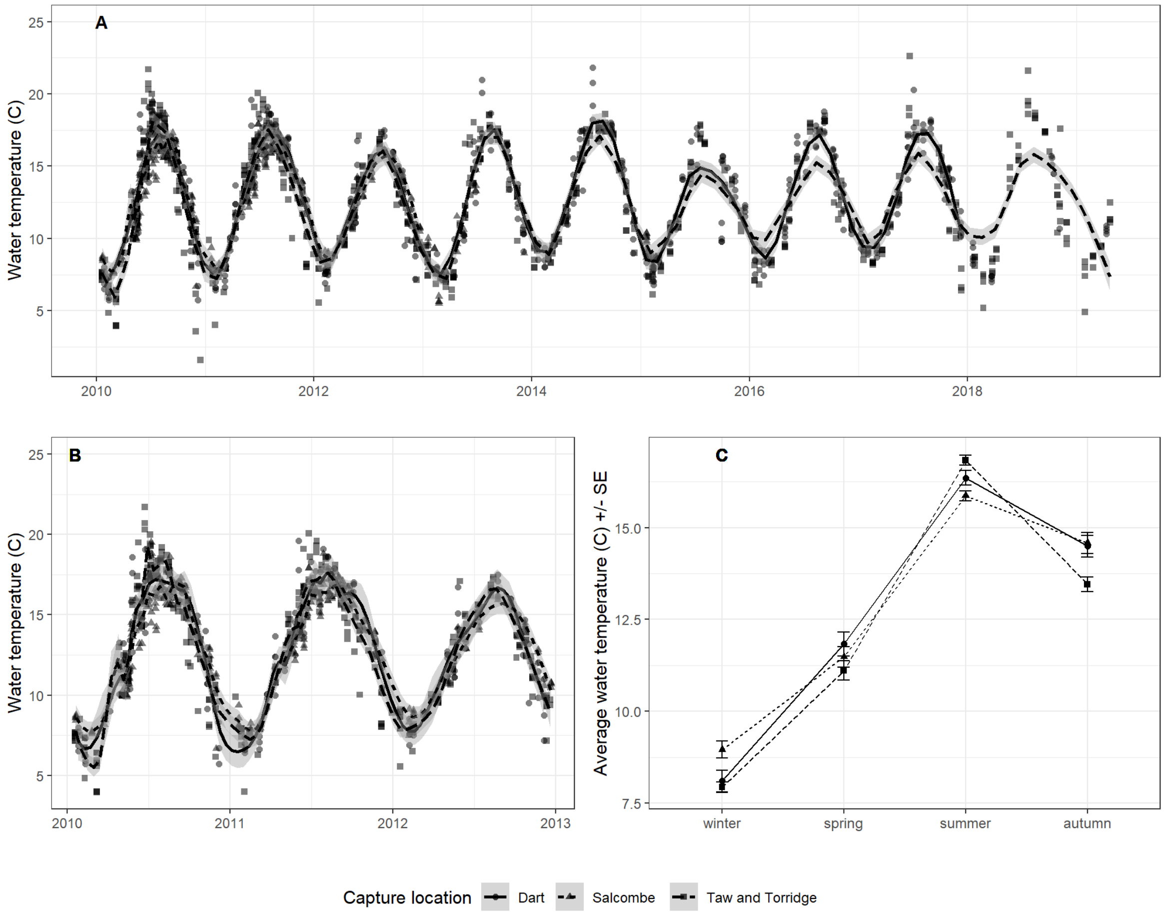


Figure 3. 5 - Water temperature recorded within the Dart estuary, Salcombe harbour, Taw and Torridge estuaries. Plot A – Time series showing all available data from 2010 to 2019 with loess interpolation (span = 0.1). Plot B – Time series showing data from 2010 – 2013 (comparable water temperature profiles from all three nursery sites) with loess interpolation (span = 0.1). Plot C – Average seasonal water temperature (2010-2013) from all three nursery sites

3.3.2 Scale collection

Scale from a total of 147 individual fish were collected. Across all nursery sites the average fork length was 301.28 mm (min: 180, max: 600), and average age was 4.1 years (min: 2, max: 13). 91 of the 147 fish (62%) were age 4, 28 were age 5 (19%) and 14 were age 3 (9.5%). The remaining 9.5% of fish were of a range of ages from 2-13.

Only the 91 individuals that were 4 years old at capture (2014 cohort) were included within further analyses. Of the 91 individuals included within further analysis, scales from 4 individuals were assigned a score of 2 and were therefore not included. The remaining fish varied in length from 266-413mm, 267-350mm & 252-320mm fork length within the Dart, Salcombe harbour and Taw/Torridge estuaries respectively (figure 3.6).

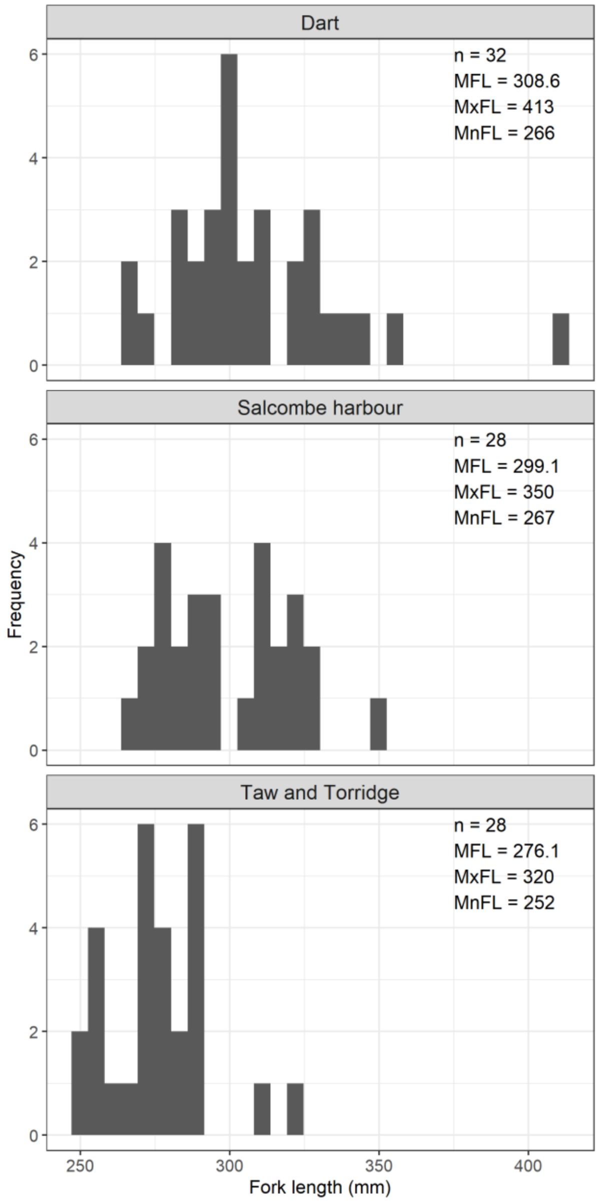


Figure 3. 6 - Length frequency histograms of European bass included within the study from each of the three nursery sites. n=Sample size, MFL = Mean fork length, MxFL= Max fork length, MnFL = Min fork length, MA = Mean age, MxA = Max age, MnA = Min age

3.3.3 Validation of Einar-Lea back calculation method

Multiple regression confirmed a positive linear relationship between scale radius and fork length ($F_{1,145}$= 259.4, $p < 0.001$, adj $R^2 = 0.639$)(Figure 3.7). Assumptions of normality and heteroscedasticity were met, and assessed through visual inspection of residual vs fitted and QQ plots. No statistical transformations were applied to the data.

Table 3. 4- Candidate linear models to test the relationship between scale radius to fork length for European bass from each of the nursery sites

Model ID	Model notation	Δ AIC
3	**Scale radius ~ fork length**	**0**
2	Scale radius ~ fork length + capture location	3.532
1	Scale radius ~ fork length * capture location	10.155
4	Scale radius ~ capture location	166.454
5	*Scale radius ~ 1*	198.344

There was no evidence to suggest that the scale radius ~ fork length relationship differed between nursery sites. All individuals were therefore pooled to form a single relationship (Table 3.4, 3.5 & Figure 3.7).

Table 3. 5 - Table of coefficients for model three (table 3.4): Scale radius ~ fork length for European bass captured across the capture locations

Coefficient	**Estimate**	**Std. Error**	**t value**	**P**
Intercept	0.362	0.188	1.922	0.057
Fork length (mm)	0.01	0.001	16.107	*<0.001*

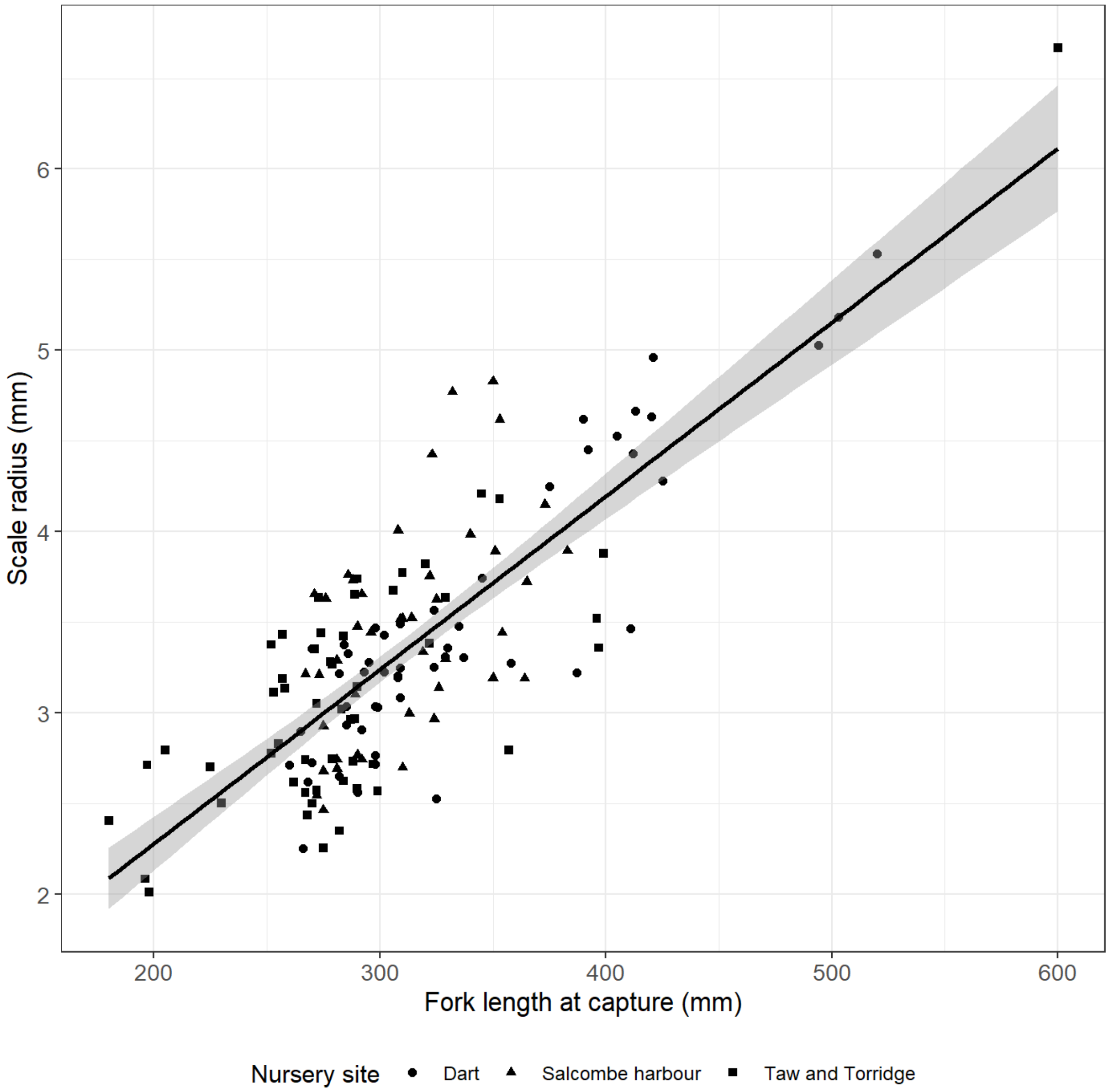


Figure 3. 7– European bass Scale radius to fork length relationship: Sale radius (mm) = 0.362 + 0.01 * Fork length at capture (mm)

3.3.3 Back calculated growth rate

No statistical transformation were applied to meet the assumptions of normality and homoscedasticity. AIC scores indicated inclusion of an interaction term between year and nursery site did not improve the model performance, suggesting that while model intercepts varied, growth rates were the same between nursery sites (Table 3.6).

Table 3. 6- Candidate linear mixed effect models to assess differences in European bass growth rate between nursery sites. Selected model is emboldened

Model ID	Model notation	Δ AIC
1	Length in year^n ~ year^n * nursery site + (1|fish ID)	0
2	**Length in year^n ~ year^n + nursery site + (1|fish ID)**	**0.355**
3	Length in year^n ~ year^n + (1|fish ID)	21.549
4	Length in year^n ~ nursery site + (1|fish ID)	1172.54
5	Length in year^n ~ 1 + (1|fish ID)	1183.803

Across all nursery sites fork length increased linearly with age at a rate of 64.4 mm per year. Notable differences were detected in the model intercepts, which were similar between the Dart and Taw/Torridge estuary (Tukey test, p = 0.486) however were 11.54 – 15.9mm higher in Salcombe harbour (Tukey test: Salcombe harbour – Dart estuary, p = 0.009. Tukey test: Salcombe harbour – Taw/Torridge estuary, p = 0.003).

Indicating that European bass grew at a similar rate in all nursery sites however achieve a higher length per year in Salcombe harbour than in the Dart and Taw/Torridge estuaries (Table 3.7 & Figure 3.8).

Table 3. 7 – Fixed and random effects of the linear mixed effect model of European bass growth rate captured from; Dart estuary, Salcombe harbour, Taw/Torridge estuaries

Fixed effects	Estimate	Std. Error	t value
Intercept (Dart estuary)	34.677	2.925	3.308
$Year^n$	64.356	0.508	126.742
Nursery site: Salcombe harbour	11.537	3.826	3.015
Nursery site: Taw and Torridge	-4.397	3.826	-1.149
Random effects			
Fish ID	187.4		
Residual	112.1		

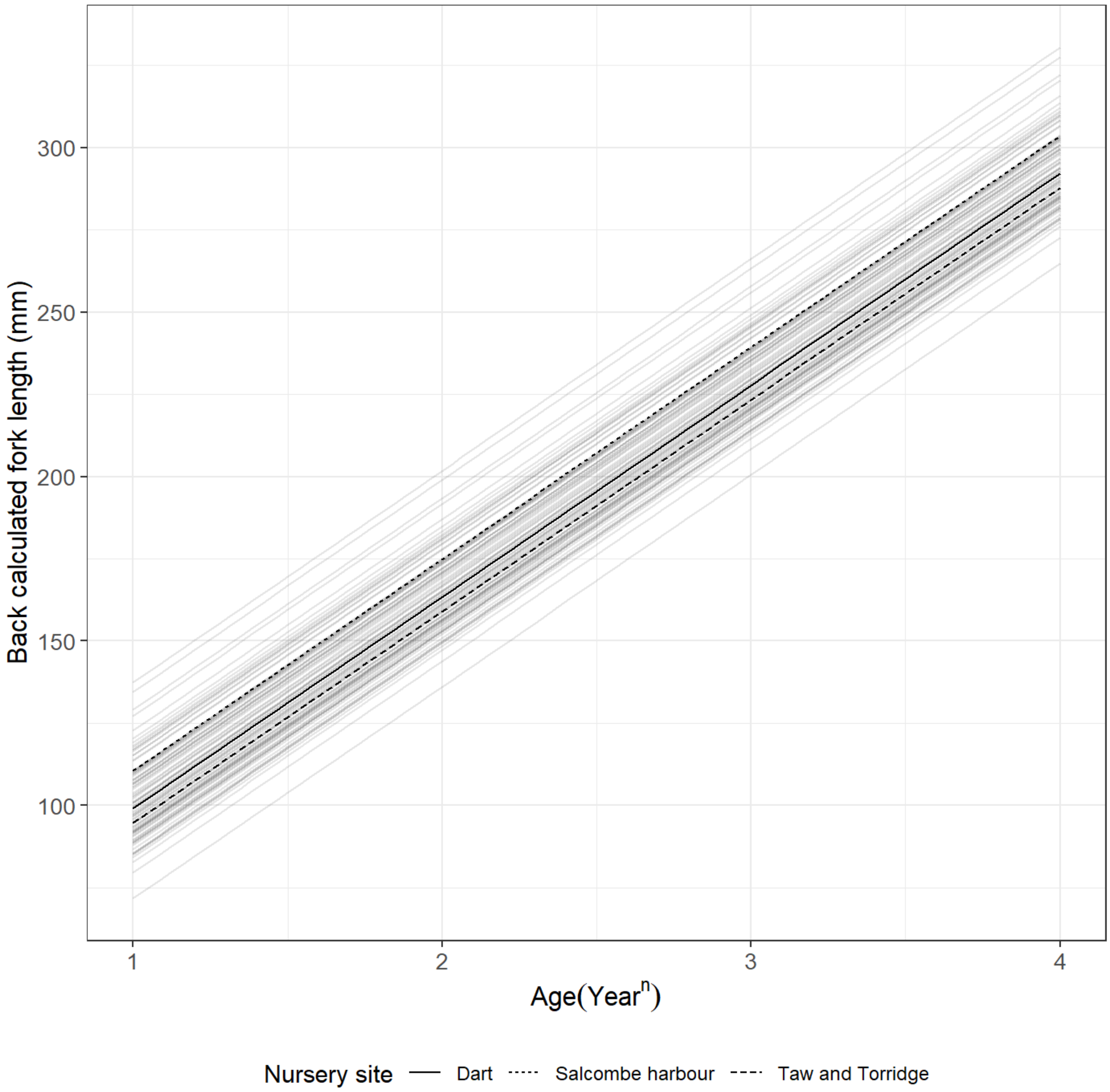


Figure 3. 8–Back calculated growth rates for European bass captured with the Dart estuary (growth rate = 34.677+64.356*Age (years)), Salcombe harbour (growth rate = 46.214+64.356* Age (years)) and the Taw/Torridge estuaries (growth rates = 30.28+64.536*Age (years)). Solid lines indicate model for each nursery site, faded lines are individual fish growth rates.

3.4 Discussion

Back calculated growth rates were similar across all the nursery sites, however model intercepts varied considerably between Salcombe harbour (46.214), and the Dart (34.677) plus the Taw/Torridge estuaries (30.28mm).

In regard to water temperature, the Dart estuary and Salcombe harbour are located approximately 20km apart on the south coast of Devon (Figure 3.2), whereas, the Taw/Torridge estuaries are located on the North coast of Devon (approximately 0.8^{o} latitude North). Despite differences in latitude between these nursery sites, water temperature was not found to be consistently lower in the Taw/Torridge estuaries than the more southerly nursery sites. However, when Salcombe harbour is compared to the Dart and Taw/Torridge estuaries, water temperature was on average 1^{o}C higher in the winter and 1^{o}C lower in the summer.

When combined the results highlight similar growth rates but varying intercepts across nursery sites, suggesting that events occurring in the first year of growth may have important implications for subsequent juvenile size and therefore survival (Pickett & Pawson, 1994).

3.4.1 Laval processes

In winter, European bass are known to form offshore spawning aggregations, typically in the western approaches and Celtic Sea (Pickett & Pawson, 1994; Pawson *et al.,* 2007). Following a planktonic phase, juveniles are reported to occupy estuarine/coastal nursery grounds as post-larvae typically at a size of 10-22mm (total length) (Aprahamian & Barr, 1985; Dando, 1985; Kelley, 1988). The differences in model intercepts reported here could therefore occur as a result of varying sizes of the fish when they first occupy the nursery sites as post-larvae.

Specifically, locally variable spawning patterns and/or transport processes of larvae from offshore spawning areas to coastal or estuarine nursery sites could result in fish entering each nursery site at different development stages and therefore sizes (Craig *et al.,* 2007). However, if this was a dominant factor then model intercepts within Salcombe harbour and the Dart estuary (located approximately 20km apart) would be expected to be similar.

3.4.2 Post-settlement processes

Alternatively, differences in model intercepts may have arisen due to differences in post-settlement growth prior to the deposition of the first year's growth band in the scales. Length at year - 0 (model intercepts) were extrapolated from the back-calculated length in years 1-4, however, extremely rapid growth within the first year may not follow the same linear trend as in years 1-4 (Kelley, 1986; Pickett & Pawson, 1994).

- ***Density-dependence***

Differences in post-settlement growth could occur as a result of local intraspecific competition for food resources (Zijlstra *et al.* 1982; Fromentin *et al.* 2001; Lorenzen & Enberg, 2001; Lekve *et al.* 2002; Craig *et al.* 2007; Ciotti *et al.,* 2013 & 2014). Density-dependent regulation of growth has been observed in wild populations of Striped bass (*Morone saxatilis*) (Martino & Houde, 2012), a genetically and ecologically similar species to European bass. Stocking density in artificial European bass farming has also been reported by a number of authors as a defining feature of growth (Hatziathanasiou *et al.,* 2002; Marco *et al.,* 2008; Sammouth *et al.,* 2009).

Little information is however available on the population sizes and/or density of European bass within specific nursery sites around the UK. Fish sampling conducted under the Water Framework Directive within Transitional and Coastal water bodies (WFD TraC) could be used to assess the relative abundance of European bass within different nursery sites. WFD TraC sampling involves collecting fish from a number of estuarine sites within the UK. Multiple capture

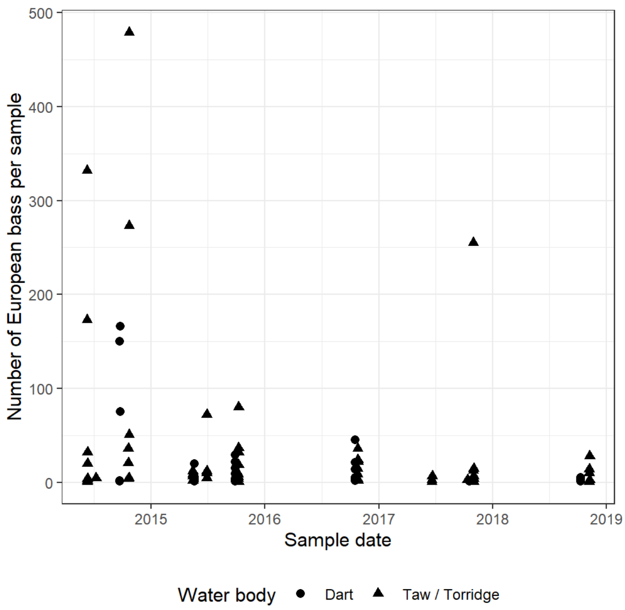


Figure 3. 7 - The number of European bass captured within WFD TRaC seine net samples in the Dart and Taw/Torridge estuaries from 2014-2019. Each point represents a single sweep of a 43m seine net. Please note no TraC fish sampling records could be located for Salcombe harbour, so is not included. Data source Environment Agency (2020).

methods are used e.g. fyke and/or seine nets (WFD-UKTAG, 2014) and metrics derived from the captured fish community e.g. species diversity, presence of indicator species, are used to qualitatively describe the fish community. Sampling effort is however low, for example typically 1-2 seine net sweeps are conducted per survey at each site. Surveys are typically conducted bi-annually (Spring & Autumn), however occasionally a higher number of surveys occur. While data is combined with that collected using a number of methods e.g. fyke netting, catch rates per sample, e.g. a single sweep of a seine net, can be extremely variable. For example, within the Taw/Torridge estuaries the minimum and maximum catch of European bass within two consecutive sweeps of a 43m seine net may vary from 1-483 individuals (Figure 3.10, Environment agency, 2020). Due to this high variance, measurement of population sizes or comparisons of relative abundance between nursery sites may therefore be inaccurate using this data. However, if complimented with additional sampling effort, mean abundance estimates may be calculated with a lower variance. WFD fish assemblage data could also be used as an independent measure of fish growth within separate nursery sites, by using the size-frequency distribution of fish captured combined with Modal Progression Analysis (Bento *et al.,* 2016). These options were however outside of the scope of the current study.

- **Seasonal water temperature differences between nursery sites**

Variability in seasonal water temperatures between nursery sites, may determine local growth rates of European bass (Pawson, 1992; Pickett & Pawson, 1994).

Relative to the other nursery sites, water temperature within Salcombe Harbour was 0.9^{o}C warmer in the winter and 0.7^{o}C colder in the summer. The Dart and Taw/Torridge are major estuaries within the Southwest UK, however Salcombe harbour is a ria system within which there are no major freshwater sources. Differences in freshwater input between Salcombe harbour - the Dart and Taw/Torridge estuaries, may therefore result in localized differences in water temperature which may have biological significance to local fish populations.

Pawson (1992) demonstrated that declines in water temperature across the south coast of the UK has a negative impact on annual recruitment rates. European bass are also thought to overwinter within their respective nursery site during the first winter, and relatively harsh winters are thought to cause significant mortality during this period (Pickett & Pawson, 1994). Therefore, variability of local water temperature (in particular within winter) between nursery sites who differ in their hydrological conditions may impact local European bass growth rates and survival (Pickett & Pawson, 1994).

- ***Habitat and/or prey availability***

A number of authors have similarly stated that local habitat and/or prey availability may also be an important factor for growth in wild fish populations (Aprahamian & Barr, 1985; Gibson, 1994; Pickett & Pawson, 1994; Green *et al.,* 2012).

Variation in both quantity and quality of accessible habitats could have influenced growth in each nursery site measured within this study. European bass have been described as an opportunistic predator, displaying substantial diet shifts with size/age (Pickett & Pawson, 1994). 0-group diet is initially dominated with plankton and progressively benthic crustaceans (e.g. shore crabs – *Carcinus maenus*) or smaller fish (e.g. sand eels *Ammodytes* spp.) with increasing size (Pickett & Pawson, 1994; Fonseca et al., 2011). In most studies, regional differences in prey availability have been cited as a key driver in feeding ecology (Pickett & Pawson, 1994), however some authors have argued that key prey species may have higher abundance or be more easily predated in specific habitats (Laffaille *et al.,* 2000 & 2001; Fonseca *et al.,* 2011; Green *et al.,* 2012). Furthermore, nutrient and/or calorie content will likely vary considerably between prey species (*Ammodytes spp.*:5.84 KJ/g^{-1} dry weight (Hislop *et al.,* 1991; Wanless *et al.,* 2005); *Carcinus maenus*: 3.69-3.72 KJ/g^{-1} dry weight (Duro, 2016)), the distribution of which may be dictated by the presence of key habitats (Moksnes , 2002; Holland *et al.*, 2005).

Therefore, variability in intertidal and subtidal habitat availability and "quality" within estuarine and coastal locations may influence the distribution and accessibility of valuable prey species, and therefore potentially effect localized growth rates (Odum, 1970; Bouwman *et al.,* 1984). The three nursery sites included within this study vary considerable in hydrology regimes, water depth, the presence of intertidal and subtidal habitat plus their extent. These environmental conditions may therefore result in distinct European bass feeding regimes and therefore growth rates in each nursery site.

3.4.3 Management implications

The high residency of European bass to nursery sites (Pawson *et al.,* 1987; Pickett & Pawson, 1994; Green *et al.,* 2012; Chapter 5), plus their potential use of estuaries as important feeding locations for mature fish (Cambiè *et al.*, 2016; Doyle *et al.,* 2017), suggests estuaries may represent significant sites of importance for this species at multiple life stages. In particular, this study highlights that growth achieved in the first year may have important implications for subsequent size at age and therefore survival. Further research attention should therefore be given to identifying drivers of growth variability across a range of nursery sites, with a particular focus on growth within the first year.

While protecting recruitment pathways is highlighted as a key mechanism to boost recovery of the Northeast Atlantic stock (Pawson *et al.,* 2005; Williams *et al.,* 2018), the ability to identify and assess fish habitat interactions, plus environmental data from nursery sites, is currently patchy and/or lacking within the UK. The majority of estuaries and ria systems along the East, South and Southwest coast of the UK are currently protected as designated Bass Nursery Areas, there however remains little understanding on how effective these site designations are at boosting recruitment. More widely, there is also lack of holistic fisheries management across Europe which incorporates the habitat requirements of the fish. This concept is widely adopted within the United States - Essential Fish Habitat (Valavanis, 2008; MSFCMA, 2018). Essential fish habitat has been introduced to Europe through the Fish Stock Recover Areas in the reformed common fisheries policy (Roberts & Hawkins, 2012). To date however this has received little political and/or management attention.

3.4.5 Conclusions

The results from this study suggest that growth within the first year may have important implications for subsequent size at age for European bass (Pickett & Pawson, 1994). The available literature does suggests that over broad time scales/inter-annual water temperature is likely to be an important factor driving growth (Kelly, 1986; Pawson, 1992; Pickett & Pawson, 1994). Hot summers and mild winters have been correlated with good year class strength and subsequent recruitment (Pickett & Pawson, 1994). However, substantial differences in size at age between nursery sites have also been evidenced within this study and the wider literature (Kelly, 1986; Pickett & Pawson, 1994). There is therefore likely to be additional environmental or biological factors which affect growth and therefore recruitment rates, which in the context of highly diminished population in the Northeast Atlantic warrant further study.

Further study should increase the number of nursery sites assessed and the year classes monitored. Additional methods, such as direct measurements of juvenile fish length (Kelley, 1986) and/or RNA:DNA ratio measurements of growth (Buckley, 1984; Mustafa *et al.,* 1991) would also compliment results.

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Chapter 4: Using feeding rates and diet to assess the suitability of compensatory saltmarsh habitat for multiple estuarine fish species in the UK

Keywords

Estuarine habitats, managed re-alignment, fish, feeding

Contributions

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4.1 Abstract

Saltmarsh provides a crucial feeding habitat for economically and ecologically important fish species. It is however estimated that as much as 50% of saltmarsh has been lost or degraded globally. Within the UK a common mitigation for intertidal habitat loss is the creation of managed re-alignment schemes. Managed re-alignment involves the creation of intertidal habitat via breaching artificial sea defences. This study aims to assess how well estuarine fish can exploit the novel habitats within re-aligned sites. Specifically, feeding rates and the similarity of prey consumed within re-aligned sites to that of surrounding established saltmarsh is assessed for each of the following species: thinlip Mullet (*Chelon ramada*), European bass (*Dicentrarchus labrax*) and common or sand gobies (*Pomatoschistus spp.*).

Five re-aligned and five nearby established saltmarsh sites were surveyed. Where fish were captured, feeding activity was recorded at 75% of the sites. Feeding rates for *Chelon ramada* and *Dicentrarchus labrax* were however up to 25% lower within the re-aligned sites than surrounding established saltmarsh, whereas *Pomatoschistus spp.* fed at the same rate. In general, prey species were similar across re-aligned and established saltmarsh, however the abundance of dominant prey species varied between re-aligned and established saltmarsh sites.

The evidence suggests that re-aligned saltmarsh habitat does provide feeding opportunities for these fishes, though not currently in the same proportions as within surrounding natural saltmarsh. Vegetation density and diversity is generally lower within re-aligned habitat, and it is likely that this may underpin how fish interact and exploit re-aligned habitats. Due to the current ecological value of these habitats and potential for further improvement, it is important to continue to assess the beneficial effects of re-aligned sites from a fisheries and conservation perspective.

4.2 Introduction

In Europe, estuaries are known to provide important nursery and feeding habitats for commercially and ecologically important species e.g. European bass (*Dicentrarchus labrax* – Pickett & Pawson, 1994; Laffaille *et al.,* 2001; Fonseca *et al.*, 2011; Green et al., 2012), Herring (*Clupea harengus* – Laffaille *et al.,* 2000; Green et al., 2012). In particular, saltmarshes are highly productive environments (Nixon, 1980; Bouchard & Lefeuvre, 2000), which are known to provide refuge (Allen *et al.,* 1994; West & Zedler, 2000) and be important feeding habitat for many fish species (Kelley, 1988; Kneib, 1997; Laffaille *et al.,* 2001; Fonseca *et al.,* 2011; Green *et al.,* 2012).

The importance of saltmarsh as a feeding habitat for juvenile fish is best illustrated by Laffaille *et al.* (2001) & Fonseca *et al.* (2011), who reported that on average 33-38% of juvenile European bass (*Dicentrarchus labrax*) entering saltmarsh have empty stomachs, whereas when leaving saltmarsh 93-98% of individuals have full stomachs. Similar results have also been reported for thinlip grey mullet *(Chelon ramada*). It was estimated that in the brief 1-2 hour tidal submersion of saltmarsh, these species are capable of consuming 7-8% of their total body weight (Laffaille *et al.,* 2001 & 2002).

Despite estuaries proving important habitat for a variety of fish species, they are typically highly modified by anthropogenic activities (Lotze *et al.,* 2006; Airoldi *et al.,* 2008) via:

- Direct removal or adaptation of intertidal habitat,
- Agricultural activities within intertidal habitat e.g. sheep grazing on saltmarsh (Laffaille *et al.,* 2000),
- Indirectly through management of adjacent land e.g. agriculture (Almeida *et al.,* 2014).

Globally it is estimated that approximately 50% of saltmarsh habitat has been lost or degraded (Adam, 2002; Barbier *et al.,* 2011). More specifically, as much as 85% of UK estuaries have been affected by historic land reclamation, with the loss of intertidal habitat ranging from 50-64% (Mclusky *et al.,* 1992, Attrill *et al.,* 1999). Historic habitat loss, is also compounded by issues such as; sea level rise, coastal squeeze and continuing human development of estuaries e.g. port developments, which may result in further 2% loss of saltmarsh habitat per year (Dixon *et al.,* 1998; Colclough *et al.,* 2003).

Saltmarsh is a protected habitat across Europe under a variety of legislative polices, notably the European Commission Habitats Directive (Council Directive 92/43/EEC), which via the Conservation of Habitats and Species Regulations 2010 (as amended) was transposed into UK law. These regulations were then consolidated under the Conservation of Habitats and Species Regulations 2017 (UK statutory instrument, 2017, 1012). The Habitats Directive seeks to maintain saltmarsh (among other habitats) in "favourable status". However if within public interest, construction proposals/developments may be consented which would result in loss of saltmarsh provided adequate mitigation measures are implemented (Mossman *et al.,* 2012).

Table 4. 1– Example aerial photography of managed re-alignment, managed retreat and established saltmarsh habitat within the UK. Photograph obtained from the southwest channel observatory

managed re-alignment

- Site name: Steart marsh
  51.199865 -3.046664

- Drainage channels and habitat features designed and mechanically created
- Sea defences actively breached

managed retreat

- Site name: Porlock marsh
  51.218292 -3.607299

- No habitat design, however features of pre-existing land (e.g. stone walls, agricultural drainage channels) may influence water movement and persist as site develops
- Sea defence may be actively breached or occur naturally as a result of extreme wave or tidal action

established saltmarsh

- Site name: East head
  50.783518 -0.910569

Over the past 20-30 years, an increasingly common mitigation tool for saltmarsh habitat loss is the construction of compensatory habitat, known as managed re-alignment (Mossman *et al.,* 2012). Managed re-alignment is a coastal management technique whereby sea defences are actively breached and tidal water encouraged to flood low lying coastal land (Lawrence *et al.,* 2018). Alternatively, Managed retreat may also occur where sea defences are naturally breached, and a decision is made to not re-inforce or repair damaged sea defences (Mossman *et al.,* 2012). These processes create new intertidal area, in which saltmarsh and/or mudflat habitat may develop (Mossman *et al.,* 2012; Lawrence *et al.,* 2018) (Table 4.1). The construction of these schemes is primarily driven by conservation legislation e.g. the Habitat Directive, however, they are also credited with providing additional benefits, such as sustainable coastal flood defence (Kentula, 2000; Esteves, 2013).

It has however been estimated that from a compensatory habitat perspective, even after a period of 50-100 years re-aligned saltmarsh (Managed re-aligned schemes and/or managed retreat) do not currently resemble those of natural/established salt marsh habitat (Garbutt *et al.,* 2006; Mossman *et al.,* 2012). In particular, it has been argued that re-aligned saltmarsh sites;

- Lack the biological complexity of established saltmarsh and are generally characterized by pioneer plant communities (Mossman *et al.,* 2012),
- Have lower topographic complexity than established saltmarsh and generally have a low density of drainage creeks (Lawrence *et al.,* 2018),
- Retain compacted soil (characteristic of prior agricultural land use) resulting in poor nutrient re-cycling (Spencer *et al.,* 2008).

It has therefore been argued that re-aligned saltmarsh does not typically provide habitats with "comparable biological characteristics to established saltmarsh" (Mossman *et al.,* 2012).

Studies investigating fish utilization of re-aligned saltmarsh sites have however indicated that they do provide valuable feeding opportunities for a wide variety of commercially and ecologically important species (Colclough *et al.,* 2005; Fonseca *et al.,* 2011; Nunn *et al.,* 2016). Within the context of historic and modern habitat loss within estuaries, this is particular important as without the process of re-aligning the coastline to create habitat, feeding opportunities for these fishes may be reduced (Mclusky *et al.,* 1992; Rochette *et al.*, 2010). Further, in lieu of pristine/ un-impacted estuaries (Best *et al.,* 2007), the effect of this habitat loss on fish production is difficult to quantify, however it is likely to have had substantial negative impacts (Mclusky *et al.,* 1992; Rochette *et al.*, 2010). Therefore, even if re-aligned sites do not provide an equivalent to established saltmarsh they are likely to provide feeding opportunities which might otherwise be absent.

As part of shoreline management plans, regional council and authorities have committed to "re-align" 10% of the UK coastline by 2030, rising to nearly 15% by 2060 (CASB, 2013; Esteves, 2013). Furthermore, re-alignment of coastline is directly applicable to "Biodiversity Net Gain" as written within the U.K. governments Environment Bill (UK Gov, 2020). As a result, the construction of managed re-alignment schemes in the U.K. is likely to increase, and the importance of these novel habitats from a fisheries perspective is of growing interest to fisheries managers (Colclough *et al.,* 2003; Fonseca *et al.,* 2011).

This study aims to compare the habitat suitability within re-aligned saltmarsh sites for three common fish species in UK estuaries: European bass (*Dicentrarchus labrax*), Thinlip grey mullet (*Chelon ramada*) and Common/Sand gobies (*Pomatoschistus spp.*). Focusing on feeding rates and a multivariate assessment of diet, this study will assess how well fish were able to feed and when they do feed what prey they consume, within five re-aligned sites compared to surrounding established saltmarsh.

4.3 Methods

4.3.1 Sample sites

Juvenile fishes were collected during surveys at five re-aligned sites in the U.K (Figure 4.1, Table 4.2). These sites were selected based on their large spatial extent, wide geographic distribution across the U.K. and the relative ages of these sites/time since first tidal inundation. In close geographic proximity to each re-aligned saltmarsh site at least one local established saltmarsh was also sampled during the same survey. The established saltmarsh was used as a reference/experimental control.

Table 4. 2– Site name, latitude and longitude, area and age of each re-aligned saltmarsh sites, plus associated established saltmarsh site(s)

Survey	Habitat type	Latitude	Longitude	Area (km^2)	Year of tidal inundation
Great orcheton fields	Managed retreat	50.3332	-3.9279	0.24	2007
	Established saltmarsh	50.33035	-3.935499	0.1	-
Wallasea island	Managed re-alignment	51.6046	0.859	1.65	2015
	Established saltmarsh	51.61569	0.782941	0.71	-
Medmerry nature reserve	Managed re-alignment	50.751	-0.8244	3.02	2013
	Established saltmarsh	50.78217	-0.91163	0.39	-
	Established saltmarsh	50.7619	-0.760567	2.93	-
Porlock marsh	Managed retreat	51.2163	-3.6068	0.75	1996
	Established saltmarsh	51.20457	-3.092042	0.11	-
Steart marsh	Managed re-alignment	51.2028	-3.0337	2.62	2014
	Established saltmarsh	51.20568	-3.03005	0.41	-
	Established saltmarsh	51.20665	-3.015694	0.37	-

At each saltmarsh juvenile fishes were captured using fyke nets which had the following dimensions: 5m leaders, 53cm net opening, with the remainder of the net measuring 2.75 meters. Mesh sizes in each respective section of the net were as follows: 10mm (leaders) 6.5 – 8mm (main body of the net). A single net was deployed in each of the three representative drainage channels distributed across each saltmarsh. Each net was deployed with the leaders facing landward, allowing fishes to swim over the net on the flooding tide, feed within the saltmarsh, and then be captured on the ebbing tide.

Fyke nets were deployed at low tide, and positioned so they were fully immersed during mid and high tide but fully exposed to the air during low tide. Each net was checked at low tide following each tidal inundation of the marsh (referred to as a net deployment), and deployed for a minimum of three tidal inundations at each site. From each net deployment, a maximum of 30 individuals of each of the following target species/taxa were randomly collected; 0-group *Dicentrarchus labrax,* 0-group *Chelon ramada* and *Pomatoschistus spp*. Individual fish were immediately euthanized via overdose with an anaesthetic agent (MS-222, Tricaine Methanesulfonate) followed by destruction of the brain (ASPA, 1986). Following confirmation of death, all specimens were stored in appropriately labelled containers filled with 80% Industrial Methylated Spirit (IMS). All samples were then returned for later laboratory analysis to identify stomach contents.

The target species were selected as they are highly abundant within estuaries across Northern Europe (Pickett & Pawson, 1994; Laffaille *et al.,* 2002; Leitão 2006). Furthermore, *Dicentrarchus labrax* and *Pomatoschistus spp.* are known as a generalist predators (Pickett & Pawson, 1994; Leitão *et al.,* 2006), whereas *Chelon ramada* feed predominantly on benthic phytoplankton and detritus (Laffaille *et al.,* 2002; Almeida, 2003; Sá *et al.,* 2006;

Kasımoğlu & Yılmaz, 2012). These species therefore represent two generalist predators and a benthic grazer, which can be used to compare habitat suitability between re-aligned and established saltmarshes.

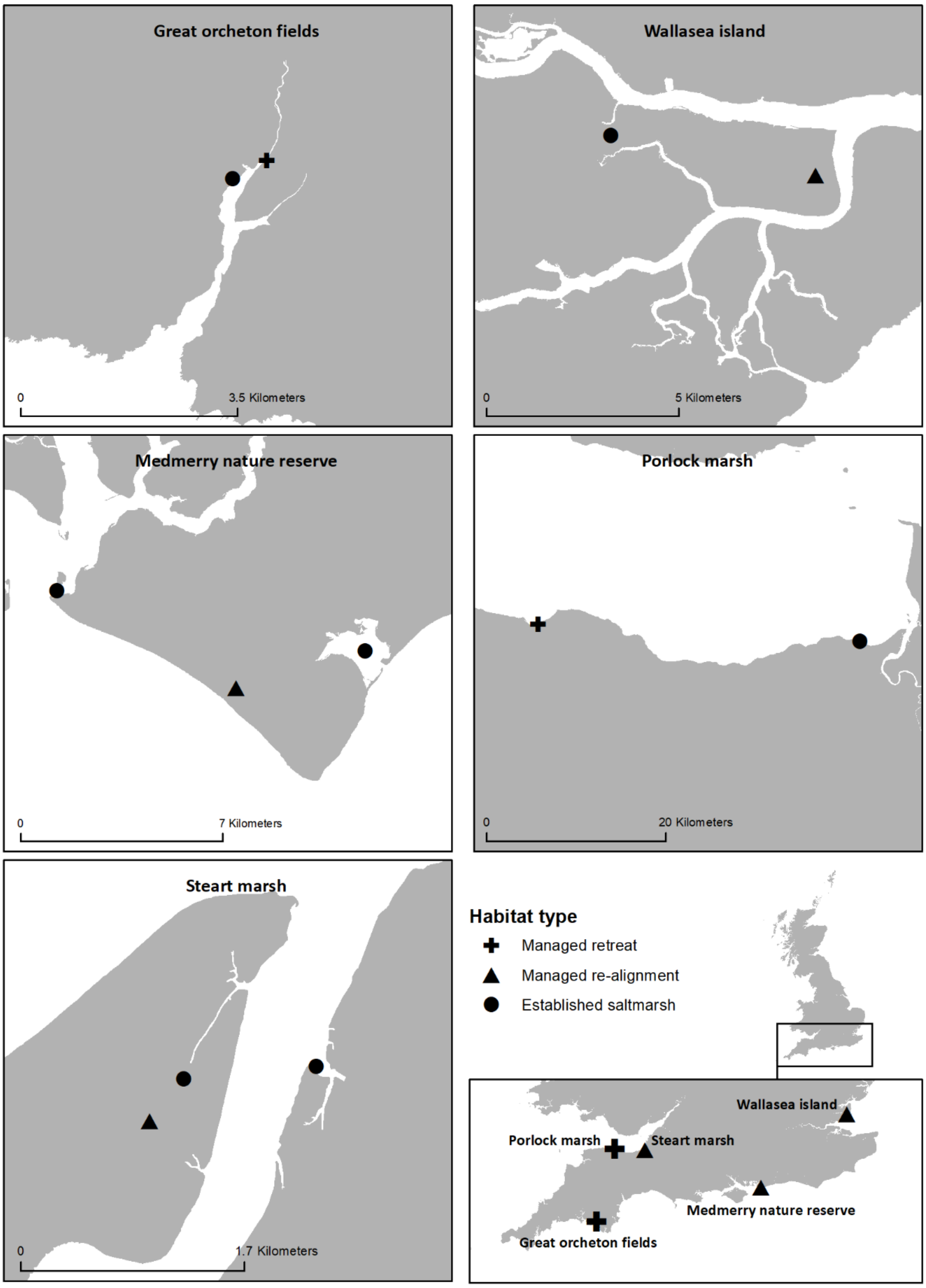

Figure 4. 1– Re-aligned and established saltmarsh sites in which juvenile fish were sampled. Re-aligned saltmarsh sites are detailed as either managed retreats or re-alignments

4.3.2 Stomach content identification
In the laboratory each fish was identified to species/taxa level. Using a 15cm measuring board the length of each fish was measured from the tip of the snout to end of the longest caudal fin ray (referred to as the total length). Excess liquid was removed, then using a digital balance each fish was weighed to an accuracy of 0.01g, then the full digestive tract removed and weighed separately. The digestive tract was then dissected under light microscopy, and all stomach content/prey species were enumerated and identified to as low a taxonomic resolution as possible. Please note that due to some prey species being semi-digested, in some instances only identification to the taxonomic level of class was possible e.g. Polychaeta. Due to rapid dehydration of tissue following emersion from IMS, all measurements of bodily tissues were conducted within a maximum of 5 minutes following emersion.

Please note that due to difficulty in distinguishing the common (*Pomatoschistus microps*) and sand goby (*Pomatoschistus minutus*), these species were grouped to *Pomatoschistus spp.* Previous work suggests no significant differences in *Pomatoschistus spp.* feeding ecology (Leitão *et al.,* 2006), therefore it was considered appropriate to pool data for these species. Other goby species captured during the survey e.g. black gobies (*Gobius niger*) or Transparent gobies (*Aphia minuta*) were not included.

4.3.3 Data analysis
Captured fishes were pooled according to the habitat they were captured in: “Re-aligned saltmarsh” or “Established saltmarsh”. No comparison was made regarding variability in fish diet between different tides/net deployments or from different creeks across each saltmarsh site. Within each survey the total length of each species captured was compared using a Kruskal-wallis test.

Subsequent data analysis was split as follows; 1) Assessment of feeding rate within re-aligned and established saltmarsh sites, 2) Assessment of diet within realigned and established saltmarsh sites.

Feeding rates

The Instantaneous Feeding Ration (IR%) was used to assess the recent foraging success for each individual fish:

$$IR\% = \frac{SW}{BW} * 100$$

IR% is calculated as Stomach Weight (SW) as a percentage of Body Weight (BW), and has been used as measure of “recent foraging success” in estuarine fish species e.g. *Dicentrarchus larbrax* and *Chelon ramada* (Pickett & Pawson , 1994; Laffaille et al., 2000 & 2001; Fonseca *et al.,* 2011).

IR% was compared between habitats using a Linear Model (LM), fit using the lm function in R package “stats” (R Core Team, 2019). Statistical assumptions were visually assessed using model diagnostics (QQplot, residuals vs fitted plot).

Candidate models were fit for each fish species/taxa individually, which included the following as fixed effects:

- **Habitat:** A categorical variable, indicating whether a fish was captured within a re-aligned or established saltmarsh
- **Survey:** A categorical variable, indicating the name of the survey that each fish was captured within. Each survey was named on the re-aligned saltmarsh site and dated according to the month and year the survey was conducted within

- **Total length:** A numerical variable, indicating the total length of each fish.

For each fish species/taxa the most complex model was initially applied, which included all variables and possible interactions (Table 4.3). Each interaction and/or variable was sequentially removed and the associated model scored according to Akaike Information Criterion (AIC). Following the rules of parsimony, the model with the lowest AIC score was selected as the best fitting model for each fish species/taxa. If AIC scores from models were ≤2 the simplest model and/or with the fewest fixed effects was selected (Zuur *et al.,* 2013). Each fish was treated as an independent replicate, and an alpha level of <0.05 was used to assess significance. All analysis was performed using R version 3.6.0 (R Core Team, 2019).

Table 4. 3 - Candidate model notations to assess feeding rate for each of the fish species/taxa included within the study

Model ID	**Notation**	**Model ID**	**Notation**
1	~ Habitat * Survey * Total Length	8	~ Habitat + Total length
2	~ Habitat + Survey * Total Length	9	~ Survey * Total length
3	~ Habitat * Survey + Total Length	10	~ Survey + Total length
4	~ Habitat + Survey + Total length	11	~ Habitat
5	~ Habitat * Survey	12	~ Survey
6	~ Habitat + Survey	13	~ Total length
7	~ Habitat * Total length	14	Null model

Diet

Chelon ramada were not included as their diet mainly consisted of diatoms and/or planktonic species, which the authors did not have the technical skills to accurately identify.

Diet data were converted to a Bray Curtis similarity matrix, with a dummy variable (1) to account for fish which had empty stomachs (Clarke *et al.,* 2006). No statistical transformation was applied to the data. A 2-way crossed multivariate PERMANOVA test was used to assess differences in diet for each species, between Survey (*Dicentrarchus* labrax: 2 levels – Steart marsh Aug 2017 & Wallasea island Jul 2017, *Pomatoschistus spp*: 3 levels – Steart marsh May 2017 + June 2018 & Wallasea island July 2017) and Habitat (2 levels – Realigned and established saltmarsh). If significant differences were detected, pairwise comparisons were used to identify at which level of each factor dietary differences occurred. All PERMANOVA tests were analysed using the statistical software PRIMER-E 7.0.13 with PERMANOVA+.

Non metric Multi-Dimensional Scaling (MDS) plots were used to visually demonstrate variability in fish diet across the habitats. MDS plots were created using the metaMDS function within R package "Vegan" (Oksanen *et al.,* 2019). The average abundance of all dominant prey species (those which accounted for >1% of overall abundance within stomachs) is presented to demonstrate which prey species drove differences in diet between habitats and surveys.

4.4 Results

Seven surveys were completed, with a total of 216 net deployments across five re-aligned and associated established saltmarsh sites. Steart Marsh was surveyed three times during 2017-2018, the remaining four re-aligned saltmarshes were surveyed once in 2017. Across all the net deployments 591 individual fish were retained for stomach content analysis, this included; 157 *Chelon ramada, 137 Dicentarchus labrax* and 297 *Pomatoschistus spp.*

Capture rates of each fish taxa varied considerably between surveys (Table 4.4), prohibiting formal comparison of feeding rates and diet for all fish taxa during each survey. Where sample size was sufficient and relatively balanced between the re-aligned and associated established saltmarsh sites, feeding rate and diet were compared (Table 4.4).

Table 4. 4 - Number of each taxa captured within each of the survey and habitat combinations. ES: Established saltmarsh, ReS: Re-aligned saltmarsh. Survey selected for further analysis are highlighted with emboldened text

Survey	**Habitat type**	***Chelon ramada***	***Dicentrarchus labrax***	***Pomatoschistus sp.***
Great Orcheton fields October 2018	ES	-	-	52
	Res	-	-	-
Medmerry June 2017	ES	**15**	1	8
	ReS	**21**	2	-
	ES	**31**	14	-
Porlock October 2018	ReS	-	-	2
	ES	-	-	11
Steart Marsh August 2017	ES	**30**	**17**	-
	ES	**30**	**1**	-
	ReS	**30**	**40**	13
Steart Marsh June 2018	ES	-	-	**27**
	ReS	-	-	**37**
Steart Marsh May 2017	ES	-	-	**52**
	ReS	-	-	**19**
Wallasea Island July 2017	ReS	-	**9**	**30**
	ES	-	**53**	**46**

The length/size of each fish taxa varied, with an average total length of 70.1mm (± 0.83 SE), 49.7mm (± 0.77 SE), 40.2mm (± 0.29 SE) for *Chelon ramada*, *Dicentrarchus labrax* and *Pomatoschistus spp.* respectively. Broadly comparable size ranges were captured of each of the target species in each habitat, however during some surveys total length varied between the habitats (Figure 4.2).

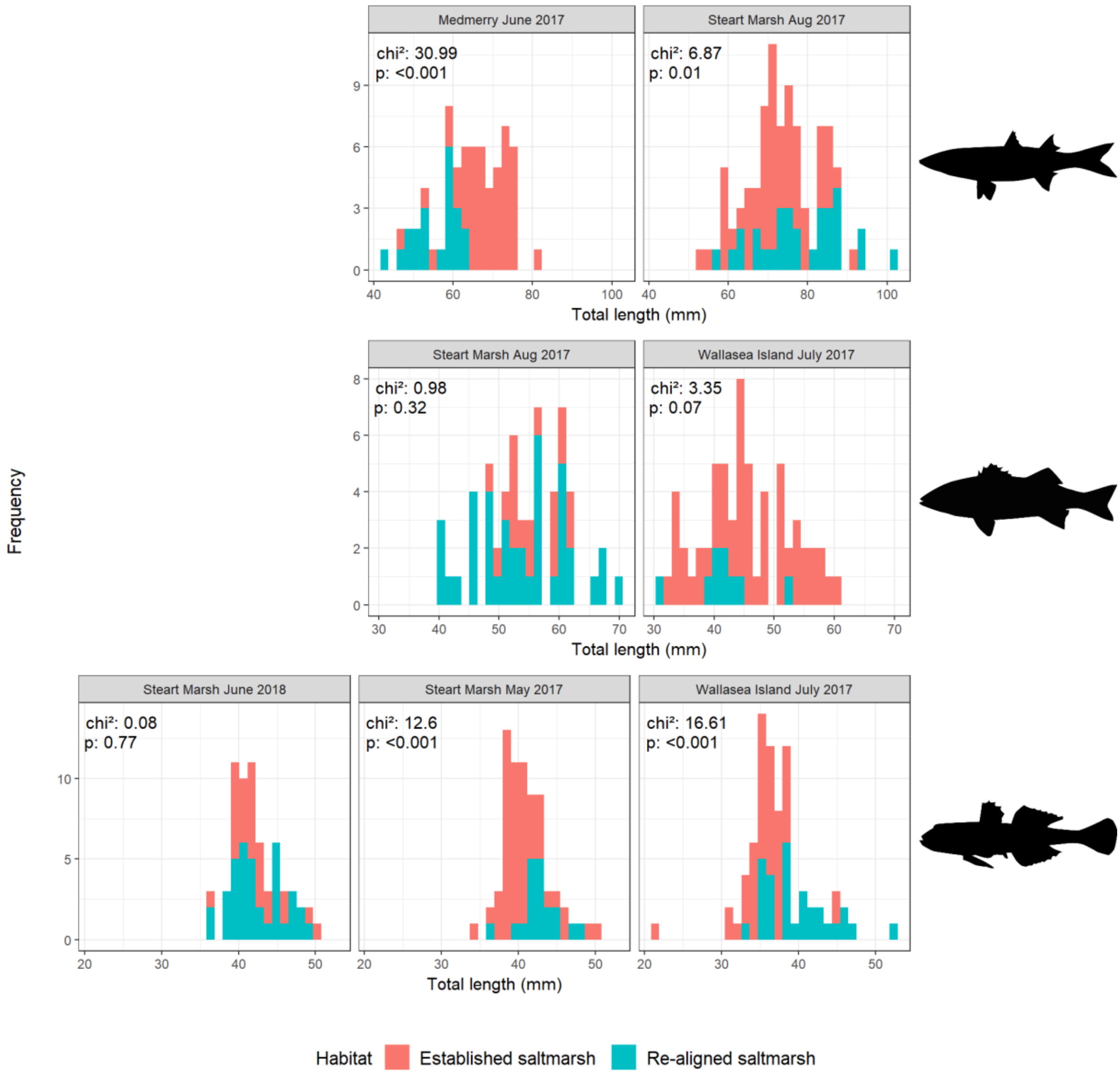

Figure 4. 2 – Length frequency plot of *Chelon ramada* (top), *Dicentrarchus labrax* (middle) and *Pomatoschistus* sp. (bottom) included within the study. Chi^2 test statistics comparing total length between habitats for each survey for each species shown in top right of each panel

4.4.1 Feeding rates

All *Chelon ramada* captured during the Medmerry June 2017 survey had empty stomachs, whereas during the Steart Marsh August 2017 survey only 4% had empty stomachs in the established and 13.3% in the re-aligned saltmarsh site.

None of the *Dicentrarchus labrax* captured during the Steart Marsh August 2017 survey had empty stomachs in the established saltmarsh, whereas 2.5% had empty stomachs in the re-aligned saltmarsh. During the Wallasea Island July 2017 survey, 7% of *Dicentrarchus labrax* had empty stomachs in the established saltmarsh, whereas 11% had empty stomachs in the re-aligned saltmarsh.

32% of *Pomatoschistus sp.* captured during the Steart Marsh survey May 2017 had empty stomachs in the established saltmarsh, and 68% had empty stomachs in the re-aligned saltmarsh. 41% captured in the Steart Marsh June 2018 had empty stomachs in the established saltmarsh, and 32% had empty stomachs in the re-aligned saltmarsh. 19.5% captured in the Wallasea island July 2017 survey had empty stomachs in the established saltmarsh, and 23.3% had empty stomachs within the re-aligned saltmarsh.

Based on the associated AIC scores, varying coefficients were included for each of the feeding rate models for each species. For *Chelon ramada* all the predictor variables plus interaction terms were included. The *Dicentrarchus labrax* feeding rate model included habitat plus survey, with no interaction term. No significant difference could be detected in *Pomatoschistus spp.* feeding rate between the May 2017 and June 2018 Steart marsh surveys (F ratio test: $F=2.721$, $P=0.07$). Therefore, the results from Steart marsh were pooled and compared to Wallasea Island July 2017. The eventual *Pomatoschistus spp.* feeding rate model included one fixed effect: survey (Table 4.5).

Table 4. 5 - Δ AIC scores for the candidate feeding rate models for each fish taxa included within the study. Selected models are highlighted by emboldened text

Model ID	***Chelon ramada***	***Dicentrarchus labrax***	***Pomatoschistus spp.***
1	**0**	1.67	6.48
2	3.46	0	0.78
3	4.49	2.72	3.44
4	5.61	2.02	1.8
5	2.51	0.73	3.05
6	4.17	**0.05**	1.75
7	13.19	2.27	23.62
8	17.17	3.97	21.88
9	4.1	12.38	0
10	4.15	13.95	0.71
11	16.6	3.05	38.97
12	2.62	12.08	**0.02**
13	15.39	11.98	22.77
14	14.91	10.08	37.12

Model coefficients suggested that *Chelon ramada* feeding rate increased with fish length within the established saltmarsh sites, and decreased in the re-aligned saltmarsh sites at Steart Marsh. No effect of length, or differences in the feeding rate between the established or re-aligned saltmarsh sites could however be detected at Medmerry Nature Reserve (Table 4.6, Figure 4.3 – top).

Dicentrarchus labrax feeding rate was significantly lower within Wallasea island than in Steart Marsh, feeding rates in established saltmarsh sites were also significantly higher than in re-aligned saltmarsh sites. In relative terms, *Dicentrarchus labrax* feeding rate was approximately 25% lower in re-aligned saltmarsh sites and 14.47% lower at Wallasea Island. Model AIC scores suggested feeding rates were similar across the size ranged sampled in this study (Table 4.6, Figure 4.3 – middle).

Pomatoschistus spp. feeding rates were significantly higher in Wallasea Island than in Steart marsh. In relative terms, feeding rates were 36.2% higher in Wallasea Island than at Steart

Marsh. Model AIC scores suggested that in Steart Marsh and Wallasea Island feeding rates were similar in established and re-aligned saltmarsh sites, and was similar across the size ranged sampled within this study (Table 4.6, Figure 4.3 – bottom).

Overall however, R^2 values for all the feeding rate models were relatively low (0.11-0.17) indicating considerably variability in feeding rates across all fish taxa (Table 4.6).

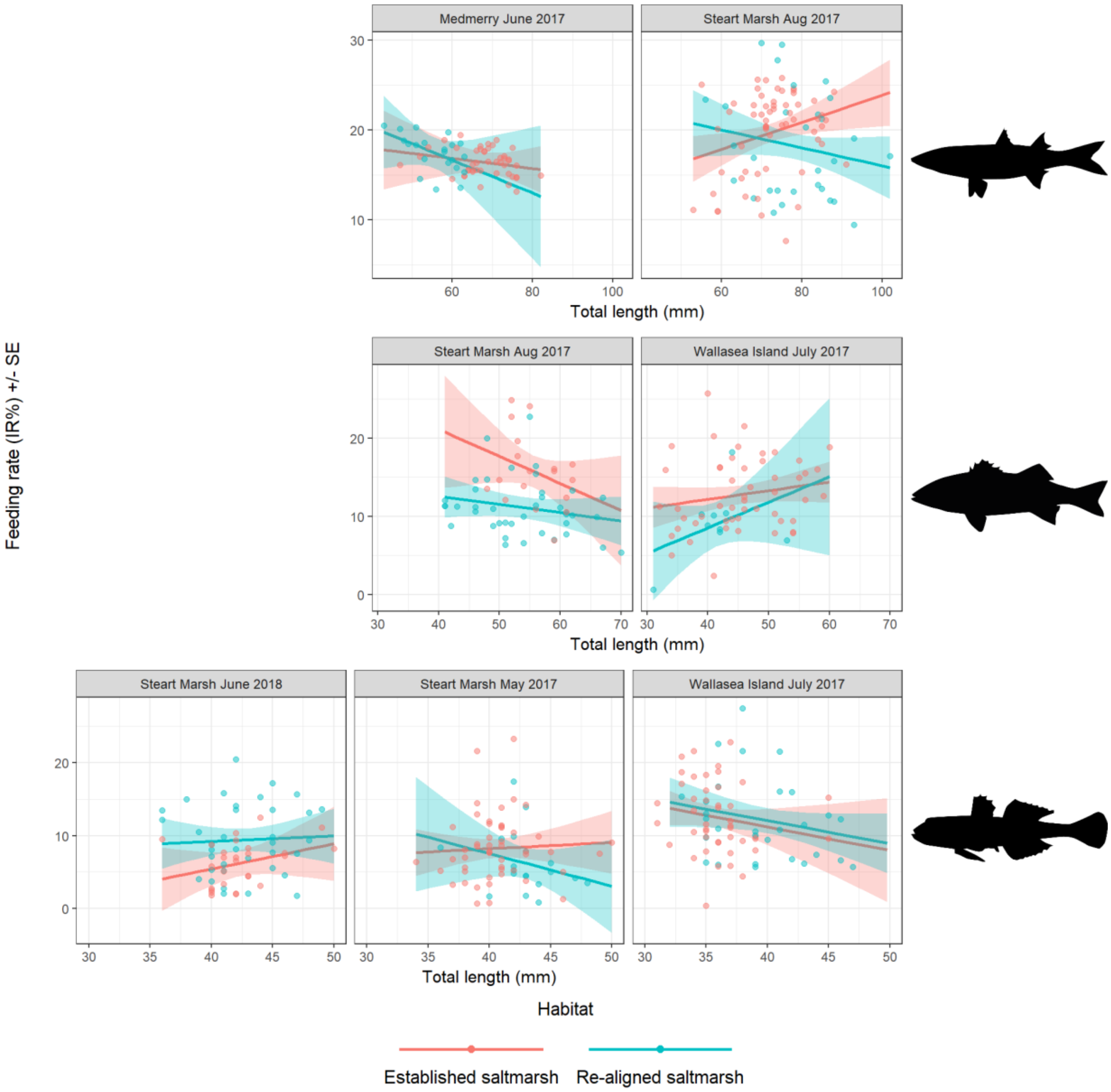

Figure 4. 3– Feeding rate (IR%) modelled against total length for; *Chelon ramada* (top), *Dicentrarchus labrax* (middle) and *Pomatoschistus sp.* (bottom) in re-aligned (blue) and established saltmarsh (red) habitat in each of the surveys. Please note visual representation includes interaction terms and fork length, whereas model outputs provided in table 6 are derived from models where terms have been removed as a result of model simplification

Table 4. 6 – Model coefficients for selected feeding rate model for each of the selected taxa within the current study. Model R^2, F value and degrees of freedom are provided under each taxa name

Taxa	Coefficient	Estimate	Standard error	T value	*p*
	Intercept – Habitat ES	20.167	5.821	3.464	<0.001
Chelon ramada	Habitat – ReS	7.477	10.111	0.740	0.460
	Survey - Steart Marsh August 2017	-11.354	7.300	-1.555	0.1222
$R^2 = 0.16$	Total length	-0.055	0.085	-0.652	0.515
$F_{7,149} = 4.303$	Habitat - ReS : Survey - Steart Marsh August 2017	9.706	12.281	0.790	0.430
	Habitat Res : Total length	-0.127	0.170	-0.748	0.455
	Survey - Steart Marsh Aug 2017 : Total length	0.206	0.104	1.974	0.05
	Habitat – ReS : Survey - Steart Marsh August 2017 : Total length	-0.122	0.193	-0.634	0.527
Dicentrarchus labrax	Intercept – Habitat ES	15.187	0.888	17.097	<0.001
	Habitat – ReS	-3.795	0.995	-3.111	<0.001
$R^2 = 0.11$					
$F_{2,113} = 7.262$	Survey - Wallasea Island July 2017	-2.180	0.977	-2.31	0.02
Pomatoschistus spp.	Intercept	7.878	0.412	19.093	<0.001
$R^2 = 0.17$					
$F_{1,206} = 42.61$	Survey- Wallasea Island July 2017	4.407	0.687	6.414	<0.001

4.4.1 Diet

A total of 3133 individual prey items from 24 species/taxa were identified from the stomachs of the captured *Dicentrarchus labrax* and *Pomatoschistus spp.* 10 of the prey species accounted for 99% of the abundance within the stomachs, the remaining 14 species accounted for <1%. The relative abundance of the "dominant" prey species (those accounting >1% abundance) in each habitat are shown in Figure 4.4.

PERMANOVA analysis suggested that *Dicentrarchus labrax* and *Pomatoschistus spp.* diet differed between surveys. *Dicentrarchus labrax* diet was also significantly different between all the established and re-aligned saltmarsh site * survey combinations (Table 4.7, Figure 4.4). No significant difference in the diet of *Pomatoschistus sp.* was found between habitats from fish captured in the Steart marsh June 2017 survey, however within Steart marsh May 2017 and Wallasea Island survey July 2018 significant differences in the diet between habitats were detected (Table 4.7, 4.8 & Figure 4.4).

Table 4. 7– PERMANOVA table of results assessing differences in the diet of *Dicentrarchus labrax* & *Pomatoshcistus spp.* from established and re-aligned saltmarsh sites (included as "habitat" within the model)

Taxa	Term	df	SS	MS	Psuedo F	P
Dicentrarchus labrax	Habitat	1	24119	24199	9.4699	<0.001
	Survey	1	34741	34741	13.641	<0.001
	Habitat : Survey	1	9633.6	9633.6	3.7825	<0.001
	Residual	115				
Pomatoschistus spp.	Habitat	1	23251	23251	17.251	0.001
	Survey	2	83870	41935	31.113	0.001
	Habitat : Survey	2	13794	6896.9	5.117	0.001
	Residual	368		1347.8		

Table 4. 8– Pairwise PERMANOVA comparison of *Pomatoschistus spp.* diet from established and re-aligned saltmarsh sites (included as “habitat” within the model) from the following surveys: Steart marsh May 17, Steart marsh June 18, Wallasea Island July 17

Survey	Term	T	P
Steart marsh May 2017	Habitat	3.066	<0.001
Steart marsh June 2018	Habitat	0.73139	0.610
Wallasea Island July 2017	Habitat	3.1425	<0.001

In general the same prey species were found at both the re-aligned and established saltmarsh sites, however their relative abundances (as measured through the fish diet) varied. Distinct differences in the relative number of dominant prey species consumed were visually apparent between the habitats (Figure 4.4). Notably, *Orchestia gammarellus and Sphaeromatidae* which cumulatively account for 50% of the total abundance for all prey species, had an overall reduced average abundance of 85.6% and 49.5% (respectively) in the re-aligned saltmarsh sites. Notable other differences in prey species across the habitats included:

1. *Delphacoides spp.* which accounted for 14.1% of all prey consumed by *Dicentrarchus labrax* within Steart marsh Aug 2017 were almost entirely absent for the respective re-aligned saltmarsh site;
2. Bivalve siphons accounted for 19.7% of the *Pomatoschistus sp.* diet with Wallasea island Jul 2017, these were approximately 16% lower in the respective established saltmarsh site.

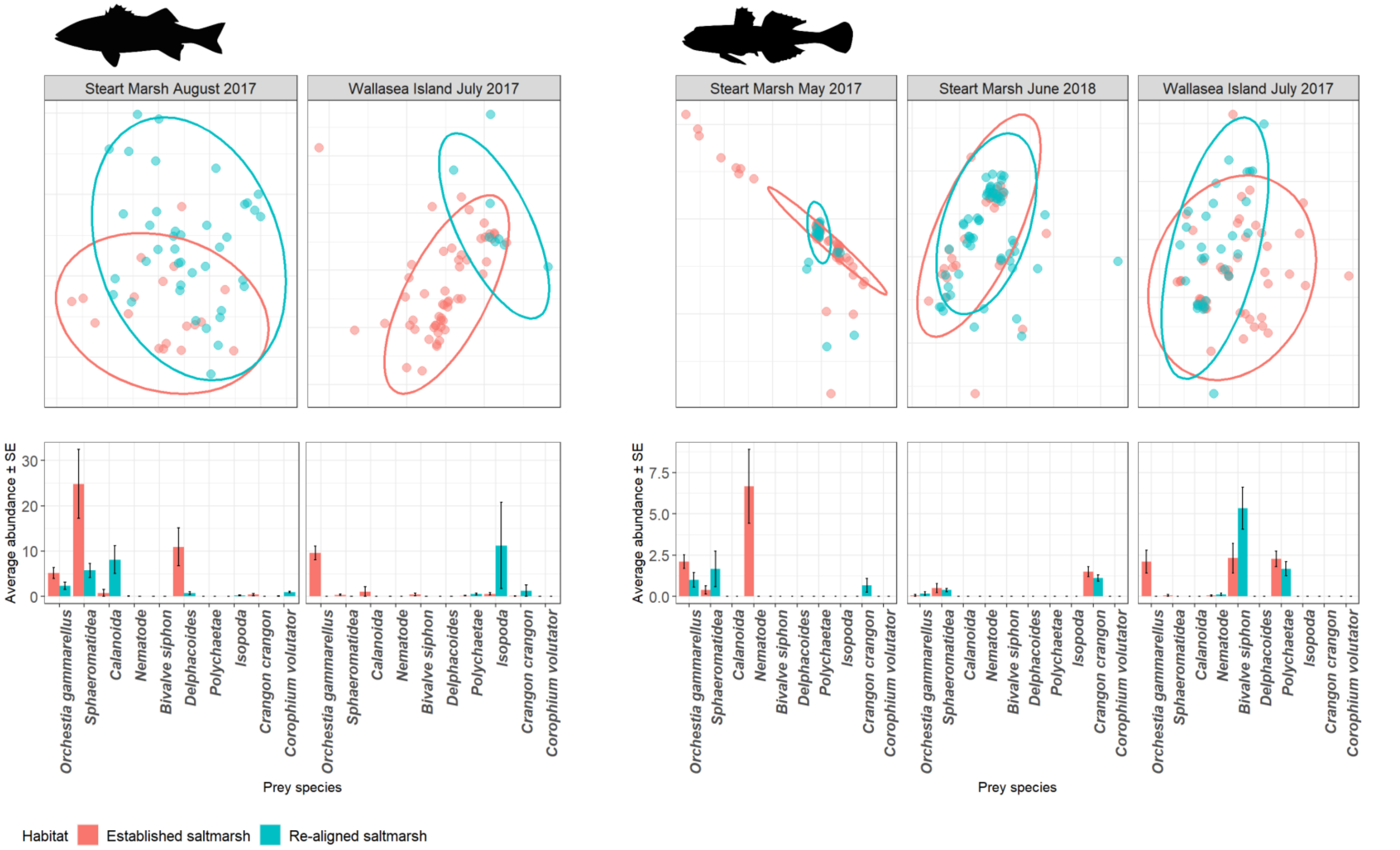

Figure 4. 4 - Non metric Multi-Dimensional Scaling (NMDS) plot demonstrating the dietary similarity of *Dicentrarchus labrax* (top left) and *Pomatoschistus spp.* (top right) captured within established and re-aligned saltmarsh sites during each of the surveys. Each point represents an individual fish. 95% ordinance ellipses used to show overlap in diet between habitats in each survey. *Dicentrarchus labrax* 2D stress value = 0.16, *Pomatoschistus sp.* 2D stress value = 0.12. Average abundance of dominant prey species per stomach for *Dicentrarchus labrax* (bottom left) and *Pomatoschistus spp.* (bottom right) captured within established and re-aligned saltmarsh sites during each of the surveys

4.5 Discussion

Overall the results indicate the re-aligned saltmarshes surveyed in this study do provide feeding habitat which is being exploited by the target fish species/taxa. There is however evidence that feeding rates for *Chelon ramada* and *Dicentrarchus labrax* are lower in re-aligned sites, furthermore apart for *Pomatoshistus sp.* during the Steart Marsh June 2018 survey, a significant difference was detected in the diet of all fish species between re-aligned and established saltmarshes. This therefore suggests that while fish do feed within re-aligned sites, for some species their feeding rate may be reduced and the relative abundances of dominant prey species may vary between re-aligned and established saltmarsh habitat.

4.5.1 *Chelon ramada*

Chelon ramada feeding rate did not differ between the re-aligned and established saltmarsh site at Medmerry Nature reserve. This is a result of all *Chelon ramada* captured on this survey being identified as having empty stomachs. Further sampling at this location would therefore be required to validate if feeding rates varied for *Chelon ramada* between Medmerry Nature Reserve and surrounding established saltmarsh.

At Steart marsh however *Chelon ramada* feeding rate increased with fish length in the established saltmarsh, whereas it decreased with fish length in the re-aligned saltmarsh. Evidence within the literature does not suggest that *Chelon ramada* switches to different prey as they grow larger (Almeida, 2003; Rita *et al.,* 2006; Kasımoğlu & Ylmaz, 2012). It is therefore likely that at any particular site, prey availability is the same for fish of all sizes. Instead differences in feeding rate may be explained by differences in vegetation between the habitats. Vegetation within saltmarsh provides crucial shelter and predation refuge from larger predatory fish and/or birds (Halpin, 2000). Typically, re-aligned saltmarsh is characterised by lower vegetation density and diversity than surrounding established saltmarsh (Mossman *et al.,* 2012). Differences in vegetation may therefore affect *Chelon ramada* feeding behaviour in re-aligned sites, potentially resulting in reduced feeding rates (Halpin, 2000).

4.5.2 Predatory fish species

Relative to the established saltmarshes, *Dicentrachus labrax* feeding rate was lower and the diet significantly different within all the re-aligned saltmarsh sites. This suggests that the habitat provided within the re-aligned sites does not currently provide the same feeding opportunities for this fish species as surrounding established saltmarsh.

Notable differences in the diet include the reduced abundance of; *Orchestia gammarellus*, *Sphaeromatidae* and *Delphacoides* within the re-aligned saltmarsh sites. *Orchestia gammarellus* & *Sphaeromatidae* are detritivores (Marsden, 1976; Schrama *et al.,* 2015), and *Delphacoides* feed directly on live plant material (Brantock & Botting, 2018). Therefore the abundance of these prey species is likely to be linked to the availability of organic matter and/or vegetation (Sprung & Dias, 2003). The generally reduced vegetation density and organic matter within re-aligned saltmarsh habitat (Mossman *et al.*, 2012) may therefore result in a reduced availability of these prey.

Pomatoschistus spp. feeding rate was not found to differ between the re-aligned and established saltmarshes, however differences within their diet were detected within the Steart Marsh May 2017 and Wallasea island July 2017 surveys. These results indicated that *Pomatoschistus spp.* will feed at the same rate in both re-aligned and established saltmarsh, however as with *Dicentrarchus labrax* they may feed on varying proportions of the same prey species in each respective habitat.

The prey species consumed by *Pomatoschistus spp.* were from a wide range of taxa and/or feeding modes, they included detritivores e.g. *O.gammarellus,* Polychaete worms and bivalves. Unlike with *Dicentrarchus labrax,* not all these prey species are directly dependent upon vegetation and/or local organic matter (Cammen, 1976; Paramor *et al.,* 2004). Due to the wide variety of prey species, and no significant difference observed in feeding rate, *Pomatoschistus spp.* may more successfully exploit the novel habitats within re-aligned saltmarsh habitat over other predatory fish species e.g. *Dicentrarchus labrax*. Though further survey work and higher sample replication would be required to fully validate this.

4.5.3 Vegetation and habitat development

Cumulatively the results suggest that the presence of vegetation and/or organic matter may be an important driver of the feeding success of *Chelon ramada* and *Dicentrarchus labrax* at re-aligned sites. Globally there is evidence that from a plant community standpoint re-aligned sites can resemble those in natural surrounding habitat within 10 years (USA- Byers & Chmura, 2007). It is however predicted that as a result of current construction designs (Mossman *et al.,* 2012; Lawrence *et al.,* 2018), and potentially the macro-tidal environment, re-aligned sites in Northern Europe may not achieve full biological equivalence to established saltmarsh within 50-100 years of tidal inundation (Mossman *et al.,* 2012).

There is however limited research on how fish interact with re-aligned habitats (Colclough *et al.,* 2003; Fonseca *et al.,* 2011; Nunn *et al.,* 2016) and as evidenced with *Pomatoschistus spp.* within the current study, fully biologically equivalent saltmarsh habitat may not be required to provide valuable feeding habitat for dependent fish populations. If the novel habitats within re-aligned sites are capable of providing functional fish feeding habitat, Colclough *et al.* (2003) argued that “these sites have the potential to make a substantial long term contribution to the stock enhancement of those coastal fish species which are known to utilise such areas as nursery grounds". Similarly however, this would require further survey work to validate.

4.5.4 Study limitations and future work

Sampling fish within intertidal habitats, such as re-aligned and established saltmarsh, is logistically and physically challenging. Furthermore, while each of the fish taxa included are relatively highly abundant within estuaries and saltmarsh habitat, their capture rates within the current study was highly varied. This resulted in relatively low sample size of each species during each survey. Furthermore, fish predation from *Carcinus maenus* also captured within fyke nets was a suspected issue at some sample sites. This further reduced the number of fish retained in each net deployment.

Future survey work should aim to increase the sample size of each fish taxa. As suggested by Colclough *et al.* (2002), this could be achieved by using a "multi-method approach" in which a variety of net designs are deployed e.g. fyke and/or seine netting. There are however logistical difficulties in deploying some net designs within vegetated-habitats e.g. seine nets. Increased sample size could also be achieved by increasing the number of surveys conducted at each re-aligned and associated established saltmarsh site. Repeated sampling would also allow the collection of additional metrics of fish habitat suitability, such as assessment of variability in fish growth (Baltz *et al.,* 1998).

A particular factor not assessed within this study is the relative ages of each re-aligned site, and how this influences fish feeding success and diet. Within the current study multiple re-aligned sites were targeted which had been tidally inundated for a variety of time frames. Unfortunately, insufficient numbers of the target fish species were captured to assess a relationship between time since tidal inundation and fish feeding success and/or diet.

Future survey work, should aim to target re-aligned sites which vary in the time since first tidal inundation, as they provide useful test sites upon which habitat development (Gray *et al.,* 2002; Mossman *et al.,* 2012), and consequent fish feeding ecologies can be monitored.

It should also be noted that inter and intra specific predation competition may also affect consumption rates (Craig *et al.,* 2007; Shoji & Tanaka, 2007). Further survey work should aim to either quantify the relative abundance of the target fish species/taxa at each site or conduct an independent assessment of prey availability.

4.5.5 Conclusions

The results suggest that the habitats within the re-alignment schemes included within this study do provide feeding opportunities for fish. Relative to the other species included, the generalist predator *Pomatoschistus spp.* exploited re-aligned habitats at an equivalent rate to that in established saltmarsh. However other species, *D.labrax* and *C.ramada,* did not feed at an equivalent rate to that within surrounding established saltmarsh.

Evidence within the peer reviewed literature suggests that re-aligned saltmarshes in Northern Europe to do not currently fully compensate for the habitat which has been lost. Complete biological equivalence, in regard to the floral diversity and density, may however not be required in regard to fish feeding rates and diets. In the context of broad scale historic and continuing modern habitat loss within estuaries, it therefore remains imperative to further study and identify how estuarine fish exploit re-aligned habitats.

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Chapter 5: Acoustic telemetry highlights localized movement of juvenile European bass (*Dicentrarchus labrax*) to coastal sites in the Southwest UK

Keywords

Acoustic telemetry, European bass, residency, nursery habitat

Contributions

All supervisors provided logistical and academic support: Elizabeth West, Tim Robbins, Shaun Plenty, Martin Attrill, Emma Sheehan.

Additional academic support provided by James Stewart of the Devon and Severn IFCA

5.1 Abstract

European bass (*Dicentrarchus labrax*) is a commercial and recreationally important fin fish native to the Mediterranean Sea and Northeast Atlantic. Shallow coastal embayments and estuaries represent important nursery habitats, which fish maintain residency to for the first 4 years of life. The high residency characteristics of this species is thought to introduce spatial structuring into wider populations and increase their vulnerability to localized population declines. Limited research has however been conducted on juvenile fish movement and residency characteristics.

Innovasea V9 acoustic telemetry tags were implanted within the intraperitoneal cavity of 146 European bass. Of these, 133 individuals were tracked via an array of 78 Innovasea receivers for an approximate period of 1 year across three coastal nursery sites in southwest, UK. While highly varied, results suggest that tagged fish were within close proximity to their respective sample site for 42.9-75.5% of the tracking period, and were not predicted to disperse further than 3.81-4.26 km during this period.

This study complements evidence within the peer reviewed literature which demonstrates the importance of estuaries to this species, and their tendency to occupy defined coastal sites over prolonged time periods. It is therefore recommended that management should be considered at a finer spatial resolution, and the impacts of further human coastal development should be considered within a local fisheries management context.

5.2 Introduction

European bass (*Dicentrarchus labrax*) is a commercially and recreationally important finfish native to the Northeast Atlantic and Mediterranean Sea (Pickett & Pawson, 1994). The species is targeted throughout its range and represents a significant commercial and recreational fishery, which in the UK are estimated to have a value of £5-6million at first sale (Barclay, 2011 from Carroll*,* 2014), and £100-200 million per year respectively (B.A.S.S, 2004 from Ares*,* 2016; Carroll*,* 2014; MRAG, 2014).

In 2010, the International Council for Exploration of the Seas (ICES) reported a dramatic decline in the North Atlantic stock (ICES divisions 4.b–c, 7.a, and 7.d–h), which in 2016 declined below "safe biological limits", a threshold known as B_{lim}. In response to ICES advice the European Commission implemented a number of strict emergency "Technical Conservation Measures" which have imposed restrictions such as; banning targeted pelagic trawling during spawning periods, restrictions on commercial and recreational landings, and increasing the minimum landing size to 42cm total length (Ares, 2016). In 2019 ICES reported that the North Atlantic stock increased above B_{lim}, however relative to historic levels the population remains in a highly impoverished state and is still below maximum sustainable yield thresholds (Figure 5.1).

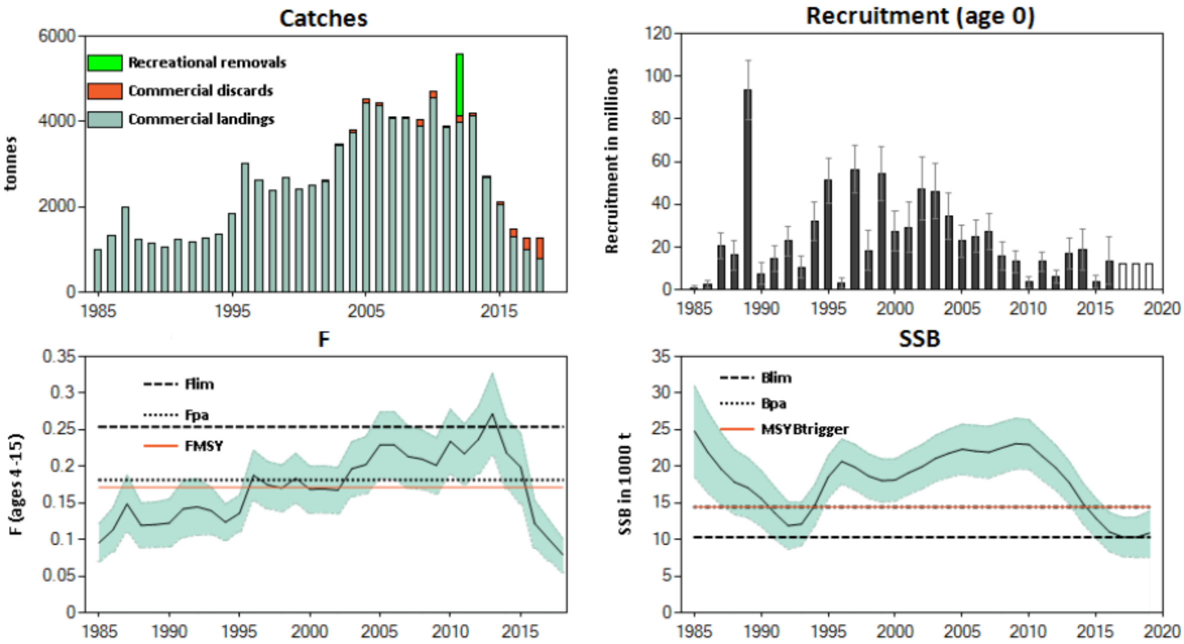

Figure 5. 1 - Sea bass in ICES divisions' 4.b–c, 7.a, and 7.d–h. Summary of the stock assessment. Catches - Total landings (commercial landings and estimated recreational removals, available for 2012 only [green bar], taking mortality of released fish into account). F - Fishing mortality is shown for the combined commercial and recreational fisheries. Discard estimates are available from 2009. Recruitment (age 0) - Assumed recruitment values are not shaded. SSB – Spawning stock biomass. Recruitment, F, and SSB are shown with 95% confidence intervals (Image source: ICES, 2019)

The decline in the Northeast Atlantic European bass stock is thought to be the result of several concomitant issues e.g. unsustainable fishing mortality (Figure 5.1 – bottom left) combined with poor recruitment (Figure 5.1 – top right). However, the life history characteristics of this species e.g. slow growth and sexual maturation rates (Pawson *et al.,* 1987; Pickett & Pawson, 1994; Pickett *et al.,* 2004; Fritsch *et al.,* 2007; Pawson *et al.,* 2007; Cambiè *et al.,* 2016; Doyle *et al.,* 2017; Pontual *et al.,* 2019) increases the likelihood of protracted recovery even if successful management interventions are implemented.

Furthermore, while mature European bass are known to make large migrations across the Northeast Atlantic (Doyle *et al.,* 2017; O'Neill, 2017; Pontual *et al.,* 2019), telemetry techniques have demonstrated that this species displays high philopatry and residency to inshore nursery and adult summer feeding sites (Pawson *et al.,* 1987; Pickett *et al.,* 2004; Fritsch *et al.,* 2007; Pawson *et al.,* 2007; Cambiè *et al.,* 2016; Doyle *et al.,* 2017; O'Neill, 2017; Pontual *et al.,* 2019). Localized movement of European bass is thought to introduce spatial structuring within wider populations which may be defined at a smaller spatial scale smaller than current management units (Cambiè *et al.,* 2016; Pontual *et al.,* 2019). Furthermore, isolation of localized populations increases dependency on local habitat availability, and vulnerability to localized population declines (Ares, 2016).

Limited research has been conducted on juvenile or sub-adult movement characteristics (<42cm total length) which relative to sexually mature conspecifics, are thought to be more resident within coastal and/or estuarine habitats (Pawson *et al.,* 1987; Pickett & Pawson, 1994). When occupying coastal and estuarine sites fish are at a higher vulnerability to the impacts of extreme environmental fluctuations and/or many human activities e.g. coastal development, habitat loss, power plant water abstraction (Edgar *et al.,* 2000; Kennish, 2002; Lotze *et al.,* 2006; Airoldi & Beck, 2007; Vasconcelos *et al.,* 2007).

In the UK, 37 Bass Nursery Areas (BNA) were designated under the *Bass (Specified Areas) (Prohibition of Fishing) (Variation) Order 1999.* This form of spatial management was introduced in 1990 and largely take the form of estuaries along the east, south and west coast of England and Wales. Within BNAs; 1) targeted commercial fishing for European bass is prohibited, 2) the use of live sand eel as a bait is prohibited; 3) fishing from a vessel is prohibited. The restrictions are typically seasonal, however vary from site to site (MAFF, 1990).

Prior mark recapture tagging studies conducted on juvenile (<32cm total length) European bass captured within designated BNAs suggested that the majority of tagged fish did not disperse further than 50km, and that these site designations would likely benefit local inshore commercial fisheries via increased recruitment rates (Pickett & Pawson, 1994; Pickett *et al.,* 2004). While mark-recapture studies provide invaluable preliminary results, recapture rates were typically low (<3%) and movement inferred between tagging and recapture locations. This may therefore result in a loss of information which has important biological and/or fisheries management implications.

Acoustic telemetry is an alternative modern tracking technique which relies on the implantation within, or attachment of, an acoustic transmitter tag to a host animal. The transmitter tag emits a uniquely-coded ping which can be detected when within transmission range of strategically placed autonomous receiver. Recent miniaturization and increased battery power of transmitter tags (Cooke *et al.,* 2013; Hussey *et al.,* 2015) allow the tagging of juvenile and/or sub-adult European bass for extended periods >2 years (Innovasea, 2016). Data derived from acoustic telemetry could identify movement/residency characteristics and highlight the importance of coastal and/or estuarine habitats for European bass.

Using acoustic telemetry, the aims of this study are to; 1) Quantify European bass site fidelity and residency to three coastal sites within the southwest UK; 2) Test how this varies between locations and with fork length; 3) Estimate how far tagged fish disperse from each site within the open coastline.

5.3 Field Methods

5.3.1 Sample sites

European bass were tracked within three coastal sites in the Southwest UK: The Dart estuary, Salcombe Harbour and the Taw/Torridge estuaries (Figure 5.2 & Table 5.1). From the closing line, the area of each site was 14.6km^2, 8.32km^2, 6.34km^2 for the Taw/Torridge estuaries, Dart estuary and Salcombe harbour respectively. All sites host a range of intertidal and subtidal sediment habitats and tidally-swept rocky reefs. Maximum water depth varied from 18m, 10m, 7m Below Chart Datum (BCD) for the Dart estuary, Salcombe and Taw/Torridge estuaries respectively. The main notable difference between the sample sites is the limited freshwater input to Salcombe Harbour. Whereas, both the Dart and Taw/Torridge are significant estuaries within the region.

All sample sites are designated as Bass Nursery Areas (MAFF, 1990), which seasonally (1st May – 31st October) prohibits commercial fishing within site boundaries and restricts some recreational fishing activities (MAFF, 1990). Furthermore, the regional fisheries body (the Devon and Severn Inshore Fisheries and Conservation Authority) introduced a local byelaw prohibiting netting (e.g. gill netting) within all estuaries in their region since 8th May 2018 (D&S IFCA, 2018) offering further protection to local fish populations using these sites.

5.3.2 Tagging procedure

From June-August 2018, 146 European bass were captured predominantly by rod and line using plastic lures. Local anglers were recruited via word of mouth and advertisement of the project on online forums. Local anglers were instructed to target fish above a minimum size threshold of 25cm fork length. This ensured that the tag to body weight ratio experienced by the fish was less than 3%, which has been previously tested as suitable for this species (Lefrancois *et al.,* 2001, Bégout Anras *et al.,* 2003).

Upon capture, all fish were temporarily placed in a container filled with aerated seawater collected at the site of capture. Fish were then transported to a central tagging location (10-15minute transport time), where they were transferred to a 500litre aerated holding tank and left to acclimatise prior to tagging.

Each fish was anaesthetized with an induction dose of 70-100mg/l MS-222 (Tricaine methanesulfonate). Fish were then positioned dorsally on a V shaped cradle, where they were ram-ventilated with a maintenance anaesthetic dose of 30-40mg/l MS-222. Induction and maintenance anaesthetic varied on an individual fish basis to ensure the required depth of anaesthesia was achieved and maintained. A single 69khz Innovasea V92X transmitter tag (tag dimensions: 29*9mm, 4.7g – air weight) was implanted within the peritoneal cavity via a small incision (10-15mm) made slightly off the mid-ventral line between the pelvic fin and anus. Transmitter tags were programmed to emit a randomised uniquely-coded ping once every 80-160 secs and had an expected battery life of 803 days. Following tag implantation, the surgical site was closed using dissolvable sutures and/or medical grade adhesive. Analgesic was topically applied to the surgical site (Lidocaine 1% solution diluted to 1:10 with NaCl saline solution). Following recovery, fish were released as close to the capture site as logistically possible. Further methodological details are provided in Annex 1.

All tagging procedures were conducted under UK Home Office license P81730EA5 by personal license holders with PILC entitlement. Dispensation was also provided by the Marine Management Organisation, Devon and Severn Inshore Fisheries and Conservation Authority, Natural England and by consent of the relevant land authority.

5.3.3 Acoustic telemetry receiver array

In total, 78 Innovasea VR2W and VR2Tx receivers were deployed (Figure 5.2 & Table 5.1). To achieve coverage of each site (which differed in size/area), each array comprised a different number of receivers; The Dart: 28, Salcombe harbour: 17, and the Taw/Torridge estuaries: 33. The receiver configuration in each array consisted of a series of detection gates which spanned the mouth of each sample site up to the mean tidal limit. Receiver gates had a mean spacing of 0.9km (± 0.09), 0.82km (± 0.4), 1.8km (± 1.6) for the Dart estuary, Salcombe harbour and the Taw/Torridge estuaries respectively. These were opportunistically attached to existing structures e.g. channel marker or moorings. All receivers were deployed from June – August 2018. Upon successful detection of each tagged fish; the time, date and tag ID was recorded on the receiver. This was periodically downloaded every 3 months.

Table 5. 1–Physical characteristics of sites, area and centroid coordinates defined under article 17 of the Habitats Directive (provided by the UK statutory nature conservation bodies)

Sample site	**Waterbody type**	**Area (km^2)**	**Number of receivers**	**Deployment date**	**Latitude**	**Longitude**
Dart estuary	Ria[1]	8.32	28	22/08/2018	50.3822	-3.6061
Salcombe harbour	Ria	6.34	17	19/06/2018	50.2377	-3.7554
Taw and Torridge estuaries	Estuary	14.6	33	19/07/2018	51.0536	-4.1504

1 – The dart estuary is technically defined as a ria system, however still has significant freshwater input via the river Dart

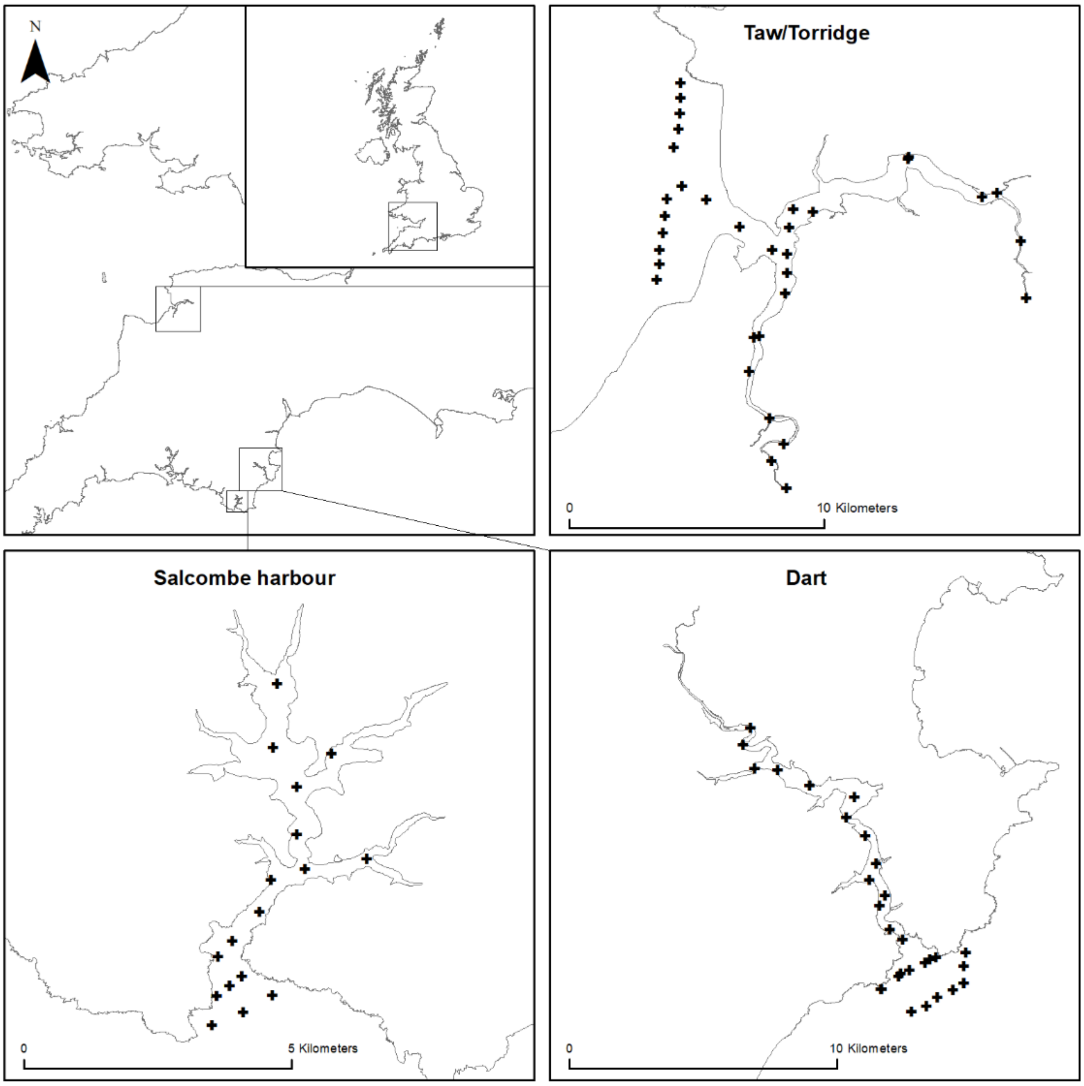

Figure 5. 2–Acoustic telemetry array within the Dart estuary (bottom right), Salcombe harbour (bottom left) and Taw/Torridge estuaries (top right). Black cross hairs represent position of acoustic receiver.

5.3.4 Range testing

In order to assess the detection efficiency of the acoustic telemetry receiver arrays within estuarine/coastal sites a range testing survey was conducted. A V9 range test tag, with comparable power output to those implanted within the fish, was deployed in a linear array of receivers in Salcombe harbour. Receivers were spaced approximately 150m apart (Figure A2.2 – Annex 2). The number of successful detections at varying distances from the range test tag were summarised.

5.4 Data analysis methods

All data manipulation and statistical analysis was conducted using R version 3.6.0 (R Core Team 2019).

To remove any influence of a post-tagging response, the first two weeks of telemetry data was removed for each fish (Doyle *et al.,* 2017). Subsequent data analysis then focussed on periods of “residence” and “absence” of each tagged fish within their respective sample site. A residence period began when a fish was detected by any receiver within each sample site, and terminated when either a fish was detected in a different sample site (iResidenceThreshold = 1) or was not detected for a period of 6 hours (iTimeThreshold=6 hours) (Doyle *et al.,* 2017). An absence period was defined by the termination of a residence period and the start of the proceeding residence period i.e. the period of time between residence events. Residence periods were defined using “RunResidenceExtraction” function within R package “Vtrack” (Campbell *et al.,* 2012).

5.4.1 Classifying residency characteristics

Time series were constructed for each fish detailing the duration of each absence period throughout the tracking period (Figure 5.3). Change point detection was used to break each time series into “segments” of time where there was a significant relative change in the mean duration of absence periods over consecutive days (cpt.mean; method:PELT; penalty: SIC - R package “changepoint” - Killick & Eckley, 2012). As described by Madon & Hingrat (2014) the PELT-TREE classification method was then used to identify and assign each segment to the following broad behaviours (R package “tree” - Ripley, 2019):

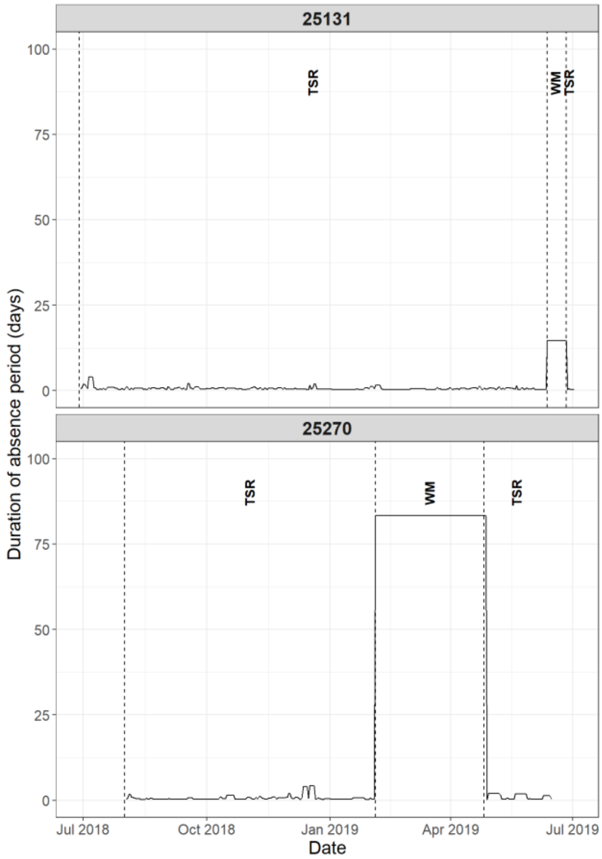

Figure 5. 3– Absence period time series for tag ID 25131 (top) & 25270 (bottom), with segments identified as “Tagging Site Residence” (TSR) and “Wider Movement” (WM). Both fish were tagged within sample site Salcombe Harbour

1. Coastal movement: Defined by a high frequency of absence periods with a low duration, during which fish were not thought capable of travelling far from the host sample site. The total duration of time fish exhibited coastal movement was combined with the total duration of all residency periods (see 5.4.1). This provided an estimate of how long each fish was either within or in close proximity to the host sample site throughout the tracking period. This was defined as “**Tagging site residence”**.

2. **Wider movement**: Defined by relatively "large" absence periods, which could happen as a result of fish conducting spawning migrations (October – April: Pickett & Pawson, 1994; Doyle *et al.,* 2017; Pontual *et al.,* 2019) or making wider movements within coastal water (Pickett & Pawson, 1994). The timing and duration of these segments are described however no further analysis is conducted on these segments.

The PELT-TREE classification method uses a regression tree to determine splitting rules for time series segments which could be identified as "coastal movement" or "wider movement". An initial supervised "training" regression tree was created using 267 segments from 14 individuals (10% of tagged fish) (R package "tree" - Ripley, 2019). In which each time series segment was manually assigned to either "coastal movement" or "wider movement". Splitting rules for these different behaviours were derived from the "training" regression tree and then applied to the remaining 1567 segments (which were not included within the "training" regression tree).

5.4.2 Assessing the influence of fork length and sample site on tagging site residence

To account for differences in the duration of time each fish was tracked (the tracking period), Tagging Site Residence (TSR) was converted to a percentage of the tracking period for each fish.

To visualize how TSR varied between sample sites and with fork length, tagged fish were binned into 10cm size classes (20-29, 30-39 & >40cm), histograms were then created for each size class * sample site combination.

Multiple regression (R package "stats" v3.6.1; R Core Team, 2019) was then used to assess for any detectable correlation between fork length and sample site on tagging site residence. Initially a regression model was fit with fork length and tagging site included as predictor variables (with an interaction term), model simplification was then conducted using Akaike Information Criterion (AIC). Following the rules of parsimony the model with lowest AIC score was selected. If AIC scores from models were =<2 the simplest model and/or with the fewest fixed effects was selected (Zuur *et al.,* 2013). Statistical assumptions were assessed via visual assessment of model diagnostic plots. Tukey pairwise comparison (stats package; R core team, 2019) was used to assess at which sample sites tagging site residence significantly differed.

5.4.3 Estimating dispersal distances from sample sites

In incidences where tagged fish were detected in locations outside of the sample site they were tagged within, Rate of Movement (ROM) was estimated using a straight line distance (avoiding land) between receivers. To make the results from the current study more broadly applicable, the average ROM of tagged fish from the current study were combined with those derived from O'Neill (2017). A linear regression was used to test a relationship between average ROM and fork length (R package "stats" v3.6.1; R Core Team, 2019). This linear relationship provided size-specific ROM estimates for European bass within the open coast from 26.2-71.4cm fork length.

When fish displayed the behaviour TSR, the estimated range a fish could achieve from their respective sample site during each individual absence period was calculated as:

Estimated range (m) = ROM estimate (m/s) * Absence period duration (s)

To estimate the potential dispersal distance of all fish from each sample site during periods of time identified as "Tagging site residence", a Linear Mixed effect Model (LMM) with the following notation was used (R package "lme4" – Bates *et al.,* 2015):

Dispersal distance = Estimated range (m) ~ Sample site + (1|tag ID) + (1|month/day)

To assess if dispersal distance differed significantly between sample sites, a model with sample site included and then removed were compared using AIC criteria. The model which scored the lowest AIC score was selected as the most appropriate model.

To account for repeated measurements and temporal auto-correlation, tag ID and time (day nested within month) were included as random factors. Model assumptions were visually assessed using model diagnostic plots. Temporal auto-correlation within model residuals was visually assessed via inspection of autocorrelation plots. Model coefficients and 95% confidence intervals (95% CI) were reported as the estimated dispersal distance of tagged fish from each sample site.

5.5 Results

A total of 146 fish were tagged as part of the study (Dart estuary – 51; Salcombe Harbour – 46; Taw/Torridge estuary - 49). Fish length ranged from 26-60cm (fork length), with a mean of 33.5cm (range: 26 - 52), 30.9cm (range: 25.4 - 38.3) and 30.3cm (range: 25.2 - 60) within the Dart estuary, Salcombe harbour and the Taw/Torridge estuaries respectively (Figure 5.4).

No immediate mortality occurred as a result of the tagging procedure, however, 12 fish were not detected >30 days post-tagging procedure. Tag ID's that were not detected >30 days post-tagging procedure were removed from further analyses. One fish (Tag ID: 25249) was tagged on 31/07/2019 in Salcombe harbour and immediately left the array of receivers. On the 14/10/2019 this individual was redetected in the Dart estuary for a period of 3 hours, 34 minutes, 12 seconds. This individual was not detected beyond the 14/10/2019.

Due to the intermittent nature of this individual being detected it was also removed from subsequent analyses.

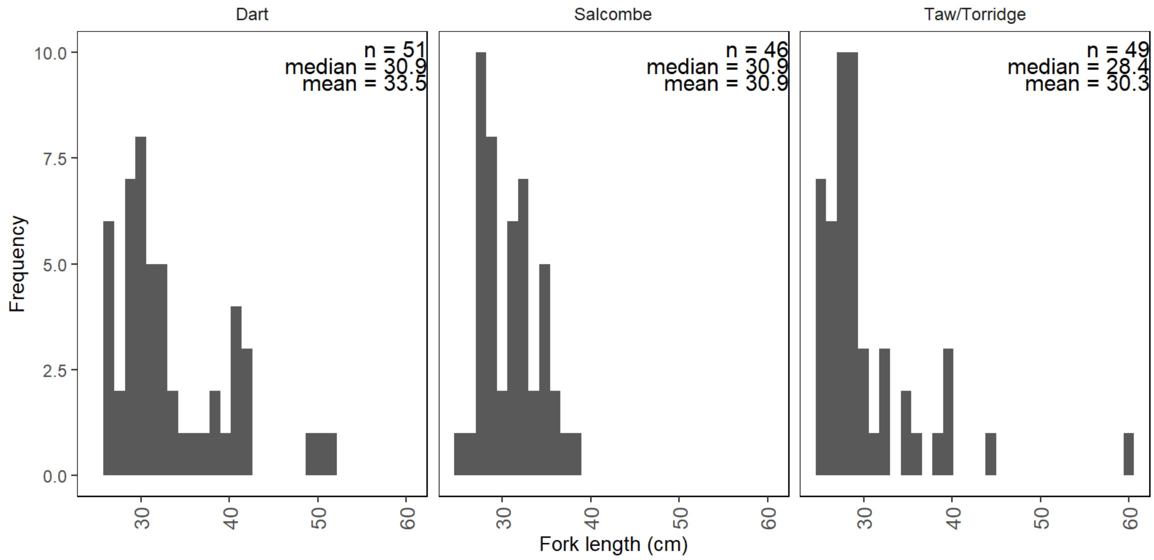

Figure 5. 4– Size distribution of tagged European bass captured within the Dart estuary, Salcombe harbour and the Taw/Torridge estuaries

5.5.1 Range testing

Range testing confirmed 60% ping detection at a range of 175m. The channel width of each tagging site rarely exceeds 300m, therefore by positioning receivers at central locations within each channel detection of tagged fish was assumed to be reliable.

5.5.2 Overall fish detection trends

Across all receivers, tagged fish were detected 2,724,548 during the tracking period (Dart estuary – 321 days; Salcombe Harbour – 385 days; Taw/Torridge estuaries - 347). Detections were highest within Salcombe Harbour (1,418,688 detections), second highest within the Dart estuary (848,917 detections) and lowest within the Taw/Torridge estuaries (393,943 detections).

5.5.3 PELT-TREE classification

From the absence period time series, a total of 1,784 unique segments were identified using the PELT change point detection method. On average 12.41 (Median: 12, Q_1: 7, Q_3: 16) change points were detected for each tagged fish. The resultant regression tree (Figure 5.5) had four terminal nodes, a residual mean deviance of 0.094 and a misclassification rate of 0.019. The classification tree was able to define the following splitting rules:

- The first node of the tree split segments into two classes, identified as “Coastal movement” with mean absence period duration <5.58 days
- The 2nd node of the tree split segments into two classes, identified as “Wider movement” with a mean duration >5.58 days

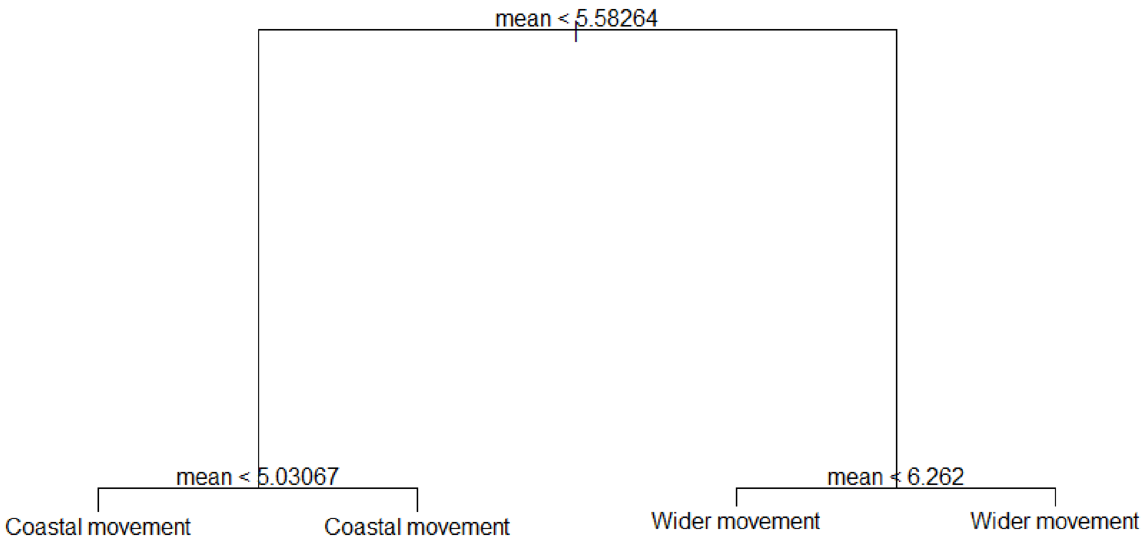

Figure 5. 5 – Regression tree for training dataset, highlighting the mean duration of absence periods (days) during periods of time when tagged European bass exhibited “Coastal movement” or “Wider movement”

Therefore during segments of time, identified through the PELT algorithm, in which the mean duration of absence period was less than 5.58days tagged fish were determined to be displaying “Tagging site residence”. During segments when the mean duration of absence periods exceeded 5.58 days, tagged fish were determined to be displaying “Wider movement”.

5.5.4 Tagging Site Residency

A total of 18,526 residence periods were detected, with an average of 139.3 residence periods per fish (Median: 98, Q_1: 57, Q_3: 208), which had an average duration of 0.64 days (Median: 0.19, Q_1: 0.062, Q_3: 0.52).

A total of 18,417 absence periods were detected, with an average of 138.3 absence periods per fish (Median: 92.5, Q_1: 51.5, Q_3: 190). Once the splitting rules derived from the PELT tree classification method (figure 5.5) were applied to the data, 129 out of 133 tagged fish were identified as exhibiting absence periods which were defined as "Coastal movement" (Dart estuary: 50; Salcombe harbour: 35; Taw/Torridge estuaries: 46). During segments of time when fish displayed "coastal movement" individual absence periods had an average duration 0.91 days (Median: 0.71, Q_1: 0.41, Q_3: 0.97), and this behaviour was sustained for an average period of 36.61 days (Median: 7, Q_1: 5, Q_3: 26).

When visually inspecting the duration of time fish displayed TSR by size class (Figure 5.6), within the Taw/Torridge fish that were 20-29.9cm had a disproportionately high TSR. Across the remaining sizes classes however, there was no visually apparent trend of particular size classes spending a higher or lower amount of time within each sample site.

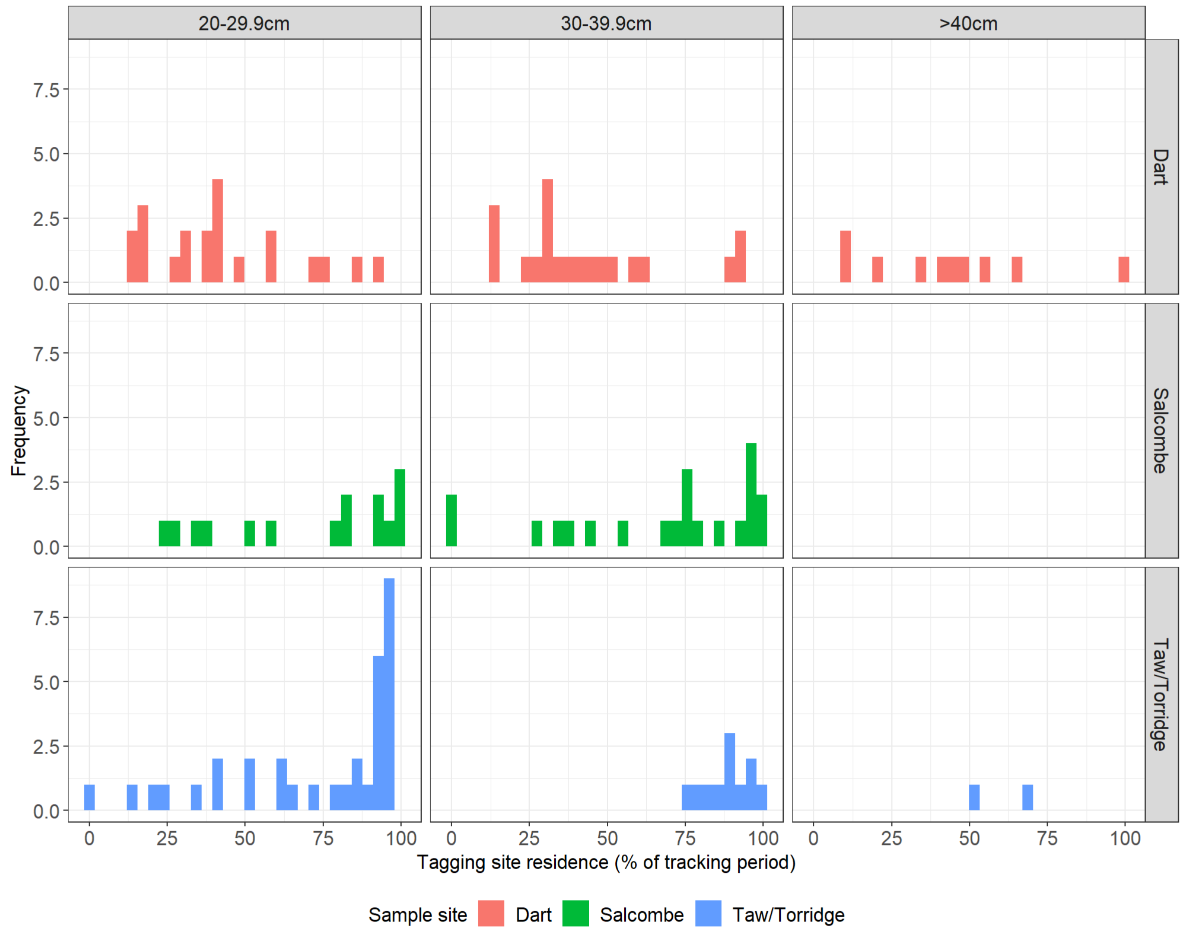

Figure 5. 6 – Histogram of tagging site residence (shown as % of tracking period) for tagged fish within each sample site within 10cm size classes.

When assessing for any statistically significant relationship of fork length and/or sample site on the duration of time fish exhibited TSR, model three achieved the lowest AIC score and was therefore selected as the most parsimonious model. Model three included sample site as the only predictor variable, suggesting fork length had no significant impact on TSR (Table 5.2).

Table 5. 2– Candidate linear models to test the effect of sample site and fork length on tagging site residence

Model ID	Model notation	Δ AIC
3	***Tagging site residence (% of tracking period) ~ sample site***	**0**
2	*Tagging site residence (% of tracking period) ~ sample site + fork length*	2.29
1	*Tagging site residence (% of tracking period) ~ sample site * fork length*	6.29
4	*Tagging site residence (% of tracking period) ~ fork length*	33.58
5	Null model	32.65

Model 3 (Table 5.3) suggested there was a highly significant difference in TSR between sample sites: LM - Adj.R^2: 0.23, $F_{2,130}$: 20.45, p: <0.001. No statistical transformations were applied to the data, however considerable variability was observed within the model residuals.

TSR was lowest within the Dart estuary with an average of 42.89% (median: 40.94 , Q_1:26.11 , Q_3: 56.91) (Tukey test Dart-Salcombe, $p \leq 0.001$; Tukey test Taw/Torridge-Dart, $p \leq 0.001$). No difference was detected between Salcombe harbour and the Taw/Torridge estuaries (Tukey test: P=0.46) in which TSR was on average 68.52% (Median: 76.78, Q_1: 42.29, Q_3: 94.76) and 75.49% (Median: 87.37, Q_1: 63.92, Q_3: 94.6)(Figure 5.7 & Table 5.3).

Table 5. 3– Coefficients for selected model, testing differences in residency characteristics between sample sites

	Coefficient	Estimate	Std. Error	t value	*p*
	Intercept (Dart estuary)	42.889	3.691	11.619	<0.001
Sample site	Salcombe Harbour	25.628	5.738	4.466	<0.001
	Taw/Torridge estuary	32.598	5.360	6.082	<0.001

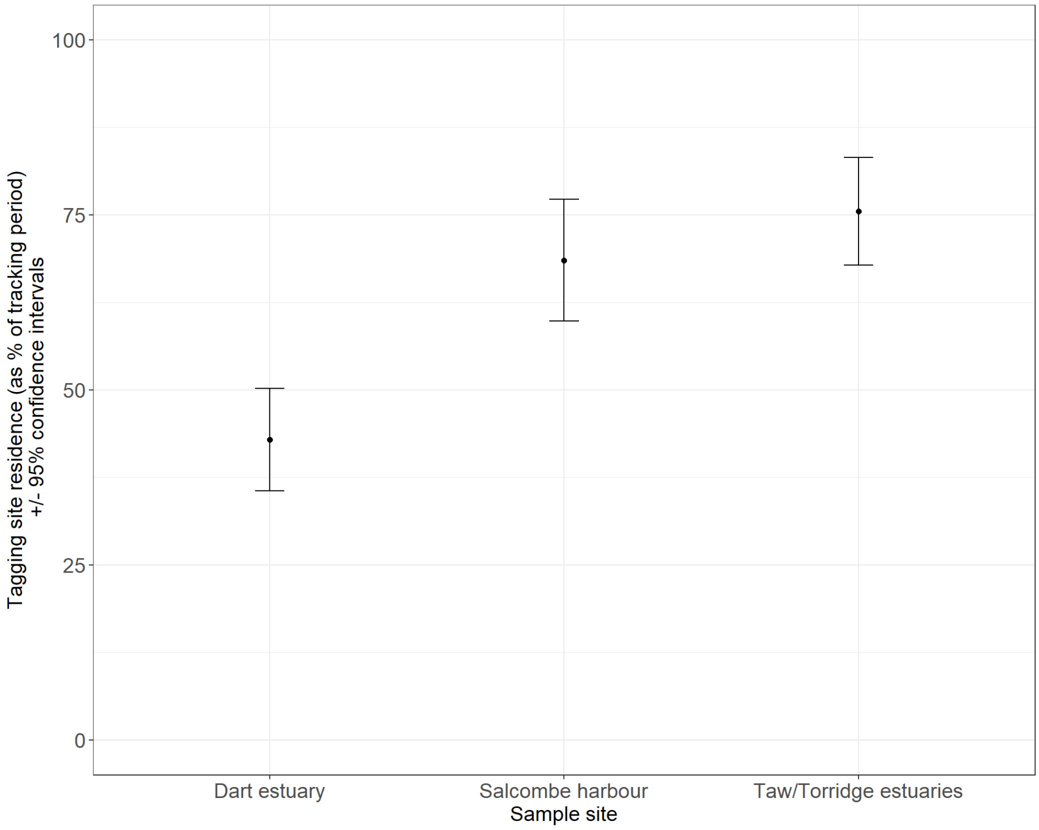

Figure 5. 7– Predicted outputs from selected model, assessing residency characteristics (± 95% CI) of tagged European bass between sample sites

Wider movement

All fish tagged as part of the study conducted wider movements, during which individual absence periods had an average duration of 23.17days (Median: 0.98, Q_1: 6.99, Q_3: 20.50).

As a result of the seasonal timing and long duration of some absence periods, 49 out of 133 tagged fish were suspected of either conducting spawning migrations or moving out of their respective sample site during the winter to seek thermal refuge in deeper water (Dart estuary – 34, Salcombe harbour – 9, Taw/Torridge estuaries – 6 fish). These fish ranged in length from 25.3-49.4cm (Median: 30.8cm, Q_1: 28.8cm, Q_3: 37.3cm), and these suspected migrations ranged in duration from 50 – 296 days; with a mean duration of 118.2 days. The median departure date was 14-02-2019, Q_1: 31-12-2018 and Q_3: 26-03-2019.The median return date was 25-06-2019, Q_1: 15-05-2019 and Q_3: 13-08-2019. The remaining 84 fish

(Dart estuary – 17, Salcombe Harbour - 27, Taw/Torridge estuary - 40), ranged in length from 25.5-60cm (Median: 29.4cm, Q_1: 28.05cm, Q_3: 32.9cm) and were detected in their respective sample sites throughout the winter (representative example demonstrated in Figure 5.3).

Calculating coastal ROM

35 fish were detected in locations outside of their respective sample site (78,837 detections); 24 fish tagged within the Dart estuary were detected within Salcombe harbour; Eight fish tagged in Salcombe harbour were detected in the Dart estuary; Three fish tagged in the Taw/Torridge estuary were detected by a third party receiver array (Swansea university-Figure 5.8). The straight line distance between the Dart estuary and Salcombe harbour (avoiding land) is calculated at 24.9km, between the Taw/Torridge estuary and the Swansea university acoustic receiver array is calculated as between 66.1-72.9km (dependent on which receiver within the Swansea university receiver array detected the tagged fish).

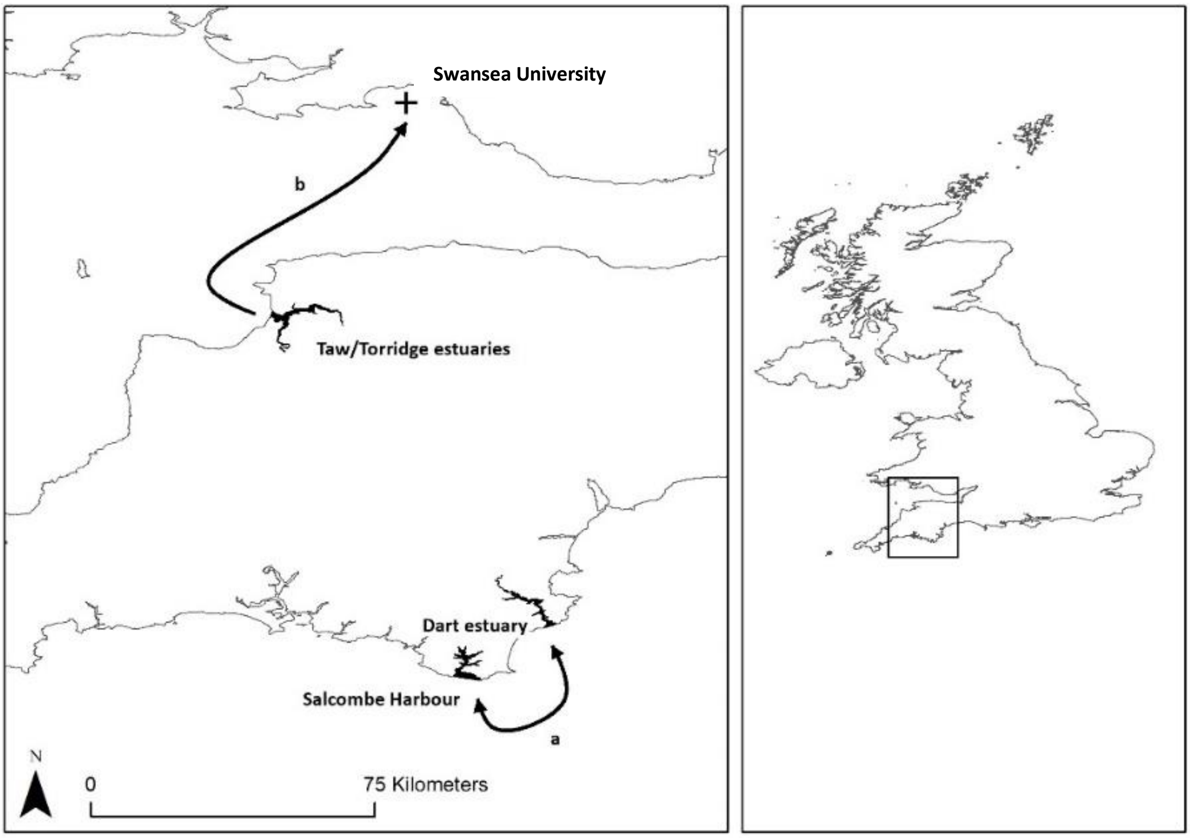

Figure 5. 8– Graphical representation of tagged fish movement between the host tagging sites to alternative locations. Please note actual route of travel is unknown. Arrows represents direction of movement. Movement "a" length = 24.9km, Movement "b" length =66.1-72.9km

Average ROM estimates from the current study were combined with those derived from O'Neill (2017). To meet the assumptions of normality a square-root transformation was applied to the data. A significant positive linear relationship was then found with fork length - LM: $F_{1,65}$: 23.715; R^2: 0.27; P: <0.001 (Table 5.4).

Table 5. 4 – Table of coefficients for linear model: ROM ~ Fork Length

Coefficients	**Estimate**	**Standard error**	**T value**	**P**
Intercept	0.047	0.056	0.844	0.402
Fork Length	0.006	0.001	4.870	<0.001

Estimated dispersal distance from sample site

To meet the assumptions of normality and homogeneity of variance a log transformation was applied to the estimated range values. Δ AIC scores indicated that inclusion of sample site improved the model performance, though Δ AIC scores indicated this effect was quite marginal (Table 5.5).

Table 5. 5- Candidate linear mixed effect models to test the effect of tagging site on dispersal distance

Model ID	Model notation	Δ AIC
1	***Dispersal distance ~ sample site + (1|tag ID)+ (1|* month/day*)***	0
2	*Dispersal distance ~ 1 + (1|tag ID)+ (1|month/day)*	2.81

During periods of tagging site residence, the LMM estimated that fish dispersed to a distance of 4.26 km (± 2.38 95% CI) from the Dart estuary, 3.17km (±2.06 95% CI) from Salcombe Harbour, and 3.81km (± 2.46 95% CI) from the Taw/Torridge estuaries (Table 5.6 & Figure 5.9).

Table 5. 6– Fixed and random effects of the random intercept linear mixed effect model for estimated dispersal distance from each sample site. Intercept, Std. Error and t value are derived directly from model outputs. The exponent of the intercept estimate and 95% confidence intervals are provided for ease of the reader

Fixed effects	**Estimate**	**Std. Error**	**t value**	**Exp (Estimate)**	**Exp (Confidence Intervals)**	
					2.5%	97.5 %
Sample site: Dart (Intercept)	8.359	0.051	165.241	4270.474	3869.191	4714.024
Sample site: Salcombe	-0.270	0.078	-3.485	3259.210	2538.076	4185.126
Sample site: Taw/Torridge	-0.123	0.072	-1.713	3775.696	2973.048	4794.949
Random effects						
Day/month	0.02					
month	0.007					
Tag ID	0.11					
Residual	0.37					

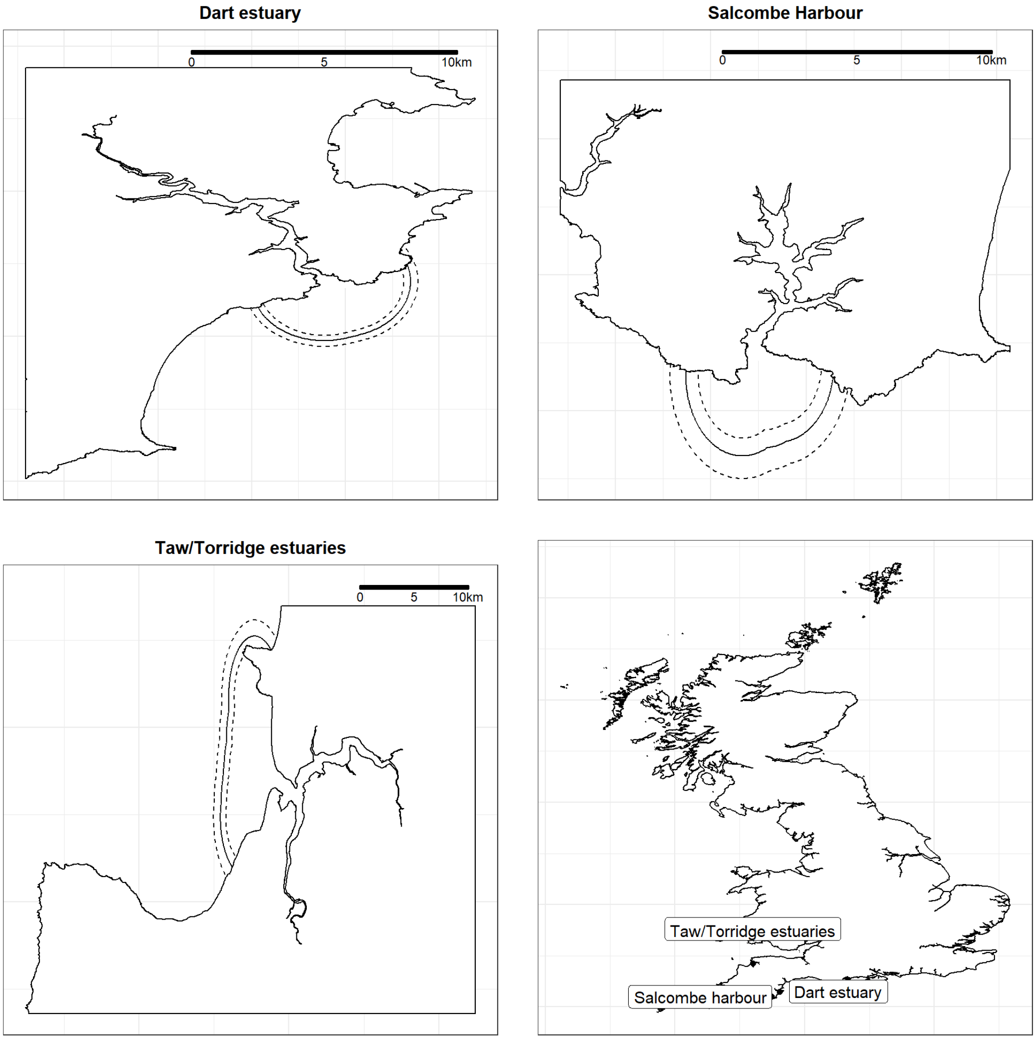

Figure 5. 9– Estimated dispersal range of tagged European bass from sample sites during periods of "Tagging site residence". Solid line represents exponent of model estimated intercept, dashed lines represent exponent of model 95% confidence intervals. Please refer to table 6.5 for model outputs and coefficients

5.6 Discussion

This study further demonstrates that European bass display localized movement patterns and high site fidelity across a range of sizes (Pickett & Pawson, 1994; Doyle *et al.,* 2017; O'Neill, 2017; Pontual *et al.,* 2019). While tagged fish did make wider movements, this publication estimates they are either within, or did not disperse further than a distance of 4.7km from, their respective sample site for 42.9-75.5% of the year. These results suggest that across the size range tagged within this study, European bass display spatially-structured movement characteristics across a significant proportion of the year.

Of particular interest was a lack of a statistical relationship between Tagging Site Residence (TSR) and fork length, and differences in TSR between sample sites. Suggesting that residency characteristics are not well-predicted by fork length, and may instead be driven by local environmental conditions (Ng *et al.*, 2007; Childs *et al.,* 2008). Furthermore 63% (89 out of the 133) of tagged fish were detected within their respective sample site throughout the winter. Pickett & Pawson (1994) suggested that 0-group European bass may seek thermal refuge in deep estuarine channels during winter, however older fish and larger 0-group may move out of estuaries during winter. The results from this study and anecdotal reports from recreational fishermen however suggest that European bass may be present within estuaries and coastal waters in the southwest UK throughout the year (Goodwin pers comms 2019).

5.6.1 Management implications

Consideration of local impacts on fish populations

Doyle *et al.* (2017), Pontual *et al.* (2019) and recent Data Storage Tagging (DST) campaigns conducted by the CEFAS, UK (unpublished results) have reported that sexually mature European bass make extensive spawning migrations across the Northeast Atlantic e.g. between the southern North and Celtic sea. These studies therefore demonstrate that European bass are capable of making large movements, however during summer months they are thought to display high fidelity to summer feeding grounds (Pickett & Pawson, 1994; Doyle *et al.,* 2017).

In the current study large absence periods were detected throughout the year, however 63% (84 out of 133) of tagged fish were not absent from their respective sample site for any period greater than 5.58days throughout winter. During this period European bass are thought to be mostly absent from coastal sites in the UK (Pickett & Pawson, 1994). These fish ranged in fork length from 25.5-60cm, and therefore represent both overwintering sub-adults and sexually mature fish which may skip a spawning migration (Pickett & Pawson, 1994; O'Neill, 2017). These data highlight that not all individuals migrate or move offshore in the winter, and that estuaries, embayments and coastal waters can remain highly utilized throughout the year. This study therefore emphasizes the importance of these ecosystems for this species (in particular by juveniles and sub-adults, Pickett & Pawson, 1994).

Estuaries, and the habitats they encompass, are however highly influenced by anthropogenic activity (Edgar *et al.,* 2000; Kennish, 2002; Lotze *et al.,* 2006; Airoldi & Beck, 2007; Vasconcelos *et al.,* 2007). This is largely thought to be a result of coastal; industrial, agricultural and/or residential development (Lotze *et al.,* 2006; Seitz *et al.,* 2014). It is estimated that as much as 85% of estuaries in the UK have been highly impacted by historic land claim, and while locally variable land claim is estimated to have resulted in 25-80% loss in estuarine intertidal habitats across the UK. As a result of sea level rise, continued habitat loss is predicted to continue at a rate of 0.2-0.7% per year (Lotze *et al.,* 2006).

While studies have failed to establish a direct link between estuarine habitat degradation and fisheries landings (Chesney *et al.,* 2000; Barnthouse *et al.,* 2013), indirect measurements of fish production in relation to lost or degraded habitats has suggested a substantial loss, ranging from 23-66%, in estuarine fish production relative to historic levels (66% loss - MClusky *et al.,* 1992; 23% loss - Rochette *et al.,* 2010). Furthermore, anthropogenic activities within estuaries e.g. farming on intertidal habitats or pollution events, have been reported to have localized negative impacts on fish feeding rates (Laffaille *et al.,* 2000) and/or cause them to absent in areas where prior abundance was recorded (Kelly, 1988; Jennings, 1990).

Within this context and as a result of the restricted movement of European bass evidenced with this study and the wider peer reviewed literature (Pawson *et al.,* 1987; Pickett *et al.,* 2004; Fritsch *et al.,* 2007; Pawson *et al.,* 2007; Green et al., 2012; Cambiè *et al.,* 2016; Doyle *et al.,* 2017; Pontual *et al.,* 2019) the impacts on local fish populations caused by further coastal development should be considered, in particular when it may affect impoverished fish populations such as European bass in the North Atlantic.

Spatial management for European bass

All the sample sites included within the current study are designated as Bass Nursery Areas, which seasonally prohibit targeted commercial fishing activity for European bass. While the effectiveness of BNA has yet to be formally assessed, Pickett *et al.* (2004) argued they benefit the fishery through increased survival of juveniles.

Further work should however be conducted to assess the benefits of spatial management for this species. This was outside the scope of the current manuscript, however, the restricted movement patterns identified within the current study and those reported by Green *et al.* (2012), Doyle *et al.* (2017) & Pontual *et al.* (2019) support the efficacy of spatial management and highlight the importance of coastal sites for this species (Pawson *et al.,* 1987; Pickett *et al.,* 2004; Green et al., 2012; Doyle *et al.,* 2017; Pontual *et al.,* 2019).

Wider management context

As a result of little evidence for genetically distinct populations across the Northeast Atlantic (Fritsch *et al.,* 2007), at the Inter-Bench Mark on New Species meeting 2012 (ICES, 2012) it was agreed by the European Commission that European bass in ICES divisions; 4b & c, 7.a, 7.d-h would be treated as one functional stock (ICES, 2012) (Figure 5.10). When put into context, European bass in the North Atlantic are currently assessed as a single management stock across approximately 597,230km^2 (Figure 5.10 – total area of ICES rectangles: 4.b–c, 7.a, and 7.d–h). However, within this study fish were not predicted to disperse wider than 4.7km^2 from their focal feeding site for significant proportion of the year. These results are also in agreement with the wider literature which demonstrate the restricted movement characteristics of this species and inter annual site fidelity to nursery sites, summer feeding grounds (Pawson *et al.,* 1987; Pickett *et al.,* 2004; Fritsch *et al.,* 2007; Pawson *et al.,* 2007; Green et al., 2012; Cambiè *et al.,* 2016; Doyle *et al.,* 2017) and spawning locations (Pontual *et al.,* 2019). This restricted movement introduces spatial structuring within the wider population, which even if genetic structuring is lacking should be considered within fisheries management policies (Cianelli *et al.,* 2013; Kritzer & Lui, 2014; Cambiè *et al.,* 2016).

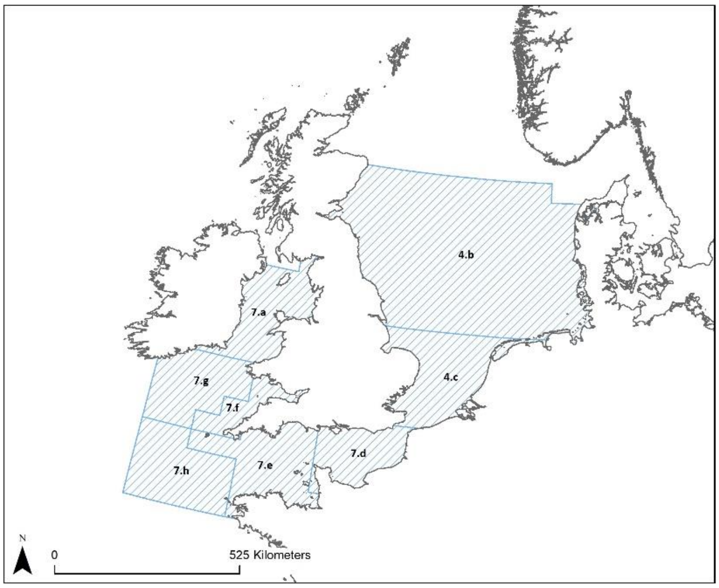

Figure 5. 10– ICES management units for European bass (*Dicentrarchus labrax*) in divisions 4.b–c, 7.a, and 7.d–h (central and southern North Sea, Irish Sea, English Channel, Bristol Channel, and Celtic Sea)

There is increasing evidence that current stock boundaries used to manage marine fisheries do not reflect the underlying biological and spatial structuring of numerous fish populations (Ruzzante *et al.,* 2000; Galley *et al.,* 2006; Wright *et al.,* 2006; Holmes *et al.,* 2008; Hutchinson*,* 2008; Reiss *et al.,* 2009; Poulsen *et al.,* 2011; Cianelli *et al.,* 2013; Kritzer & Liu, 2014; Neat *et al.,* 2013). As a result of either human-induced or environmental events, spatial structuring could result in variability in local population abundances (Cianelli *et al.,* 2013; Ares, 2016), which, if not reflected in management actions could have substantial impacts on the resilience of the wider population, as well as negatively impact on the dependent commercial and recreational fisheries (Cianelli *et al.,* 2013).

5.6.2 Study limitations

PELT-TREE classification method

The PELT-TREE classification method relies on change point detection to split/segment the absence period data into periods in which the mean duration of absence periods significantly changes. The user then determines if these segments relate to periods of "coastal" or "wider" movement. These segments are then used to train a supervised classification tree, which defines splitting rules. These splitting rules are then applied to the remaining data (i.e. the data not included within the supervision classification tree).

With no aprior knowledge of European bass residence/absence within coastal sites, determining which segments related to coastal or wider movement is semi-subjective. However, when put into context the classification tree defined "Coastal movement" as any absence period with a duration less than 5.58 days. This is equivalent to 97% of all absence periods recorded within the study. While the remaining 3% of absence periods had a high duration, coastal residence absence periods were well represented within the analysis.

Dispersal estimates

The dispersal estimates calculated as part of this study did not account for any tidal influences, which can cause significant variability in water velocity at different states of the tidal cycle (springs vs neap tides) and between sample sites. For example, in the Taw/Torridge estuary the tidal range can vary from 5-8m during spring and neap tides, whereas within the Dart estuary and Salcombe harbour the tidal range can vary between 4-5m. The resultant tidal flows are likely to significantly alter the potential range a fish could travel from each sample site during an absence period.

To account for the variable influence of tidal streams, the average ROM in coastal waters was calculated for each fish and used to estimate the potential range achievable during each absence period. It is acknowledged by the authors that when tidal streams are relatively high fish may be able to achieve a larger range from each sample site, and conversely a lower range during lower tidal streams. However, average ROM was thought to provide the best approximation of coastal movement speed. In future studies, further work should be conducted to incorporate tidal streams into dispersal estimates.

5.6.3 Conclusions

This study has contributed to the growing evidence that European bass display high residency to specific sites at various life stages. In particular, this study emphasis that juvenile and sub-adult fish are strongly associated with coastal and estuarine waters. The authors therefore recommend that management of European sea bass, and the potential impacts of human activity on this species, should be considered at a smaller geographic scale than that of current management units.

Further research should investigate the beneficial effects of spatial management for this species, and/or review the efficacy of existing spatial management such as designated Bass Nursery Areas.

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Chapter 6: Environmental drivers and spatio-temporal patterns in European bass (*Dicentrarchus labrax*) movement within coastal sites in the Southwest UK

Keywords

Acoustic telemetry, European bass, Water temperature

Contributions

All supervisors provided logistical and academic support: Elizabeth West, Tim Robbins, Shaun Plenty, Martin Attrill, Emma Sheehan.

Additional academic support provided by James Stewart of the Devon and Severn IFCA

6.1 Abstract

European bass are an ecologically and economically important demersal fish species commonly found in estuaries and coastal sites across Northern Europe. Since 2010, populations across the Northeast Atlantic have however rapidly declined. Due to the high potential for interactions with human activities, it remains highly important to document and identify fish movement characteristics in relation to the dynamic conditions experienced by these fish.

This study utilized acoustic telemetry to track 146 fish for an approximate period of 1 year, across three coastal sites in the southwest UK. A Generalized Linear Mixed Model (GLMM) with a binomial error structure was used to investigate environmental drivers for presence/absence within each sample site. When fish were present, detection rates were summarised across the tidal cycle and mapped throughout each sample site.

While fish movement was highly variable, local water temperature was the most important predictor for presence/absence in the two estuaries sampled. No detectable effect of water temperature was however found on fish presence/absence within Salcombe harbour. The presence of European bass throughout the year in Salcombe harbour and the seasonal stability of water temperature suggests that ria sites may provide winter refuge from sharp declines in water temperature and salinity. Tidally-driven movement was also apparent at all sites, although fishes were also able to maintain positions at particular locations.

The potential importance of ria systems for this species within winter has been highlighted, and results suggests their presence during winter should be accounted for in fisheries management policies.

6.2 Introduction

Coastal ecosystems, such as estuaries and embayments, represent important nursery and productive feeding sites for a variety of commercially and ecologically important fish species (Pickett & Pawson, 1994; Wennhage *et al.,* 2007; Seitz *et al.,* 2013). In temperate regions, these ecosystems host an array of habitats such as; submerged mud & sand flats, saltmarshes, seagrass beds, rocky & biogenic reefs, which provide shelter and important foraging opportunities for fishes (Pickett & Pawson, 1994). Estuaries and coastal ecosystems have however been described as "the most anthropogenically-degraded habitat-types on earth, with few estuaries in temperate and tropical regions existing in a near pristine state" (Edgar *et al.,* 2000). These ecosystems also experience high environmental fluctuations, which can have a high influence on both habitats and resident fish populations (Pickett & Pawson, 1994; Ladd et al., 2019). It is therefore imperative to increase our biological understanding of estuarine ecosystem functioning, and how dependent fish populations exploit these environments.

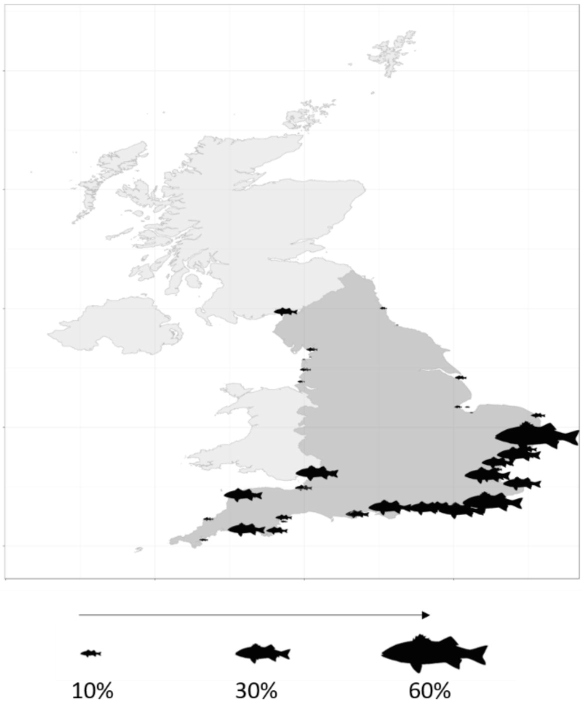

Figure 6. 1– Average relative abundance (presented as percentage of total catch) of European bass within Water Framework Directive Transitional and Coastal water bodies 1991-2019

European bass (*Dicentrarchus labrax*) is a dominant component of estuarine and coastal fish assemblages in Northern Europe (Pickett & Pawson, 1994) (Figure 6.1). Within these ecosystems European bass occupy a high trophic level throughout maturity, and therefore likely fulfil a crucial ecological role within these environments (Pickett & Pawson, 1994). The species is also highly valued for commercial and recreational fisheries, which in the UK have an estimated value of £5-6million at first sale (MMO,2020), and £100-200 million per year respectively (B.A.S.S, 2004 from Ares*,* 2016; Carroll*,* 2014; MRAG, 2014).

In 2010 the International Council for Exploration of the Seas (ICES) reported a dramatic decline in the North Atlantic European bass stock (ICES divisions 4.b–c, 7.a, and 7.d–h), which in 2016 declined below "safe biological limits", a threshold known as B_{lim}. In response to ICES advice the European Commission implemented a number of strict emergency "Technical Conservation Measures" which have imposed restrictions such as; banning targeted pelagic trawling during spawning periods, restrictions on commercial and recreational landings, and increasing the minimum landing size to 42cm total length (Ares, 2016). In 2019 ICES reported that the North Atlantic stock increased above B_{lim}, however relative to historic levels the population remains in a highly impoverished state and is still below maximum sustainable yield thresholds (ICES, 2019).

Within the UK, 34 separate sites (largely estuaries) were designated and protected as Bass Nursery Areas (BNA) (MAFF, 1990). Within site boundaries targeted commercial fishing for European bass is prohibited, there are also restrictions on recreational fishing activities such as prohibited use of specific baits e.g. live sand eel (*Ammodytes sp.*). These designated sites, and estuaries more widely, are highly utilized by this species at a variety of life stages (Kelley 1988; Pickett & Pawson, 1994; Laffaille *et al.,* 2001; Fonseca *et al.,* 2011; Green *et al.,* 2012; Cambiè *et al.,* 2016; Doyle *et al.,* 2017; O'Neill, 2017). During winter, European bass are thought to be largely absent from coastal sites as they conduct wide-ranging offshore spawning migrations when sexually mature, or seek thermal refuge in deeper water if immature (Pickett & Pawson, 1994; Doyle et al., 2017; O'Neill, 2017). Therefore BNA sites are predominantly protected on a seasonal basis, from 1st May – 31st October.

There however remains very little understanding on the spatio-temporal distribution of European bass, or how this varies in relation to the dynamic environmental conditions experienced by these fish in inshore areas (Pickett *et al.,* 2004). Using acoustic telemetry, Doyle *et al.* (2017) & O'Neill (2017) cumulatively tracked 74 individual European bass in coastal and estuarine sites in south Ireland. The studies found that tagged fish occupied small home ranges (0-5km) for extended periods however, fish movement also co-varied with environmental conditions such as tidal state and ambient light conditions.

Acoustic telemetry is a tracking technique which relies on the implantation within, or attachment of, an acoustic transmitter tag to a host animal. The transmitter tag emits a uniquely-coded ping, which can be detected when within range of strategically placed acoustic receivers. This technique has successfully been used to track a number of coastal and estuarine fish species including European bass e.g. *Alosa fallax* (Davies, Britton, Nunn *et al.,* 2020), *Anguilla anguilla* (Bultel *et al.,* 2014), *Dicentrarchus labrax* (Doyle *et al.,* 2017 & O'Neill, 2017), *Morone saxatilis* (Ng *et al.,* 2007), *Pomadasys commersonnii* (Childs *et al.,* 2008), *Sparus aurata* (Abecasis & Erzini, 2008).

As a result of the ecological and economic importance of this species and the diminished stock levels in the North Atlantic, it remains imperative to identify movement ecology and space use to support conservation and fisheries management policies. This is particularly important within inshore areas, such as estuaries or coastal embayments, where fish may interact with a range of anthropogenic activities or extreme environmental fluctuations.

Using acoustic telemetry the aim of this study is identify and report the spatio-temporal movement trends, and assess environmental co-variates for the presence/absence of European bass within multiple coastal sites in the southwest U.K.

6.3 Field Methods

6.3.1 Sample sites

European bass were tracked within three coastal sites in the southwest UK: The Dart estuary, Salcombe Harbour and the Taw/Torridge estuaries (Figure 6.2 & Table 6.1). From the closing line, the area of each site was; 8.32km^2, 6.34km^2, 14.6km^2 for the Dart estuary, Salcombe harbour and the Taw/Torridge estuaries respectively. All sites host a range of intertidal and subtidal habitats e.g. sediment based and tidally-swept rocky reefs. Max water depth varied from; 18m, 10m, 7m Below Chart Datum (BCD) for the Dart estuary, Salcombe and Taw/Torridge estuaries respectively. The main notable difference between the sample sites is the limited freshwater input to Salcombe Harbour, which is classified as a Ria system. The Dart estuary is also classified as a ria system, however unlike Salcombe harbour it still retains a major freshwater source/river - the river Dart.

All sample sites are designated and protected as Bass Nursery Areas (MAFF, 1990). Furthermore, the regional fisheries body (the Devon and Severn Inshore Fisheries and Conservation Authority) introduced a local byelaw prohibiting netting (e.g. gill netting) within all estuaries in their District from 8th May 2018 (D&S IFCA, 2018) offering further protection to local fish populations using these sites.

6.3.2 Tagging procedure

From June-August 2018, 146 European bass were captured predominantly by rod and line using plastic lures. Local anglers were recruited via word of mouth and advertisement of the project on online forums. Local anglers were instructed to target fish above a minimum size threshold of 25cm fork length. This ensured that the tag to body weight ratio experienced by the fish was less than 3%, which has been previously tested as suitable for this species (Lefrancois *et al.,* 2001, Bégout Anras *et al.,* 2003).

Upon capture, all fish were temporarily placed in a container filled with aerated seawater collected at the site of capture. Fish were then transported to a central tagging location (10-15minute transport time), where they were transferred to a 500litre aerated holding tank and left to acclimatise prior to tagging.

Each fish was anaesthetized with an induction dose of 70-100mg/l MS-222 (Tricaine methanesulfonate). Fish were then positioned dorsally on a V shaped cradle, where they were ram-ventilated with a maintenance anaesthetic dose of 30-40mg/l MS-222. Induction and maintenance anaesthetic varied on an individual fish basis to ensure the required depth of anaesthesia was achieved and maintained. A single 69khz Innovasea V92X transmitter tag (tag dimensions: 29*9mm, 4.7g – air weight) was implanted within the peritoneal cavity via a small incision (10-15mm) made slightly off the mid-ventral line between the pelvic fin and anus. Transmitter tags were programmed to emit a randomised uniquely-coded ping once every 80-160 secs and had an expected battery life of 803 days. Following tag implantation, the surgical site was closed using dissolvable sutures and/or medical grade adhesive. Analgesic was topically applied to the surgical site (Lidocaine 1% solution diluted to 1:10 with NaCl saline solution). Following recovery, fish were released as close to the capture site as logistically possible. Further methodological details are provided in Annex 1.

All tagging procedures were conducted under UK Home Office license P81730EA5 by personal license holders with PILC entitlement. Dispensation was also provided by the

Marine Management Organisation, Devon and Severn Inshore Fisheries and Conservation Authority, Natural England and by consent of the relevant land authority.

6.3.3 Acoustic telemetry receiver array

In total, 78 Innovasea VR2W and VR2Tx receivers were deployed (Figure 6.2 & Table 6.1). To achieve coverage of each site (which differed in size/area), each array comprised a different number of receivers; The Dart: 28, Salcombe harbour: 17, and the Taw/Torridge estuaries: 33. The receiver configuration in each array consisted of a series of detection gates which spanned the mouth of each sample site up to the mean tidal limit. Receiver gates had a mean spacing of 0.9km (± 0.09), 0.82km (± 0.4), 1.8km (± 1.6) for the Dart estuary, Salcombe harbour and the Taw/Torridge estuaries respectively. These were opportunistically attached to existing structures e.g. channel marker or moorings. The majority of receivers were deployed from June – August 2018. Upon successful detection of each tagged fish; the time, date and tag ID was recorded on the receiver. This was periodically downloaded every 3 months. Please note the duration of time receivers were deployed (the deployment duration) varied between receivers due to loss caused by: storm damage and theft (Table 6.2).

Table 6. 1–Physical characteristics of sites, area and centroid coordinates defined under article 17 of the Habitats Directive (provided by the UK statutory nature conservation bodies)

Sample site	**Waterbody type**	**Area (km^2)**	**Number of receivers**	**Deployment date**	**Latitude**	**Longitude**
Dart estuary	Ria[1]	8.32	28	22/08/2018	50.3822	-3.6061
Salcombe harbour	Ria	6.34	17	19/06/2018	50.2377	-3.7554
Taw and Torridge estuaries	Estuary	14.6	33	19/07/2018	51.0536	-4.1504

1 – The dart estuary is technically defined as a ria system, however still has significant freshwater input via the river Dart

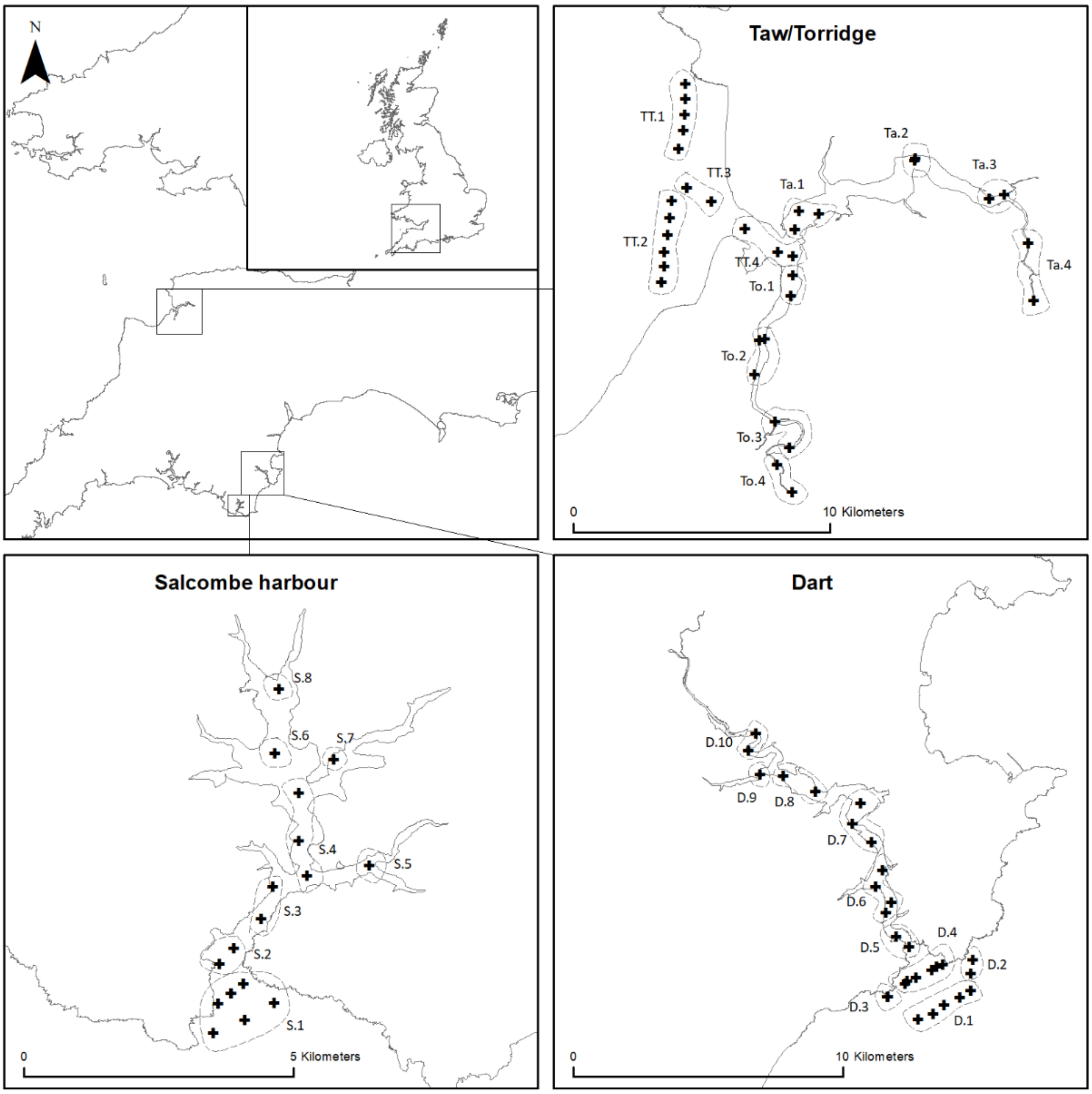

Figure 6. 2– Acoustic telemetry array within the Dart estuary (bottom right), Salcombe harbour (bottom left) and Taw/Torridge estuaries (top right). Black cross hairs represent position of acoustic receiver. Dashed lines and text annotations indicate receivers grouped into stations (see 6.4.2)

Table 6. 2- Receiver grouping station latitude, longitude and deployment information

Station ID	Latitude	Longitude	Number of receivers	Deployment date	Latest download date	Deployment duration (days)
			Dart estuary			
D.1	50.323345	-3.546654	5	22/08/2018	24/01/2019	155
D.2	50.332179	-3.531058	2	22/08/2018	24/01/2019	155
D.3	50.323335	-3.569906	1	22/08/2018	24/01/2019	155
D.4	50.333944	-3.557221	6	23/08/2018	09/07/2019	320
D.5	50.344243	-3.568457	2	23/08/2018	09/07/2019	320
D.6	50.362978	-3.579637	4	23/08/2018	09/07/2019	320
D.7	50.380965	-3.592631	3	23/08/2018	09/07/2019	320
D.8	50.395761	-3.621897	2	23/08/2018	09/07/2019	320
D.9	50.396986	-3.643136	1	23/08/2018	09/07/2019	320
D.10	50.410979	-3.644471	2	23/08/2018	09/07/2019	320
			Salcombe harbour			
S.1	50.213571	-3.769646	6	19/06/2018	04/07/2019	380
S.2	50.225033	-3.777894	2	19/06/2018	04/07/2019	380
S.3	50.235150	-3.764986	2	19/06/2018	04/07/2019	380
S.4	50.246556	-3.756459	3	19/06/2018	04/07/2019	380
S.5	50.240683	-3.742593	1	03/07/2019	04/07/2019	1
S.6	50.259623	-3.765283	1	19/06/2018	04/07/2019	380
S.7	50.259154	-3.746456	1	19/06/2018	04/07/2019	380
S.8	50.270768	-3.765514	1	04/08/2018	04/07/2019	334
			Taw/Torridge estuaries			
TT.1	51.106743	-4.245765	5	19/07/2018	10/11/2018	114
TT.2	51.057508	-4.253515	6	19/07/2018	10/11/2018	114
TT.3	51.079193	-4.233520	2	19/07/2018	08/07/2019	354
TT.4	51.061591	-4.200255	3	19/07/2018	08/07/2019	354
Ta.1	51.072900	-4.176889	3	20/07/2018	06/07/2019	351
Ta.2	51.092246	-4.119970	1	20/07/2018	06/07/2019	351
Ta.3	51.078219	-4.071353	2	20/07/2018	06/07/2019	351
Ta.4	51.064046	-4.053491	2	20/07/2018	06/07/2019	351
To.1	51.047359	-4.187349	2	21/07/2018	07/07/2019	351
To.2	51.021469	-4.201283	3	21/07/2018	07/07/2019	351
To.3	50.999673	-4.191441	2	21/07/2018	07/07/2019	351
To.4	50.978280	-4.186949	2	21/07/2018	07/07/2019	351

6.3.4 Range testing

In order to assess the detection efficiency of the acoustic telemetry receiver arrays within estuarine/coastal sties a range testing survey was conducted. A V9 range test tag, with comparable power output to those implanted within the fish, was deployed in a linear array of receivers in Salcombe harbour. Receivers were spaced approximately 150m apart (Figure A2.2 – Annex 2). The number of successful detections at varying distances from the range test tag were summarised.

High background noise is also known to cause interference with acoustic telemetry studies, because it inhibits the ability of the receivers to detect tagged animals (Reubans *et al.,* 2019). Guidance from the acoustic telemetry equipment provider (Innovasea), suggests the following:

- Environments with background noise <300mv typically provide very good - good detection rates
- Environments with background noise 300-650mv typically provide moderate detection rates, however detections will be reduced
- Environments with background noise 650-950mv typically provide low detection rates

Due to the highly tidal environment in which the receivers were deployed, turbulent water flow was thought to be the most likely cause of high background noise. In locations of high tidal flow e.g. estuary mouths, Innovasea VR2Tx receivers were deployed (Table 6.3, Figure A2.2 – Annex 2). These receivers are equipped with additional background noise sensors, which record noise in Millivolts (mv) at an hourly resolution.

Table 6. 3– Deployment location for acoustic receivers additional background noise sensors deployed with acoustic telemetry arrays in each sample site. Receiver station IDs are displayed spatially on Figure 6.2

Sample site	**Deployment location**		
	Latitude	**Longitude**	**Receiver station ID**
Dart estuary	50.340719	-3.562905	D.5
Salcombe Harbour	50.223432	-3.778764	S.2
Taw/Torridge estuary	51.066597	-4.208707	TT.4

To assess the relative levels of background noise within each sample site, background noise measurements were summarised as follows. For every tidal cycle throughout the monitoring period 12 equally-split bins were created based on the duration of that respective tidal cycle. The average background noise for each tidal bin was calculated and displayed using a polar bar plot. The relative levels of background noise were qualitatively described.

6.4 Data analysis methods

All data manipulation and statistical analysis was conducted using R version 3.6.0 (R Core Team 2019).

6.4.1 Overall fish detection trends

To remove any influence of a post-tagging response, the first two weeks of telemetry data was removed for each tagged fish (Doyle *et al.,* 2017). Each fish was then assigned to a 10cm size class (20-29.9, 30-39, >40cm fork length), detection records were then presented in an abacus plot with fish arranged by the length. This enabled visualization of broad scale patterns of presence/absence within each of the sample sites and how this varied with the size of tagged fish. Patterns in how often fish were detected in each sample site were then qualitatively described.

Previous results (Chapter 5) reported that tagged fish would enter each sample site and be present for an average duration of 0.64 days, which would be followed by a period of absence which had an average duration of 0.91 days. These results indicated that tagged fish were regularly entering and then exiting each sample site. Anecdotal reports from local fishermen suggested that fish may time arrival at or just before low tide, and follow the flooding tide landward into intertidal areas. Subsequent data analysis within this study was therefore focussed on a tidal cycle level. Tidal cycles were defined as the time from each low water to the proceeding/following low water (mean duration 12.4 hours/0.5 days - Figure 6.3). Spatio-temporal trends of fish detections within tidal cycles were identified, and environmental co-variates of fish presence/absence per tidal cycle were assessed.

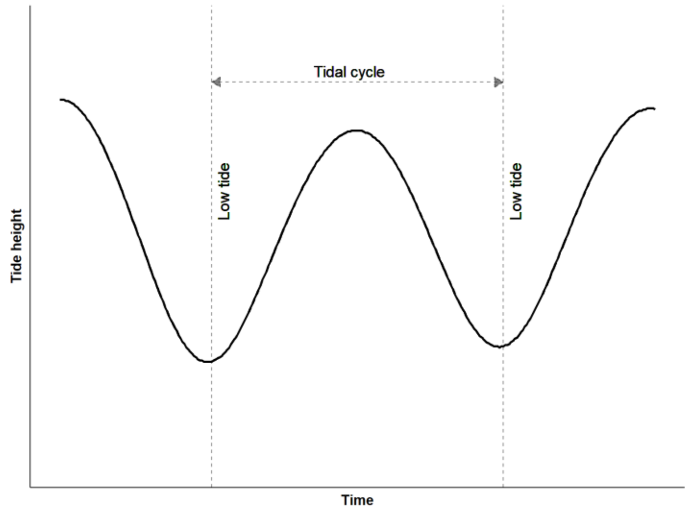

Figure 6. 3– Graphical definition of tidal phase used to define presence/absence of tagged fish within each sample site

6.4.2 Spatial-temporal detection trends of European bass within tidal cycles

In order to visualize the spatio-temporal trends in European bass movement/activity, the proportion of detections at various receiver stations were mapped. Data from individual receivers were grouped into "stations" (Figure 6.2 & Table 6.2), receiver grouping was based on the following:

1- Where receivers were deployed in relative close geographic proximity, data were grouped into a single station

2- Where receivers were part of single small detection gate (3-4 receivers), data were grouped into a single station. Large receiver gates were split into multiple coarse groups.

For every tidal cycle throughout the monitoring period, 12 equally-split bins were created based on the duration of that respective tidal cycle. The number of fish detections at each station in each tidal bin was calculated, and then converted to a percentage of the total detections at each station on the respective tidal cycle. The percentage detections were then averaged across all tidal cycles during the deployment duration of that particular station (Table 6.2).

The average percentage detections for each tidal bin at each station was displayed spatially as a polar bar plot overlaid on a map of each sample site. These plots were designed to demonstrate if fish were detected at each station, at what point in the tide this activity occurred. The relative differences in fish activity at each station was then qualitatively described.

6.4.3 Presence/Absence of European bass per tidal cycle

A Generalised Linear Mixed Model (GLMM) with a binomial error structure and logistic link function was used to test for European bass presence/absence (binary response = 1/0) within each tidal cycle in each sample site (R package "lme4", Bates *et al.,* 2015). The following were included as fixed effects to test for any detectable correlation with the tagged fish presence/absence:

- **Fork length:** The length of each fish, measured from the tip of the snout to the fork of the caudal fin.

- **Water temperature (^{o}C):** Average water temperature for each tidal cycle. Water temperature was monitored at 30 minute intervals using HOBO U24-002-C loggers at the mouth/seaward entrance of each sample site (Table 6.4, Figure A2.3 Annex 2).

Table 6. 4– Deployment locations of HOBO U24-002-C water temperature loggers within each of the sample sites

Sample site	Latitude	Longitude
Dart estuary	50.340871	-3.563458
Salcombe harbour	50.224283	-3.7792
Taw/Torridge estuaries	51.0772	-4.230317

- **Fractional tide height:** Maximum tide height within each respective tide cycle, relative to the maximum tide height recorded for each sample site over the monitoring period. Due to large differences in tidal range between sample sites (Table 6.7), actual tide height was correlated with sample site (data not shown here). Therefore a fractional tide height was included as a relative measure of tide height within each sample site.
- **Sun altitude:** The sun's average altitude (radians above the horizon) for each respective tidal cycle. Sun altitude was calculated using R Package "suncalc" (Thieurmel & Elmarhraoui, 2019) at an hourly resolution, an average was then calculated for each tidal cycle. Values -1:0 indicate a night time tidal cycle and 0:1 indicate a daytime tidal cycle.
- **Local rainfall:** A binary variable indicating the occurrence (1) or absence (0) of rainfall at a Met Office weather station local to each sample site (Table 6.5, Figure A2.3 – Annex 2) on the day of the focal tidal cycle. Due to geographic proximity, sample sites Dart estuary and Salcombe harbour shared data from the same weather station at Slapton.

Table 6. 5– Location of local weather stations for each of the sample sites

Sample site	Met office weather station name	Latitude	Longitude
Dart estuary + Salcombe Harbour	Slapton	50.29	-3.65
Taw/Torridge estuary	Chivenor	51.09	-4.15

All covariates were assessed for collinearity using variance inflation factors and multi-panel scatter plots (Zuur *et al.,* 2013). No significant collinearity was detected. All continuous covariates were standardized to have a mean of 0 using the following:

$$x(standardized) = x - mean(x)/sd(x)$$

To account for non-independence of samples due to repeated observations from each individual fish, tag ID was included as a random effect. Temporal autocorrelation in model residuals was assessed, and none was visually apparent within ACF plots.

Table 6.6 shows all covariate combinations included within the GLMM. The corresponding models were ranked according to Akaike Information Criterion (AIC). The model with the lowest AIC score was selected as the best fitting model. If AIC scores were <2 the model with the fewest terms was selected (Zuur *et al.,* 2013).

Table 6. 6– Combinations of fixed effects included within GLMM to assess environmental drivers for European bass presence/absence per tidal cycle in each of the; Dart estuary, Salcombe harbour, Taw/Torridge estuary

Model ID	Fixed effects	Model rationale
1	Sample site + fork length + water temp + fractional tide height + sun altitude +local rainfall	All co-variates
2	fork length + water temp + fractional tide height + sun altitude +local rainfall	All co-variates, sample site removed
3	Sample site + water temp + fractional tide height + sun altitude +local rainfall	All co-variates, fork length removed
4	Water temp + fractional tide height + sun altitude +local rainfall	All environmental co-variates
5	Fractional tide height + sun altitude +local rainfall	All environmental co-variates, water temperature removed
6	Water temp + sun altitude +local rainfall	All environmental co-variates, fractional tide height removed
7	Water temp + fractional tide height +local rainfall	All environmental co-variates, sun altitude removed
8	Water temp + fractional tide height + sun altitude	All environmental co-variates, local rainfall removed
9	Sample site + fork length + sample site: water temp + sample site: fractional tide height + sample site: sun altitude + sample site: local rainfall	Sample site, fork length and all environmental co-variates with sample site interactions
10	Sample site + sample site: water temp + sample site: fractional tide height + sample site: sun altitude + sample site: local rainfall	Sample site and all environmental co-variates with sample site interactions
11	Fork length + sample site: water temp + sample site: fractional tide height + sample site: sun altitude + sample site: local rainfall	Fork length and all environmental co-variates with sample site interactions
12	Sample site: water temp + sample site: fractional tide height + sample site: sun altitude + sample site: local rainfall	All environmental co-variates with sample site interactions
13	Sample site: fractional tide height + sample site: sun altitude + sample site: local rainfall	All environmental co-variates with sample site interactions, water temperature removed
14	Sample site: water temp + sample site: sun altitude + sample site: local rainfall	All environmental co-variates with sample site interactions, fractional tide height removed
15	Sample site: water temp + sample site: fractional tide height + sample site: local rainfall	All environmental co-variates with sample site interactions, sun altitude removed
16	Sample site: water temp + sample site: fractional tide height + sample site: sun altitude	All environmental co-variates with sample site interactions, local rainfall removed
17	Null model	No fixed effects

6.5 Results

6.5.1 Range testing

Range testing confirmed 60% ping detection at a range of 175m. The channel width of each tagging site rarely exceeds 300m, therefore positioning receivers at central locations within each channel detection of tagged fish was assumed to be reliable except in situations of high background noise.

Background noise readings at points of high tidal flow were variable between each of the sample sites. Throughout the tidal cycle in the Dart and Salcombe harbour background noise were on average below 291mv, indicating good detection rates across the tidal cycle (Innovasea, 2019). In the Taw/Torridge estuary however, average background noise ranged from 414-666mv. These results suggest that detections may be reduced, in particular during mid tidal phases at the deployment location of the noise sensor (Figure 6.4).

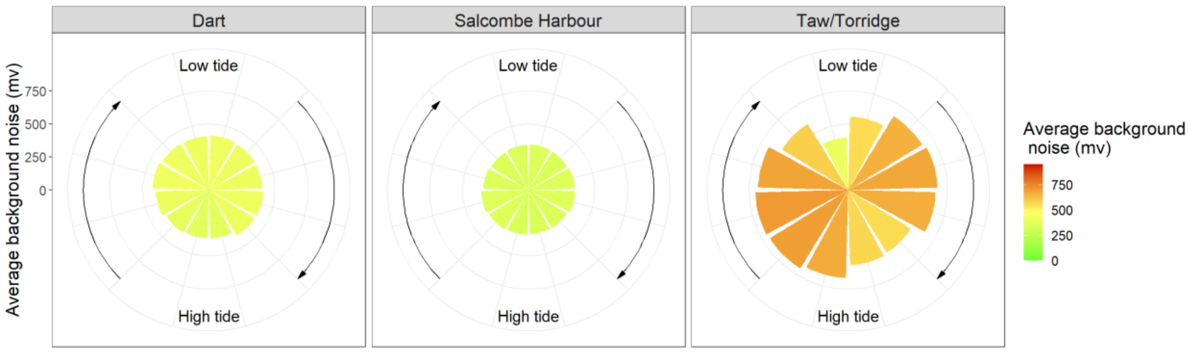

Figure 6. 4– Background noise readings from VR2Tx receivers deployed within each of the sample sites. Size and colour of bar plots scaled between 0-950mv to display average background noise levels relative to advice published by Innovasea (2019)

6.5.2 Environmental variables

Over the project duration seasonal trends in water temperature were observed, where water temperature ranged from 4.1-26.5°C between winter and summer. Differences in temperature profiles (Figure 6.5 -average daily water temperature with GAM smoother) were visually apparent between the sample sites. Within the Dart and Taw/Torridge estuaries greater fluctuations between winter and summer water temperatures occurred relative to Salcombe Harbour (Figure 6.5, Table 6.7). All other variables (fractional tide height, sun altitude and local rainfall) were comparable across sample sites throughout the monitoring period.

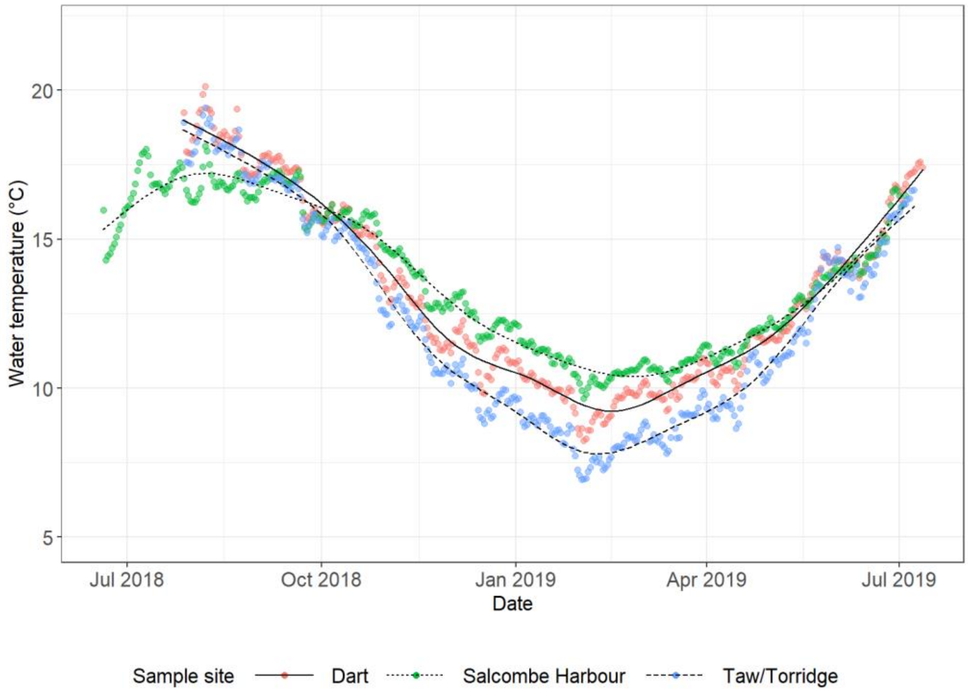

Figure 6. 5- GAM smoother applied to daily average water temperature records from each of the sample sites throughout the monitoring period.

Tidal range varied considerably between the sample sites: 5.3-8.8m Above Chart Datum (ACD). While actual tide height values were not included as a fixed effect within the GLMM, these are presented to provide context to the spatio-temporal detection trends.

Table 6. 7– Water temperature and tidal range recorded within each of the sample sites throughout the tracking period

Sample site	Water temperature (°C)			Tide height (m ACD)		
	Min	Max	Range	Min	Max	Range
Dart estuary	4.10	26.50	22.40	0.14	5.44	5.30
Salcombe Harbour	7.12	24.68	17.56	0.23	5.59	5.36
Taw/Torridge estuaries	4.70	26.00	21.30	-0.53	8.27	8.8

6.5.3 Overall fish detection trends

A total of 146 fish were tagged as part of the study (Dart estuary – 51; Salcombe Harbour – 46; Taw/Torridge estuary - 49). Fish length ranged from 26-60cm (fork length), with a mean of 33.5cm (range: 26 - 52), 30.9cm (range: 25.4 - 38.3) and 30.3cm (range: 25.2 - 60) within the Dart estuary, Salcombe harbour and the Taw/Torridge estuaries respectively (Figure 6.6).

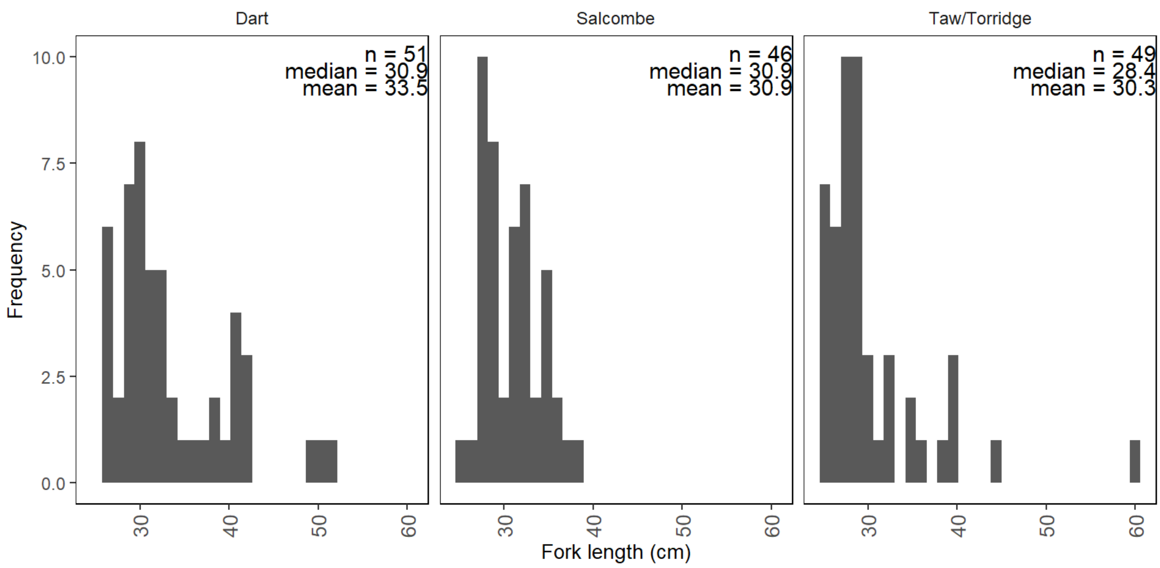

Figure 6. 6- Size distribution of tagged European bass captured within the Dart estuary, Salcombe harbour and the Taw/Torridge estuaries

No immediate mortality occurred as a result of the tagging procedure. However, 12 fish were not detected >30 days post-tagging procedure. Tag ID's that were not detected >30 days post-tagging procedure were removed from further analyses. One fish (Tag ID: 25249) was tagged on 31/07/2019 in Salcombe harbour and immediately left the tagging site. On the 14/10/2019 this individual was redetected in the Dart estuary for a period of 3 hours, 34 minutes, 12 seconds. This individual was not detected beyond the 14/10/2019. Due to the intermittent nature of this individual being detected it was also removed from subsequent analyses.

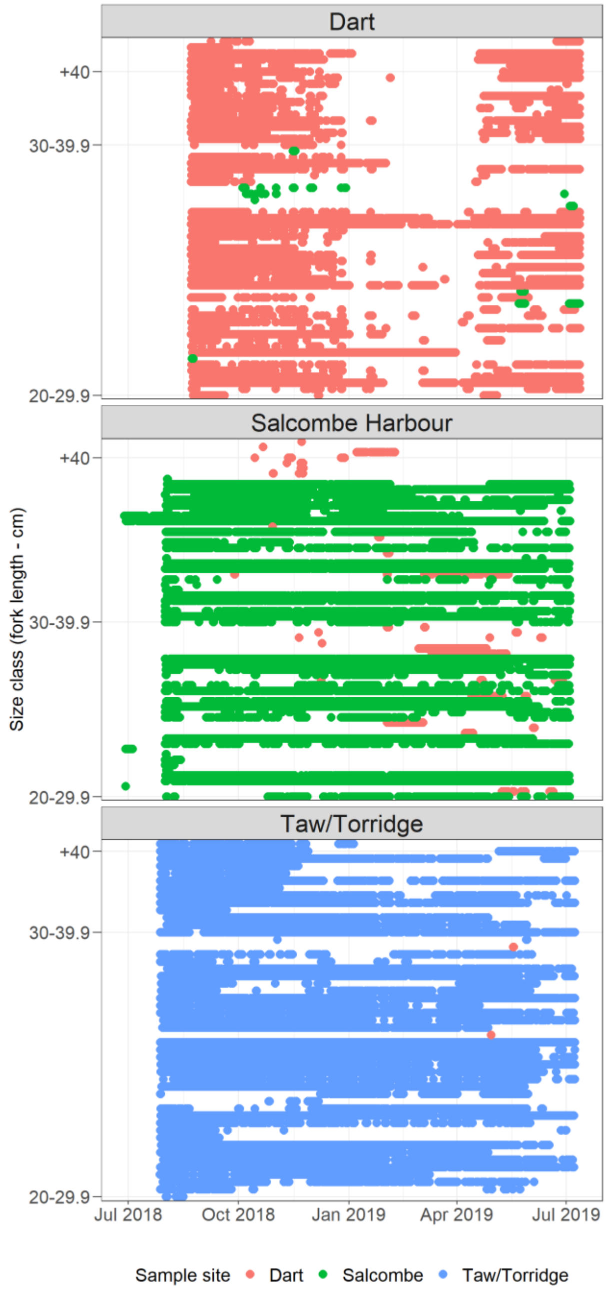

Figure 6. 7 - Abacus plot displaying presence/absence of tagged fish within each of the sample sites. Each row represents each individual fish. Sample site in which each respective fish was tagged is demonstrated with colour, and detections from the acoustic array in each sample site shown in each panel. Tagged fish split into 10cm size classes and arranged in ascending order on y axis.

Across all receivers, tagged fish were detected 2,724,548 times during the tracking period (Dart estuary – 321 days; Salcombe Harbour – 385 days; Taw/Torridge estuaries - 347). Detection rates were highest within Salcombe Harbour (1,418,688), second highest within the Dart estuary (848,917) and lowest within the Taw/Torridge estuaries (393,943) .

Seasonal differences in tagged fish detections were visually apparent between sample sites (Figure 6.7). Fish tagged within the Dart estuary were detected regularly from August 2018 – January 2019. From January-April 2019 tagged fish were largely absent from the Dart estuary, however 9 of the 51 fish tagged in the Dart were also detected in Salcombe harbour during this period (mean length: 31.38cm, range: 28.2-41.1cm) (Figure 6.7). Following May 2019 tagged fish were detected regularly within the Dart estuary until the end of the monitoring period. Fish tagged in Salcombe harbour were detected regularly throughout the monitoring period. From August 2018 – January 2019 & June – July 2019, 8 fish from Salcombe harbour were also intermittently detected within the Dart estuary (mean length: 30.73 cm, range: 27.5-33.2cm). In the Taw/Torridge estuary the majority of fish were detected regularly, however 10 fish were absent from December 2018 – May 2019. From May-June 2019, 2 fish tagged in the Dart estuary were detected in the Taw/Torridge estuary (fork length: 28.2 & 29.8cm).

6.5.4 Spatio-temporal detection trends

Spatio-temporal detection trends were highly varied throughout each of the sample sites (Figure 6.8, 6.9, 6.10, Table A2.1 – Annex 2). Generally fish detections occurred throughout the tidal cycle in both the Dart estuary and Salcombe harbour, whereas in the Taw/Torridge estuary detections were proportionally highest during the tidal extremes; at low and high tide (Figure 6.10, A2.1 – Annex 2). Within all of the sample sites there is evidence of proportionally higher fish detections at low tide near the seaward entrance (Figure 6.8: D.2, D.3, D.5. Figure 6.9: S.1. Figure 6.10: TT.3, A2.1 – Annex 2). With increasing landward distance into each of the sample sites, increasing detections occur at a later stage in the flooding tide (Figure 6.8, 6.9, 6.10, A2.1 – Annex 2). The receiver stations located either furthest landward (Figure 6.8: D.10. Figure 6.9: S.6, S.8. Figure 6.10: To.3, To.4, Ta.4, A2.1 –

Annex 2) or located in side-channels (Figure 6.8: D.9. Figure 6.9: S.7, A2.1 – Annex 2), recorded a higher proportion of detections at high tide or the tidal bins pre and/or proceeding high.

“Moderate” background noise was however recorded within the Taw/Torridge during mid tidal cycles, suggesting that the acoustic telemetry array underestimated fish activity during these periods. Therefore, the extreme nature of fish detections during high and low tide within the Taw/Torridge should be interpreted with caution.

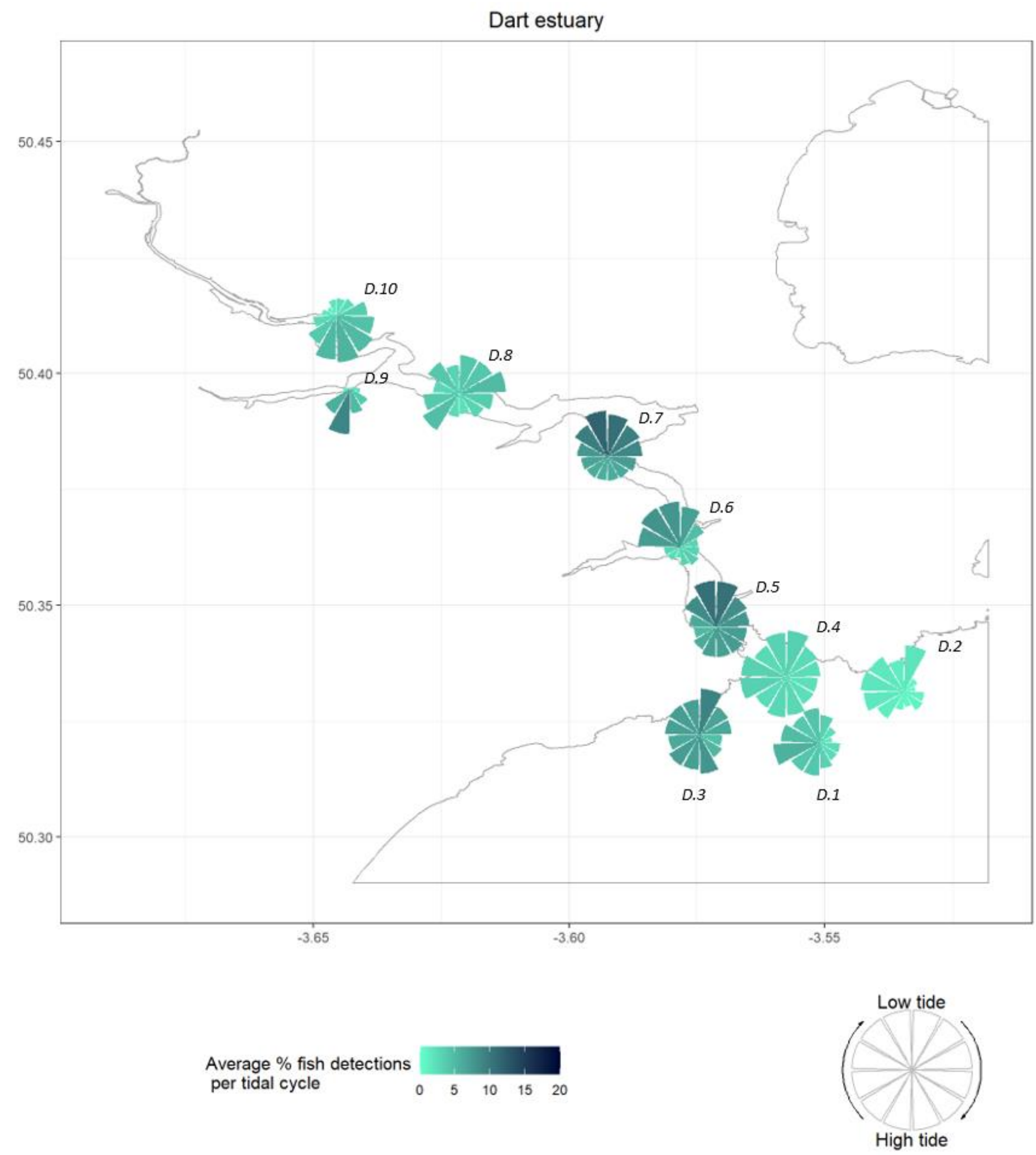

Figure 6. 8 - Average % of fish detections throughout the tidal cycle at various acoustic receiver stations within the Dart estuary. The size of the each bar represents the relative difference in detections across the tidal cycle at each station, bar charts are colour coded on the same scale

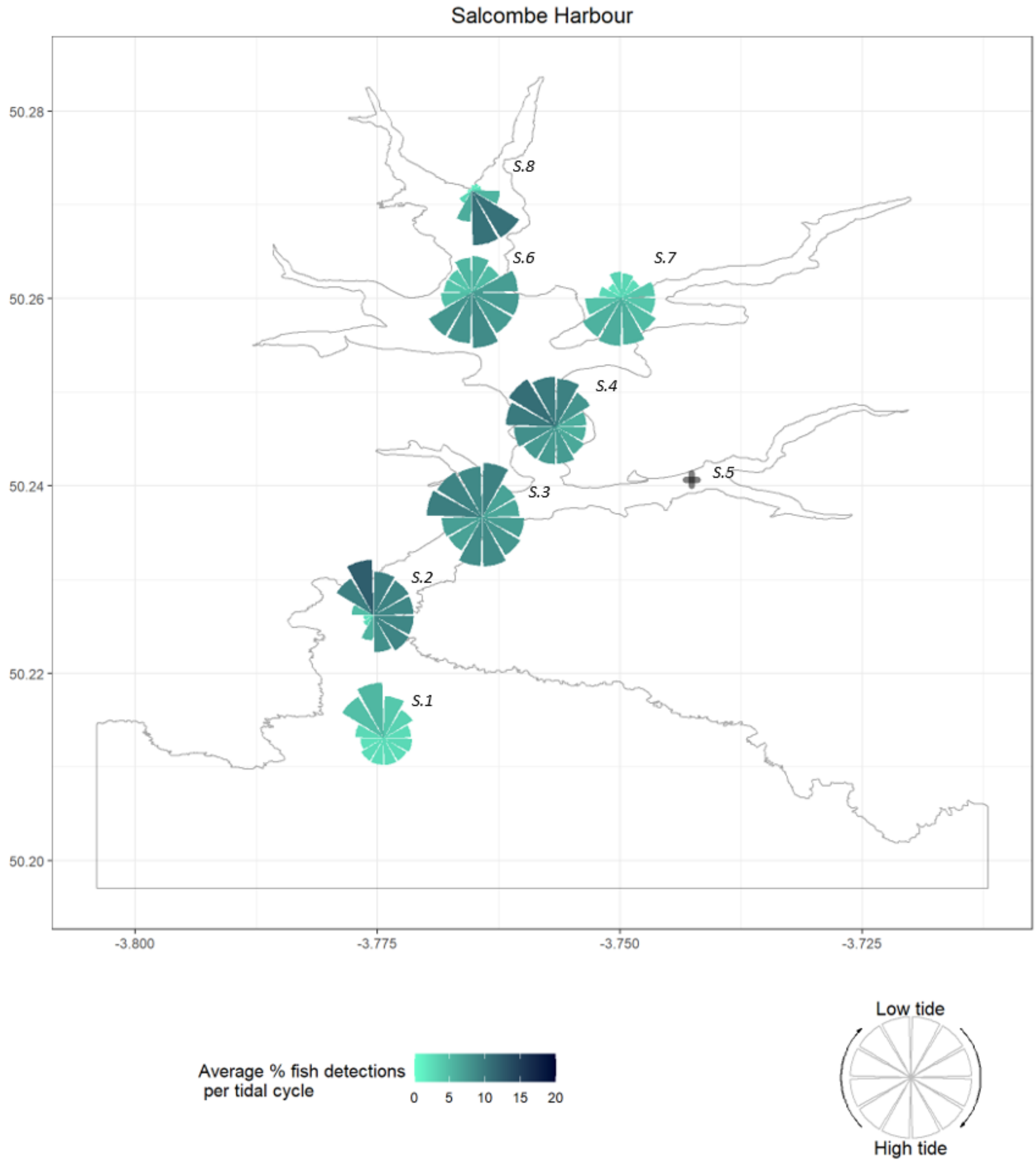

Figure 6. 9 - Average % of fish detections throughout the tidal cycle at various acoustic receiver stations within Salcombe harbour. The size of the each bar represents the relative difference in detections across the tidal cycle at each station, bar charts are colour coded on the same scale. Station s.5 is not shown as a result of a short deployment period (1 day)

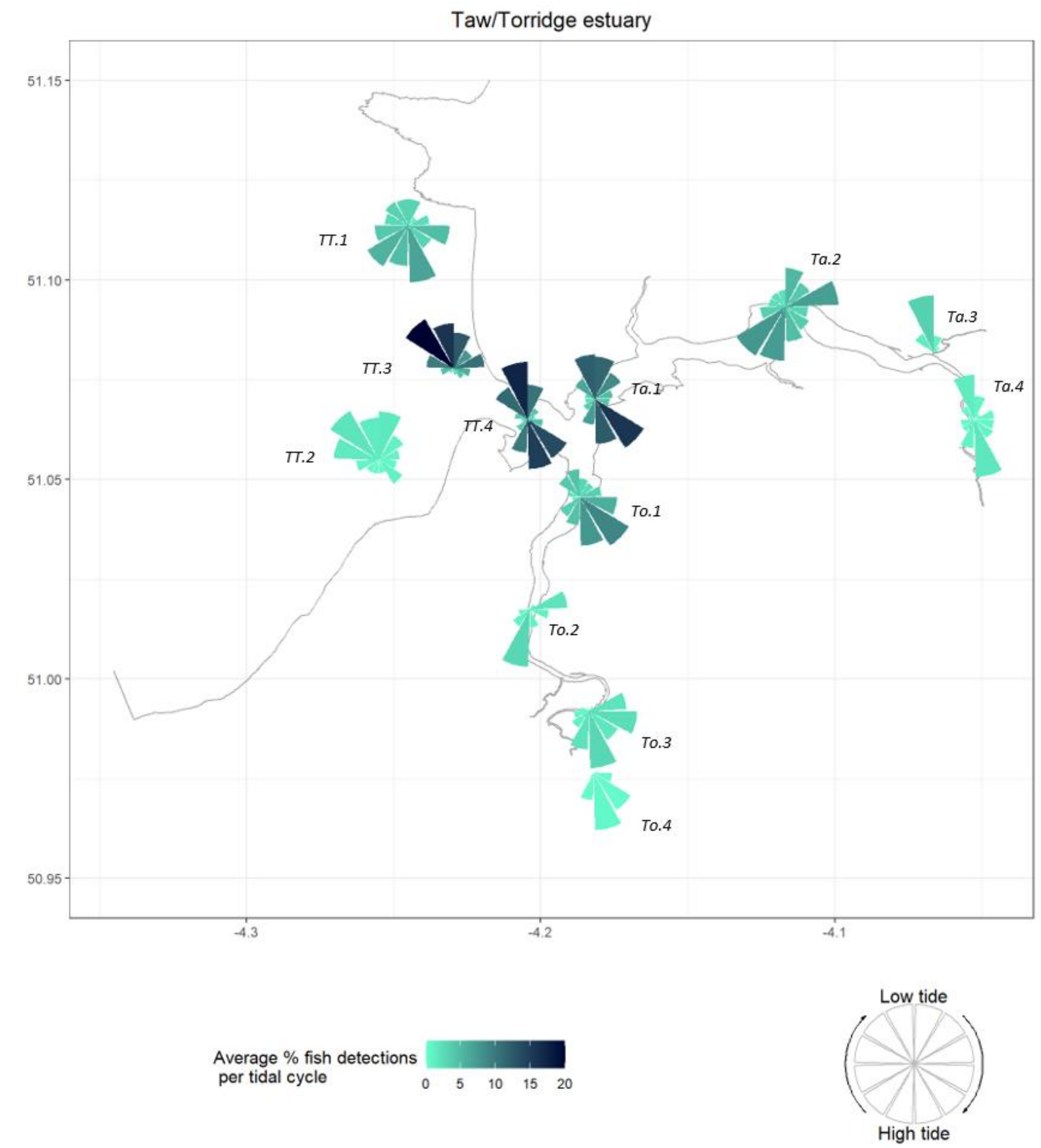

Figure 6. 10 - Average % of fish detections throughout the tidal cycle at various acoustic receiver stations within the Dart estuary. The size of the each bar represents the relative difference in detections across the tidal cycle at each station, bar charts are colour coded on the same scale

6.5.5 European bass presence/absence per tidal cycle

AIC scores indicated inclusion of sample site interactions significantly improved model performance, the best fitting model included sample site plus all possible environmental covariates with sample site interactions (Table 6.8). Inclusion of fork length did not improve the model fit so was not included as an explanatory variable.

Table 6. 8– Δ AIC scores for candidate GLMMs assessing covariates on the presence/absence of tagged European bass per tidal cycle

Model ID	Δ AIC	Model ID	Δ AIC
10	0	1	6524.97
9	1.83	4	6530.03
12	8.76	6	6537.62
11	32	2	6541.3
16	160.06	7	6579.31
14	256.43	8	6621.45
15	441.63	13	9889.87
3	6523.04	5	11436.86
		17	11936.11

Table 6. 9- Model results for best-fit GLMM model based on AIC rankings. Parameter estimates (β) in terms of log odds ratio. Exp(β) represents odds ratios for ease of reader and used to demonstrate effect size

Fixed effects	β ± SE	Exp(β)	Z	*p*
Sample site (Dart estuary) – intercept	**-1.11 ± 0.208**	**0.33**	**-5.334**	**<0.001**
Sample site (Salcombe harbour)	**1.877 ± 0.325**	**6.534**	**5.775**	**<0.001**
Sample site (Taw/Torridge estuaries)	**1.565 ± 0.303**	**4.783**	**5.166**	**<0.001**
Sample site (Dart): Water temperature	**1.941 ± 0.026**	**6.964**	**75.078**	**<0.001**
Sample site (Salcombe harbour): Water temperature	-0.009 ± 0.022	0.991	-0.392	0.695
Sample site (Taw/Torridge): Water temperature	**0.358 ± 0.014**	**1.431**	**26.238**	**<0.001**
Sample site (Dart): Fractional tide	**0.125 ± 0.019**	**1.133**	**6.577**	**<0.001**
Sample site (Salcombe harbour): Fractional tide	0.002 ± 0.02	1.002	0.094	0.925
Sample site (Taw/Torridge): Fractional tide	**-0.133 ± 0.013**	**0.876**	**-10.163**	**<0.001**
Sample site (Dart): Sun altitude	**0.243 ± 0.019**	**1.276**	**12.806**	**<0.001**
Sample site (Salcombe harbour): Sun altitude	**-0.16 ± 0.017**	**0.852**	**-9.272**	**<0.001**
Sample site (Taw/Torridge): Sun altitude	**-0.213 ± 0.016**	**0.808**	**-13.596**	**<0.001**
Sample site (Dart): Local rainfall	**0.199 ± 0.036**	**1.22**	**5.457**	**<0.001**
Sample site (Salcombe harbour): Local rainfall	**-0.298 ± 0.034**	**0.742**	**-8.828**	**<0.001**
Sample site (Taw/Torridge): Local rainfall	**-0.208 ± 0.029**	**0.812**	**-7.063**	**<0.001**
Random effect				
Tag ID	2.157			

The GLMM indicated that fish presence/absence varied between the sample sites, with a probability of 24.8%, 86.7% and 82.7% of tagged fish being present on any particular tidal cycle within the Dart estuary, Salcombe harbour and the Taw/Torridge estuaries respectively.

In the Dart and Taw/Torridge estuaries water temperature was the most important predictor for tagged fish presence/absence, with increasing temperature resulting in a higher probability of presence. Water temperature was however not found to be a significant predictor of presence/absence in Salcombe Harbour (Table 6.9 & Figure 6.11).

The second most important predictor was sun altitude, with statistically significant trends for all sample sites. Within the Dart estuary a positive trend was detected, indicating an approximate 11% higher probability of presence during daylight tidal cycles. In Salcombe Harbour and the Taw/Torridge the opposite was however detected with an approximate 14-18% higher probability of presence during night time tidal cycles (Table 6.9 & Figure 6.11).

While statistically significant relationships were detected for the remaining variables (Fractional tide height and local rainfall), relative to water temperature and sun altitude their effects were considered marginal (Table 6.9 & Figure 6.11).

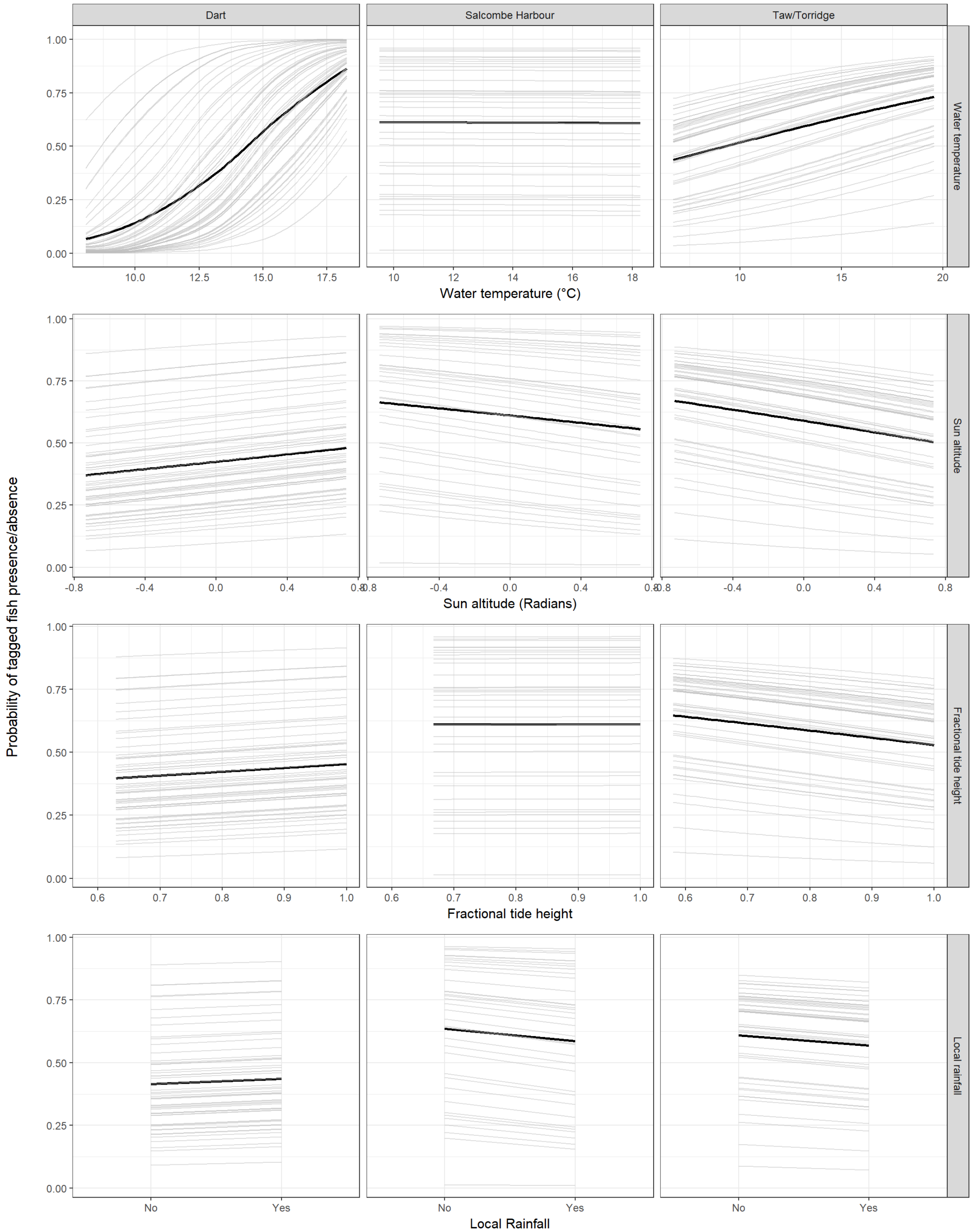

Figure 6. 11- Visual representation of optimal model, Mod 10 showing the effects of water temperature, sun altitude, fractional tide height and local rainfall on tagged fish presence/absence in each of the; Dart estuary, Salcombe harbour and the Taw/Torridge estuary. Solid line represents "group" response, greyed lines represent individual fish response

6.6 Discussion

Mapping of spatial temporal detection trends suggest that when tagged fish were present within the respective sample sites, there was evidence of movement associated with the tidal cycle however detections also occurred at a variety of locations irrespective of the tidal cycle.

The relationship between European bass presence/absence to environmental conditions is locally variable, however is principally driven by local water temperature.

6.6.1 Spatial-temporal detection trends

Within the Dart estuary and Salcombe harbour detections occurred throughout the tidal cycle, indicating that tagged fish were present across most of the spatial extent of these systems throughout the tide. Similar results were reported by Doyle *et al.* (2017), where tagged European bass would display residency to specific receivers within Cork Harbor for extended periods (average residency duration - 12 hours). This behavior was noted to occur repeatedly by Doyle *et al.* (2017), and suggests that European bass may hold position at specific locations within estuaries throughout tidal cycles.

Relative peaks in detections at low water near the seaward entrance of all the systems, and increasing proportional detections at later stages in the tide also suggests tidal associated movement. Notably higher proportions of detections at the most landward stations at high tide suggest these locations are mostly utilized at high tide. These results are supported by anecdotal reports from local fishermen, which suggest that either a proportion of the local fish population move with the tide and/or some individuals hold station at particular habitats which provide optimal feeding opportunities (Cooper 2016; Bradshaw, 2016). Similar tidal movement has also been reported for other estuarine fish species e.g. Thinlip mullet - *Chelon ramada* (Almeida, 1996) and Spotted grunter - *Pomadasys commersonni* (Childs *et al.,* 2008).

6.6.2 Environmental drivers for European bass presence/absence in coastal sites

Presence/absence of European bass was found to be principally driven by local water temperature. This has similarly been found for other estuarine-fish species worldwide (Morin *et al.,* 1992, Thiel *et al.,* 1995, Harrison & Whitfield, 2006; Childs *et al.,* 2008), and is known to be an important factor in European bass survival and growth (Pickett & Pawson, 1994). It should however be noted that the Dart and Taw/Torridge estuaries are fed by "spate rivers", which experience high freshwater input within the winter. Therefore, while not measured within the current study a combination of low salinity and/or seasonal declines in water temperature are likely to have highly influenced the tagged fish presence/absence in these sites.

No detectable influence of water temperature could however be found for European bass within Salcombe Harbour. Salcombe harbour is classified as a ria system within which there are no major freshwater sources, whereas the other sites are major estuaries within the region. The lack of major freshwater input within Salcombe harbour, is likely to influence local water temperature and salinity. Salinity was not measured, however the minimum water temperature recorded in Salcombe was 7.12 ^{o}C whereas the minimum recorded within the Dart and Taw/Torridge estuaries was 4.1-4.7^{o}C. This local variability in water temperature is likely to be driven by the lack of a major river flowing into Salcombe harbour, which may maintain more stable water conditions similar to that of the open coastline.

European bass is at it's Northern range limit within the U.K. (Pickett & Pawson, 1994), and are thought to negatively affected by cold water and therefore seek thermal refuge in winter (Pickett & Pawson, 1994). Therefore European bass are generally considered to be seasonally absent from U.K. coastal sites (Pickett & Pawson, 1994). Evidence from other studies suggests that 0-group bass may occupy deep estuarine channels, however older fish move into deeper coastal water to seek thermal refuge (Kelley, 1988 & 2002). Furthermore, while this species is considered to be euryhaline, abrupt salinity changes are known to cause mortality (Pickett & Pawson, 1994).

The evidence reported in this study suggests that in sites where water temperature (and potentially salinity) is more seasonally stable, such as rias, European bass may be present throughout the year. Furthermore, the presence of 9 of the 51 tagged fish from the Dart estuary within Salcombe harbour during the winter, possibly suggests that estuarine resident fish may utilize local coastal rias during extended periods of lower water temperature and/or salinity.

Prior acoustic telemetry studies conducted on European bass in Ireland (Doyle *et al.,* 2017; O'Neill, 2017), reported that the majority of fish were indeed absent during the winter (November-May/June) and were suspected of conducting offshore spawning migrations (Pickett & Pawson, 1994). Fish tagged by Doyle *et al.* (2017) & O'Neill (2017) were >37.2cm fork length, within the current study fork length ranged from 26-60cm (Overall mean: 31.6cm). Coastal winter presence of European bass recorded within this study may therefore be due to differences in the length of fish included between these studies. However, O'Neill (2017) reported that 11 out of 44 fish they tagged were repeatedly detected throughout the winter in coastal sites. These results therefore suggest that not all European bass conduct offshore winter spawning migrations.

6.6.3 Management implications

The results from this study suggest that European bass may be present in some coastal sites throughout the year. In particular ria systems may host both resident fish populations and those from surrounding estuaries.

Coastal rias are relatively common across the south UK e.g. Southampton Water, Poole Harbour, Chichester Harbour, and more generally across the Northern range limit of European bass e.g. Abers within Brittany, Northern France. Within the U.K. a number of rias are designated and protected as Bass Nursery Areas (MAFF, 1990), which are typically protected from commercial fishing activities on a seasonal basis (1st May – 31st October). Further work may therefore be needed to identify broader residency of European bass within rias, and assess if seasonal management of these sites provides adequate fisheries protection. Inshore fisheries authorities within the U.K. have recently implemented netting restrictions within estuaries and shallow embayments (e.g. Cornwall IFCA & The Devon and Severn IFCA), which reinforces and extends the protection afforded by BNAs. This has however not yet been universally adopted across the UK.

6.6.4 Conclusions

This study has provided detailed observations on the movement of European bass in relation to a suite of environmental variables within multiple coastal sites in the U.K.

Mapping spatio-temporal trends support the idea of tidal associated movement of European bass within estuaries and coastal sites, however individuals may also hold position at specific locations. Primarily presence/absence was found to be driven by local water temperature, however salinity may also be an important variable. Other variables including; sun altitude, tide height & daily rainfall were also found to have a significant effect though their influence was marginal.

The authors have highlighted that within coastal rias, water temperature and salinity is likely to be more seasonally stable than within estuaries. This should be accounted for within protective legislation such as BNAs and/or local fisheries byelaws.

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Chapter 7: General discussion

Combined across the chapters within this thesis various aspects of the inshore movement and feeding ecology of European bass have been assessed. The findings of which have broad scale implications for European bass fisheries management.

7.1 PhD focus

The thesis was specifically focussed on addressing the following objectives; 1) the feasibility of localised management/conservation policies to improve local European bass populations within the D&S IFCA district; 2) Identifying; movement, feeding and growth within estuarine habitats from a fisheries management perspective; 3) effectiveness of designated Bass Nursery Areas within the D&S IFCA's district.

The following is an overview of the research findings and how they relate to these objectives:

7.1.1 Assessing the feasibility of localised management/conservation policies to improve local European bass populations

Results from chapter 5 highlight high site fidelity and residency of European bass to specific designated Bass Nursery Areas (BNA) within the Devon and Severn Inshore Fisheries and Conservation Authority's (D&S IFCA) district. Combined with wider literature, these results support the evidence that individuals of this species occupy geographically specific locations across a range of ages (Pickett & Pawson, 1994; Pickett *et al.,* 2004; Green *et al.,* 2012; Cambiè *et al.,* 2016; Doyle *et al.,* 2017; O'Neill, 2017; Pontual *et al.,* 2019).

Fish movement was tracked within and adjacent to designated Bass Nursery Areas (BNA) over a period of 1 year. The results demonstrated that European bass regularly move in and then out of BNA boundaries. Fish were however estimated to remain within an area of <4.26km of BNA boundaries for a significant proportion of the year (42.9-75.5% - variable between sample sites). Fish were also detected making large absence periods (5.58-296 days), however, following large absence periods tagged fish returned to the same BNA and began to display repeated movements within and adjacent to the site they were tagged (Doyle *et al.,* 2017; O'Neill, 2017; Pontual *et al.,* 2019) (Figure 7.1). Therefore, while fish may make wider movements/migrations, the restricted nature of this species movement characteristics may introduce spatial structuring within the wider Northeast Atlantic stock.

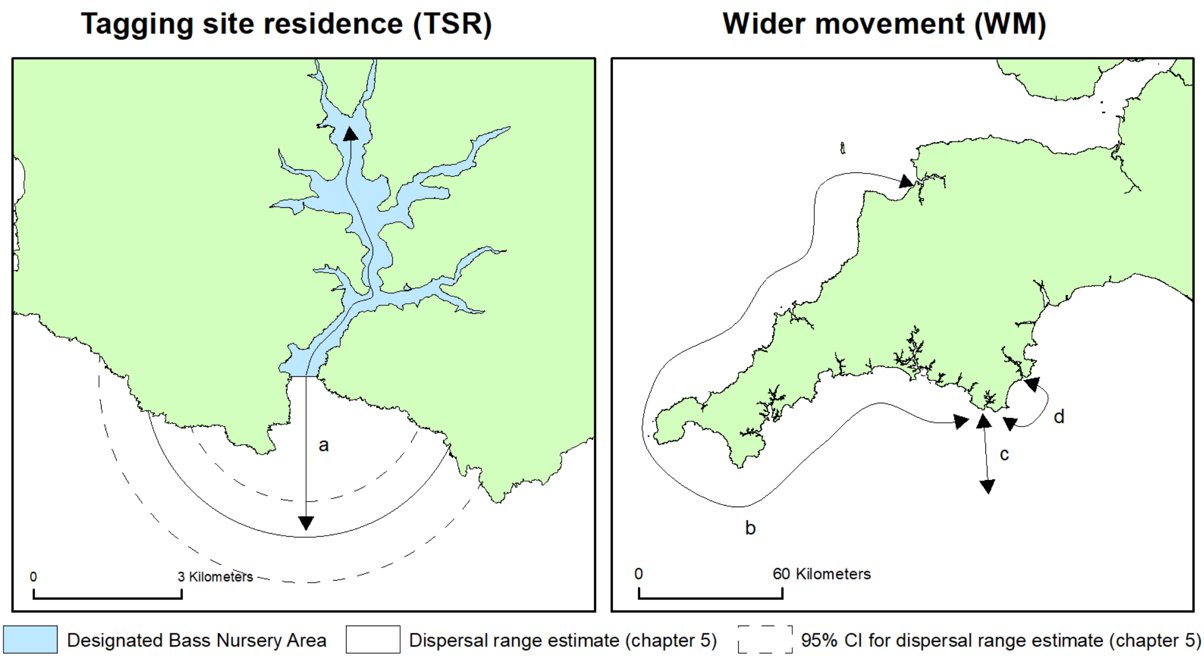

Figure 7. 1 –Example figure of European bass movement characteristics – "Tagging site residence" and "Wider movement" within and adjacent to sample site Salcombe harbour. Arrow "a" indicates tagging site residence: repeated short-range movement in and out of sample site (Dispersal distance varied between sample sites). Arrow "b" & "d" indicate recorded wider movement between all sample sites. Arrow "c" indicates wider movement: extended absence periods (5.58-296 days)

Current stock identity assessments have primarily used genetic markers to identify discrete populations across the species range. Results from which have reported low genetic diversity and suggested a single panmictic population across the Northeast Atlantic. The movement characteristics of this species, however, may create “meta-populations” which are geographically discrete (Akçakaya *et al.,* 2007) and persist at smaller spatial scales than current recognized management units (Cambiè *et al.,* 2016).

O’Neill (2017) argued that genetic homogeneity across the Northeast Atlantic may be due to two primary factors; 1) migration of sexually mature individuals across the region; 2) communal spawning locations combined with variable larval transport process to inshore coastal sites, and corresponding recruitment to the local area (Pickett *et al.,* 2004). It has also been highlighted that only a few genetic migrants per generation are sufficient to maintain genetic homogeneity across a population (Carvalho & Hauser, 1995; Naciri *et al.,* 1999; O’Neill, 2017).

Due to the low genetic diversity of European bass across the Northeast Atlantic, a single fisheries management stock has been identified by ICES. As stated previously this approach may underestimate the underlying population structure which is defined by locally restricted movement patterns. If the underlying population structure remains unacknowledged, current stock assessments may over or under estimate local geographic distribution and Spawning Stock Biomass. This would in turn have significant implications on; 1) assessing the relative impacts of fisheries management interventions, 2) assessing the impacts of human activities on local fish populations e.g. coastal development.

Therefore in light of the evidence provided within this thesis and within the wider literature, it is argued that a more regionalized fisheries management approach would be appropriate for the Northeast Atlantic European bass stock.

7.1.2 Identifying; movement, feeding and growth within estuarine habitats from a fisheries management perspective

Results from chapters 2-6 highlight that estuarine habitats support a range of commercial fisheries within the UK (Seitz *et al.,* 2014), in particular those exploited by the inshore commercial fishing fleet. More specifically, estuaries have been highlighted as sites of high significance for European bass as both nursery habitat (Pickett & Pawson, 1994), but also as feeding habitat for sexually mature fish (Cambiè *et al.,* 2016; Doyle *et al.,* 2017). Estuaries in general are however highly adapted by a range of human activities and environmental fluctuations, resulting in substantial alteration and/or loss of habitats (Chapter 2, Seitz *et al.,* 2014).

Estuaries and associated habitats (e.g. Saltmarsh) are protected under UK and European legislation, notably via a variety of site designations e.g. Marine Conservation Zones (Marine and Coastal Access Act 2009), Special Areas of Conservation (Council Directive 92/43/EEC) or Sites of Special Scientific Interest, Water Framework Directive (Council Directive 2000/60/EC), as well as indirectly through the Birds Directive (Council Directive 2009/147/EC). These designations are however often narrowly focussed, and very few protect habitats from a fisheries perspective. Furthermore, because a feature-based approach is currently applied to protected marine habitats a wide range of exploitative activities e.g. trawling, aggregate dredging, renewables development are often permitted within protected site boundaries (Roberts & Hawkins, 2012).

Concurrently management of commercial and recreational fisheries for European bass, are typically aimed at maintaining the Spawning Stock Biomass by sustainably limiting fishing pressure. Designated Bass Nursery Areas within the UK, do provide protection for fish that reside within designated sites (Pickett *et al.,* 2004), there however remains no consideration for habitat preservation upon which the fish are dependent. It has therefore been argued that future fisheries management should adopt a more holistic approach, which both maintain fish populations but also preserve and restore the habitats that are essential in supporting dependent fish populations (Seitz *et al.,* 2014; NOAA, 2019). This concept is commonly referred to as Essential Fish Habitat (ESH), and is fundamental principle of the Ecosystem Based approach to Fisheries Management (EBFM).

ESH is a general term for a particular habitat which provides a critical ecosystem service to a fish species; i.e. habitats that are necessary for fish; spawning, breeding, feeding, or growth to maturity (NOAA, 2019). EBFM and ESH are specifically mentioned within several high level European and UK conservation policies, notably; Marine Strategy Framework Directive (MSFD), Common Fisheries Policy (CFP) and Marine Spatial Planning Directive (MSPD).

Specifically within the reformed Common Fisheries Policy Reform it was proposed, that EU member states establish a network of marine reserves known as “Fish Stock Recovery Areas” (proposed under Amendment 68, Part 3, Article 7a) (Roberts & Hawkins, 2012).These areas are proposed to cover 10-20% of the territorial waters of EU member states to protect habitats which provide essential ecosystem services to commercially important fin and shell fish species. These areas could either add to the coverage of MPAs in the Natura 2000 network (sites designated as Special Areas of Conservation or Special Protection Areas), or existing Natura 2000 sites could also be designated as “Fish Stock Recovery Areas” (Roberts & Hawkins, 2012).

At the time of writing Fish Stock Recovery Areas have received little political and/or fisheries management attention, furthermore following Britain’s exit from the European Union it is uncertain if Fish Stock Recovery Areas will be introduced within the U.K. However, due to the evidence which suggests European bass highly utilize estuarine and coastal habitats at a variety of life stages, combined with human pressure on these ecosystems, further research and/or fisheries management attention should investigate the potential benefits of holistic approaches which both; 1) sustainably manage fishing pressure from commercial and recreational fisheries, 2) account for habitats which support the fishery.

7.1.3 Assessing effectiveness of designated Bass Nursery Areas within the D&S IFCA's district

Designated Bass Nursery Areas (BNA) were designed to provide spatial protection for undersized European bass (Pickett *et al.,* 2004). These site designations typically provide seasonal protection from any targeted commercial fishing, as well as prohibition of certain baits e.g. live sand eels within site boundaries (MAFF, 1990).

Pickett *et al.* (2004) conducted a mark re-capture study on juvenile European bass captured within 11 BNAs from 1988-1994. The study attached coded ID tags to 6438 individual bass, out of which 238 (3.7%) were recaptured. The time at liberty was variable however, 36% of recaptures occurred within 1 year of tagging, 58% within 2 years and 95% within 5 years. Typically the recapture locations were within 50km of the release site, and the authors argued that protection of nursery habits would therefore largely benefit the local commercial and recreational fisheries. Therefore, appropriate management of these sites may result in improved recruitment to local fisheries (Picket *et al.,* 2004).

In regard to the direct protection offered by BNA within the D&S IFCA district, chapter 5 highlights that all tagged fish regularly moved in and then out of the boundaries of the BNAs monitored. Residency periods from across the acoustic telemetry arrays had an average duration of 0.64 days, and absence periods had an average duration of 0.91 days when exhibiting Tagging Site Residence, and up to 256days when exhibiting the behaviour "Wider

Movement”. The results therefore suggest that tagged fish spent a higher proportion of time outside of BNA boundaries, where they are within the wider coastal environment. However, tagged fish were estimated to be within 4.26km of their host BNA for significant proportions of the year. Furthermore, the repeated nature of returns to the BNAs monitored suggests these sites are highly utilized by local fish populations.

A wide variety of environmental variables were found to correlate with fish presence/absence to BNAs, however water temperature and/or salinity was found to have the most significant effect. Fish which inhabited estuaries exhibited a clear seasonal trend with decreasing water temperature resulting in a lower probability of being present. Whereas, within Salcombe harbour, where there is no major freshwater inflow, no influence of water temperature could be detected. It is therefore argued that the seasonal stability of water conditions within Salcombe harbour, resulted in a high proportion of fish maintaining residency throughout the winter.

The overwintering behaviour of European bass to coastal sites is not currently reflected within BNA legislation, with 85.2% of designated BNA offering only seasonal protection. Many other designated BNAs are coastal rias and/or natural harbours which experience limited freshwater input e.g. Poole harbour, Southampton water. Within the D&S IFCA district specifically, a local byelaw was introduced in May 2018 which prohibited the use of net fishing within all estuaries and coastal rias. It is therefore argued that the seasonal element of BNA legislation may not be relevant to the residency characteristics of local European bass populations within these sites.

While variable between sites, European bass display residency to designated Bass Nursery Areas throughout the year. BNA site designations typically protect European bass on a seasonal basis, throughout spring – autumn. The seasonal element of the protection offered by BNA designations may not be relevant to the residency characteristics of local fish populations, particular in sites which experience low fresh water inflow.

7.2 Key messages

The key research findings of this thesis are as follows:

1. European bass exhibited spatially restricted movement patterns which may create meta-populations across the wider North Atlantic. Regionalized fisheries management policies may be appropriate.
2. Estuaries and associated habitats are highly utilized by European bass at a variety of life stages. The habitat requirements of European bass should be integrated within management policies.

7.3 Broader research and fisheries management applicability

Survey work associated with chapters 3, 5, 6 focussed on three survey sites within the southwest UK: The Dart, Salcombe harbour and Taw/Torridge estuaries. 75% of estuaries and ria systems across England and Wales have an area of <11 km^2 (Figure 7.2). The Dart (8.7km^2), Salcombe harbour (11.2 km^2), Taw/Torridge estuaries (14.1 km^2) are therefore considered to be representative of wider estuaries and ria systems across England and Wales which have not been directly sampled as part of this thesis.

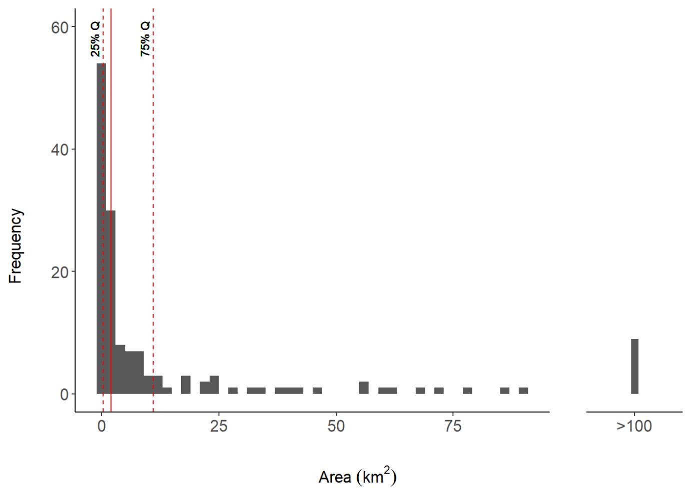

Figure 7. 2 – Area (km^2) of estuaries and ria systems within England and Wales. Solid red line indicates median, and dashed lines represent interquartile range (Data source: JNCC, 2018).

Human activity, hydrology and the extent of seabed habitats (e.g. saltmarsh, mudflats, reef) vary between the sample sites included within this thesis, and more broadly across coastal sites across the UK, therefore local environmental conditions may influence growth patterns and movement characteristics of local fish populations. However, due to consistent fish behavioural and growth patterns observed across the survey sites studied within this thesis, it is likely that these results are more broadly applicable than just to coastal sites within the D&S IFCA district. Therefore, while there is a focus on European bass populations within the D&SIFCA district within this thesis, the results have broad scale applicability for European bass populations outside of the D&S IFCA district.

7.4 Future research recommendations

The following is recommendations of future research:

1. Chapter 3 highlighted that factors which influence growth within the first year could have significant implications for latter European bass growth, survival and recruitment. Further studies should identify the broad scale feeding ecology of Age0 European bass across a range of nursery sites, and the factors which influence feeding success and corresponding growth.
2. Chapters 5 & 6 highlighted the high residency of European bass to estuarine and costal sites. While these sites are protected via a variety of designations e.g. Bass Nursery Areas and Special Areas of Conservation, a range of human activities may still be permitted which could negatively impact local fish populations. Space use within Bass Nursery Areas should be monitored to assess activity hot spots for a range of different age classes.
3. BNA boundaries are high varied between sites (Figure 7.3). Due to the repeated nature of tagged fish returning to their respective BNA, further work should

investigate appropriate BNA boundary demarcation to mitigate movement bottlenecks at the entrance to designated sites.

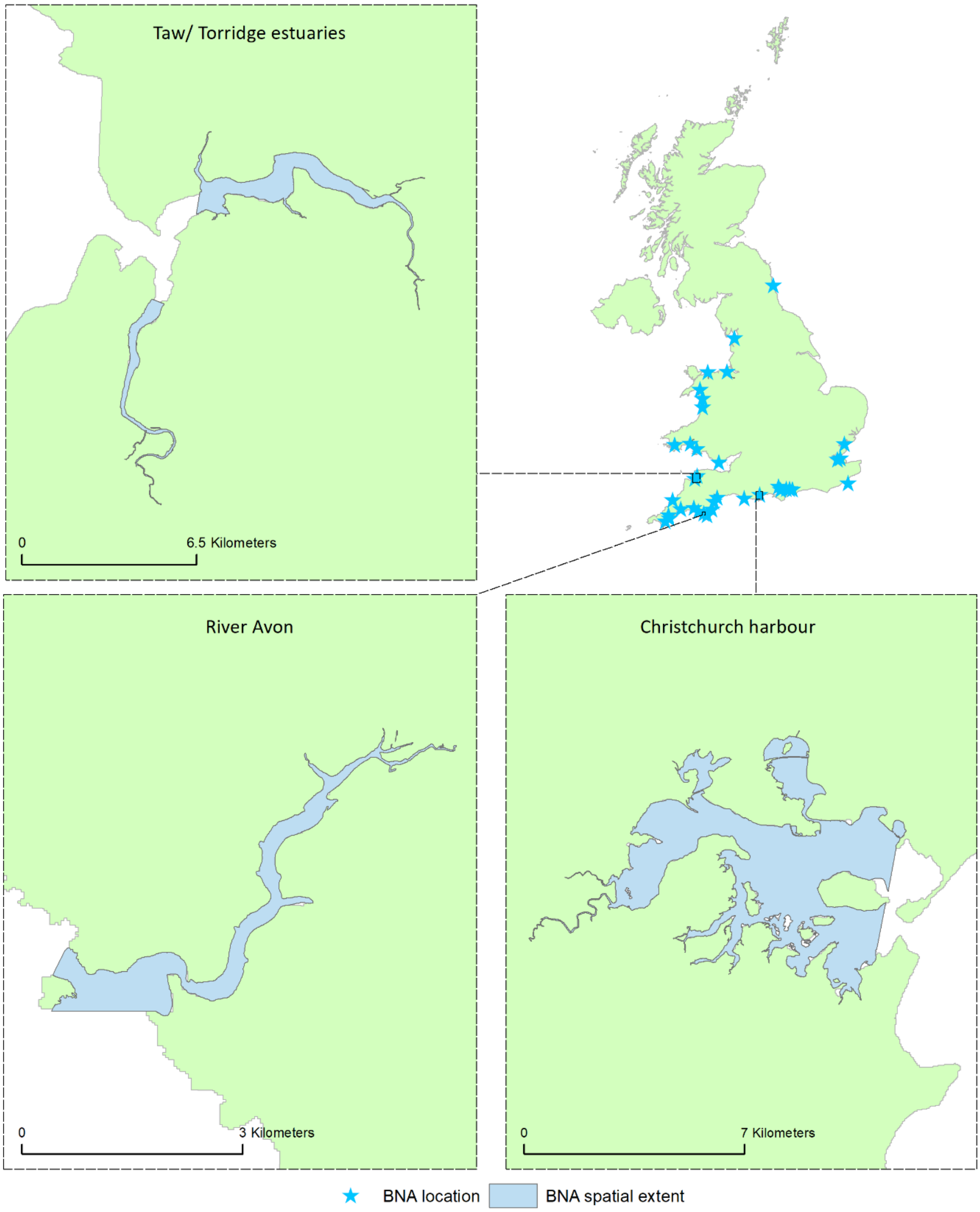

Figure 7. 3– Spatial extent of three designated Bass Nursery Areas across the UK. Shown to demonstrate variability in site boundary demarcation

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Annex 1 –Tagging protocol

A1.1 Introduction

The following text is the methodology used to tag European bass with acoustic telemetry tags. Data from this tagging effort was used to inform the outputs of chapters 5 & 6. All tagging procedures were conducted under Home office license P81730EA5 by personnel license holders with PILC entitlement. Dispensation was also provided by the Marine Management Organisation, Devon and Severn Inshore Fisheries and Conservation Authority, Natural England and by consent of the relevant land authority.

A1.2 Methods

A1.2.1 Tagging sites

European bass were captured, tagged and then released within three estuarine/coastal sites in the Southwest UK; the Dart estuary, Salcombe harbour and the Taw/Torridge estuaries (Figure A1.1). The Dart and Taw/Torridge are major estuaries in the region with large freshwater influences and an approximate area of 8.3 and 14.6km^2 respectively. Salcombe harbour is a coastal ria system with very limited freshwater input and an approximate area of 6.3km^2.

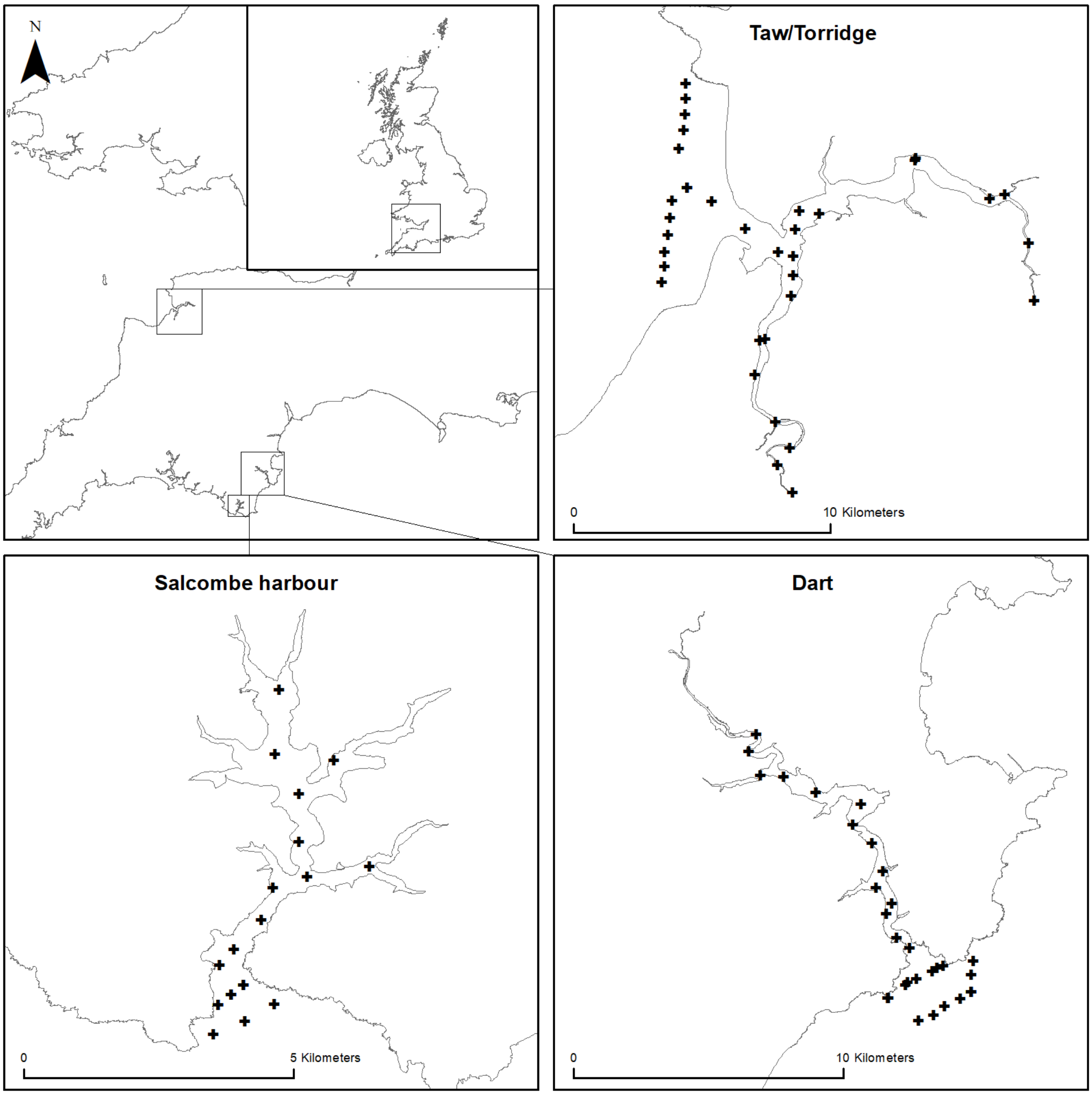

Figure A1. 1 - Acoustic receiver deployment locations within Salcombe harbour (bottom left), Dart (bottom right) and Taw/Torridge estuaries (top right)

A1.2.2 Acoustic telemetry receiver array

In total 78 Innovasea VR2W and VR2Tx receivers were deployed throughout the coastal sites: Dart estuary - 28; Salcombe harbour – 17; Taw/Torridge estuaries – 33. These were opportunistically attached to existing structures e.g. channel marker or moorings. This receiver configuration consisted of a series of detection gates which spanned the seaward entrance to the approximate mid-spring limit of each system. All receivers within Salcombe Harbour were deployed prior to all tagging procedures on 19th June 2018. Due to logistical constraints within the Dart and Taw/Torridge estuaries receivers were deployed approximately two weeks following tagging.

Range testing confirmed 60% ping detection at a range of 175m. The channel width within all coastal sites rarely exceeds 300m at high tide, therefore by positioning receivers at central locations within each channel, detection of tagged fish was assumed to be reliable. Upon successful detection of each tagged fish; the time, date and tag ID was recorded on the receiver. This was periodically downloaded every 3 months throughout the project.

A1.2.3 Tagging procedure

From June-August 2018, 146 European bass were captured within the three coastal sites, predominantly by rod and line using plastic lures. Innovasea V9-2L (29*9mm, 4.7g – air weight) tags were the acoustic transmitter tags used within the current study. The correct tag to animal size was determined following recommendations within Lefrancois *et al.* (2001) and Bégout Anras *et al.* (2003), in which it is estimated that European bass could accommodate a tag burden equivalent to 3.5% of the total body weight of the fish without causing a detectable negative effect on feeding or growth. Weight measurements were not directly collected during this study however using the following weight to length relationship for European bass (Henderson, 2017 – unpublished data), the tags in this thesis were equivalent to 1.55% of the smallest fish included:

$$\text{Weight (g)} = 1\text{E-}05 * \text{Length (mm)}^{3.0735}$$

Upon capture, each fish was given a visual pre-operative assessment as detailed in table A1.1. Any individual which scored 2 or less was removed from the study. Fish were then transported via an aerated covered bucket to a central tagging location (10-15minute transport time), where they were transferred to an aerated 500litre holding tank prior to tagging. Stocking density within all holding tanks was kept below 5kg/m^3. To ensure water conditions were stable and similar to the environment the fish were captured; water temperature, salinity, dissolved oxygen and ammonia (NH_3) measurements were taken every 20minutes. If necessary, fresh salt water was pumped to holding tanks from adjacent to the tagging site to stabilise or refresh the water conditions in the holding tanks.

Table A1. 1 - Visual pre and post-operative assessment scoring criteria

Score	Criteria
1	**Extremely poor physical condition.** Severe scale loss, heavy haemorrhaging, moribund
2	**Poor physical condition:** Moderate scale loss, torpid/lethargic behaviour
3	**Moderate physical condition**: Minor scale loss, minor haemorrhaging or blemishes present and alert behaviour
4	**Good physical condition**: No major scale loss, minor haemorrhaging or blemishes present and alert behaviour
5	**Excellent physical condition**: No major scale loss, alert swimming behaviour, with no significant blemishes

Each fish was individually anaesthetized with an induction dose of 70-100mg/l MS-222 (Tricaine methanesulfonate). Due to low Ph of MS222 a buffering agent (Sodium bicarbonate) was added until an equivalent Ph to sea water was achieved. Due to variability in the time taken for individual fish to progress through the stages of anaesthesia (Table A1.2), induction dose was adjusted on an individual basis to decrease the time taken to achieve surgical plane anaesthesia. Once surgical plane anaesthesia was achieved (Table A1.2), fish were placed upside down on a V shaped cradle where they were ram-ventilated with a maintenance anaesthetic dose of 30-40mg/l MS-222 (Plus a buffering agent – Sodium bicarbonate). Maintenance anaesthetic dose varied to ensure fish were held at surgical plane anaesthesia during the tagging procedure.

A single 69khz Innovasea V92L transmitter tag was implanted within the peritoneal cavity via a small incision (10-15mm) made slightly off the mid-ventral line just above the pelvic fin (Figure A1.2). Transmitter tags were programmed to emit a uniquely-coded ping at a randomized rate of once every 80-160secs, and had an expected battery life of 803 days. All transmitter tags were independently checked for successful transmission of tag ID prior to implantation. Following tag implantation, the surgical site was closed using dissolvable sutures. If the surgical site was not adequately sealed medical grade adhesive (e.g. vetbond) was also applied. The sealed surgical site was then topically flushed with a pre-prepared analgesic solution (Lidocaine 1% solution diluted to 1:10 with NaCl saline solution) with an approximate dose of 1ml/kg.

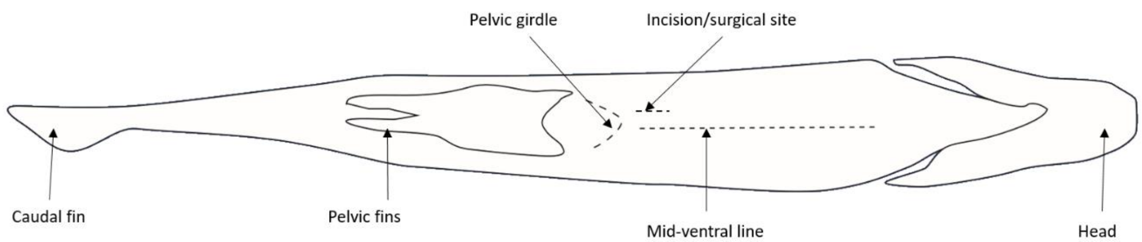

Figure A1. 2 - Annotated diagram of ventral view of European bass, including mid-ventral line and position of surgical site

The fork length of each fish was measured, and scales collected for age determination. Each fish was then gently lowered into an oxygenated 500litre recovery tank, within which a maximum stocking density of 5kg/m^3 was maintained. During recover, the gills of each fish were ram-ventilated with water from the holding tank using a handheld water pump until recovery stage 2 was achieved (Table A1.2). Once recovery stage 2 was achieved each fish was monitored for a minimum period of 1 hour to observe any latent signs of post-operative signs of distress. Enrichment was provided in the pre-operative holding and post-operative recovery tanks in the form of locally collected floating seaweed. To ensure water conditions were stable within recovery tanks; water temperature, salinity, dissolved oxygen and ammonia (NH_3) measurements were taken every 20 minutes.

Table A1. 2 - Visual symptoms for varying stages of anaesthesia and corresponding recovery. Table adapted from Sneddon (2012)

	Stage	**Plane**	**Level of Anaesthesia**	**Equilibrium**	**Visual symptoms**
Anaesthesia	1		Lightly sedated	Normal	Disorientated behaviour
	2		Excited	Difficulty	Excited and “struggled” swimming behaviour
	3	1	Light anaesthesia	Difficulty	Loss of consciousness begins, equilibrium maintenance begins to fail, most reflexes (pedal, corneal, palpebral) absent, gill ventilation regular.
		2	Surgical anaesthesia	Loss	Equilibrium lost, muscles relaxed, most reflexes (vestibulo-ocular, pedal, palpebral, corneal) absent, regular gill ventilation
		3	Deep anaesthesia	Loss	Intercostal muscles relaxed, gill ventilation slow and irregular, ability to maintain respiration is endangered, pupillary light reflex may be slow or absent, vestibulo-ocular reflex is absent
	4		Overdose	Loss	Too deep, all muscles, including diaphragm and intercostal muscles are paralyzed. All reflexes absent
Recovery	4			Loss	Fish is unconscious or semi-conscious and in the lateral recumbency. Some reflexes are still diminished or absent (tested via tail pinching)
	3			Difficulty	Fish is conscious and all reflexes are present, but may not be able to control it’s body position
	2			Normal	Fish can either maintain itself in a sternal position, or can move independently, but may still show symptoms of sedation or erratic swimming behaviour
	1			Normal	All functions are normal, unless altered directly by the experimental procedure

Lidocaine/Lignocaine was selected as an appropriate analgesic agent based on; 1) advice from the within-institute Named Veterinary Surgeon (NVS) and Named Animal Care and Welfare Officer (NACWO), 2) it's prior successful use in laboratory trails with a variety of fish species (Park *et al.,* 1988; Sneddon, 2012), and 3) the reduced risk of negative side effects when compared to Non-Steroidal Anti Inflammatory Drugs (NSAID) or Opioids (Wolfensohn & Lloyd, 2008).

Lidocaine/Lignocaine is a local anaesthetic agent, which has analgesic properties by acting locally on a variety of nerve cell functions e.g. inhibition of action potentials, blocking sodium channels (from Sneddon, 2012 - Peck & Hill, 2004; Rang et al., 2007). "Pain" sensation is therefore locally inhibited by blocking nociceptive transmissions (Sneddon, 2012).

A1.4 Results

A total of 146 fish were tagged as part of the study. Fish length ranged from 25.2-60cm (fork length), with a mean of 30.7cm (± 0.471 SE). All metadata for each individual tagged fish is presented within Table A1.3. Induction anaesthetic dose varied from 70-100 mg/L, however for 95.2% of the tagged fish 80-90mg/L were sufficient to induce anaesthesia to a surgical plane. Maintenance anaesthetic varied from 30-40 mg/L, however for 96.6% of the fish 40mg/L was sufficient to maintain surgical plane anaesthesia. Induction time typically varied from 2-24.14minutes, however on average was achieved in 6.50 minutes (± 0.31 SE). Please note one individual achieved surgical plane anaesthesia in 49 minutes (tag ID: 25172). This individual was however tracked for a subsequent period of 338.5 days suggesting no lasting negative affect. The duration of the surgical procedure varied from 0.5-26.2minutes, however was completed in an average time of 3.8 minutes (± 0.19 SE). No immediate mortality occurred as a result of the tagging procedure.

Table A1. 3 – Tagging metadata for European bass equipped with acoustic telemetry tags. Please note n/a means not recorded.

Fish information				Surgeon ID	Surgical scores		Anaesthetic dose (MS222 mg/L^{-1})		Induction time (mins)	Surgery duration (mins)
Transmitter ID	Fork length (cm)	Sample site	capture date		Pre-op	Post-op	Induction	Maintenance		
25131	35	Salcombe	28/06/2018	surgeon 1	5	5	70	30	00:05:17	00:08:00
25132	26.7	Salcombe	28/06/2018	surgeon 1	5	5	70	30	00:07:23	00:12:00
25133	28.1	Salcombe	28/06/2018	surgeon 5	5	5	70	30	00:04:52	00:31:00
25134	35	Salcombe	27/06/2018	surgeon 1	5	5	70	30	00:03:29	00:07:00
25182	36.5	Salcombe	01/08/2018	surgeon 3	5	4	80	40	00:07:08	00:11:00
25183	31.4	Salcombe	01/08/2018	surgeon 3	5	5	80	40	00:04:22	00:07:00
25233	30.9	Salcombe	31/07/2018	surgeon 3	5	5	80	40	00:05:37	00:09:00
25234	27.1	Salcombe	31/07/2018	surgeon 5	5	5	80	40	00:05:45	00:09:00
25235	30.8	Salcombe	31/07/2018	surgeon 5	5	5	80	40	00:02:59	00:06:00
25236	28.1	Salcombe	31/07/2018	surgeon 5	5	5	80	40	00:08:19	00:08:00
25237	28.6	Salcombe	31/07/2018	surgeon 5	5	5	80	40	00:05:43	00:08:00
25238	28.9	Salcombe	31/07/2018	surgeon 5	5	4	80	40	00:10:18	00:11:00
25239	31	Salcombe	31/07/2018	surgeon 5	5	5	80	40	00:10:18	n/a
25240	29	Salcombe	31/07/2018	surgeon 3	4	5	80	40	00:07:46	00:11:00
25241	27.5	Salcombe	31/07/2018	surgeon 3	4	5	80	40	00:05:57	00:10:00
25242	32.4	Salcombe	31/07/2018	surgeon 3	5	5	80	40	00:18:42	00:23:00
25243	27.5	Salcombe	31/07/2018	surgeon 3	5	5	80	40	00:13:54	00:17:00
25244	27.2	Salcombe	31/07/2018	surgeon 3	5	5	80	40	00:08:37	00:12:00
25245	28.8	Salcombe	31/07/2018	surgeon 3	5	5	80	40	00:07:36	00:11:00
25246	29.6	Salcombe	31/07/2018	surgeon 3	5	5	80	40	00:06:10	00:10:00
25247	31.3	Salcombe	31/07/2018	surgeon 3	4	5	80	40	00:05:07	00:09:00
25248	32.2	Salcombe	31/07/2018	surgeon 3	5	5	80	40	00:06:41	00:10:00

25249	31	Salcombe	31/07/2018	surgeon 3	5	5	80	40	00:08:03	00:14:00
25250	35.3	Salcombe	31/07/2018	surgeon 5	5	5	80	40	00:04:38	00:08:00
25251	29	Salcombe	31/07/2018	surgeon 5	4	5	80	40	00:06:08	00:09:00
25253	27.5	Salcombe	31/07/2018	surgeon 5	5	5	80	40	00:05:28	00:08:00
25254	36.4	Salcombe	31/07/2018	surgeon 3	5	5	80	40	00:11:17	00:16:00
25255	33.2	Salcombe	31/07/2018	surgeon 5	5	5	80	40	00:04:09	00:08:00
25256	29.2	Salcombe	31/07/2018	surgeon 5	4	5	80	40	00:03:58	00:07:00
25257	32.3	Salcombe	31/07/2018	surgeon 5	5	5	80	40	00:05:45	00:08:00
25258	34	Salcombe	31/07/2018	surgeon 5	4	5	80	40	00:07:56	00:11:00
25259	29.5	Salcombe	31/07/2018	surgeon 5	5	5	80	40	00:07:38	00:11:00
25260	25.4	Salcombe	31/07/2018	surgeon 5	5	5	80	40	00:03:28	00:08:00
25261	27.3	Salcombe	31/07/2018	surgeon 5	5	4	80	40	00:03:21	00:06:00
25262	31.9	Salcombe	31/07/2018	surgeon 5	5	5	80	40	00:05:43	00:09:00
25263	32.6	Salcombe	31/07/2018	surgeon 5	5	5	80	40	00:05:36	00:08:00
25264	32.9	Salcombe	31/07/2018	surgeon 5	5	5	80	40	00:04:46	00:08:00
25265	28.1	Salcombe	31/07/2018	surgeon 5	5	5	80	40	00:05:28	00:08:00
25266	29.2	Salcombe	31/07/2018	surgeon 5	5	5	80	40	00:05:39	00:21:00
25267	28.9	Salcombe	31/07/2018	surgeon 5	5	5	80	40	00:04:09	00:08:00
25268	32.5	Salcombe	01/08/2018	surgeon 5	5	5	80	40	00:05:21	00:08:00
25269	35.4	Salcombe	01/08/2018	surgeon 5	5	5	80	40	00:05:55	00:09:00
25270	37.3	Salcombe	01/08/2018	surgeon 5	5	5	80	40	00:04:22	00:07:00
25271	38.3	Salcombe	01/08/2018	surgeon 5	5	5	80	40	00:04:44	00:08:00
25272	35.1	Salcombe	01/08/2018	surgeon 3	5	5	80	40	00:06:33	00:11:00
25179	25.2	Taw/Torridge	20/07/2018	surgeon 5	5	5	90	40	00:04:05	00:07:49
25180	29	Taw/Torridge	20/07/2018	surgeon 5	4	5	90	40	00:04:21	00:07:48
25153	28.2	Taw/Torridge	18/07/2018	surgeon 3	4	5	90	40	00:06:00	00:09:00
25152	29.9	Taw/Torridge	18/07/2018	surgeon 3	4	5	90	40	00:05:00	00:08:00
25151	27.8	Taw/Torridge	18/07/2018	surgeon 3	5	5	90	40	00:08:00	00:12:00
25144	27	Taw/Torridge	18/07/2018	surgeon 2	5	5	90	40	00:03:00	00:05:00

25143	29	Taw/Torridge	18/07/2018	surgeon 3	5	5	90	40	00:05:00	00:08:00
25142	27.5	Taw/Torridge	18/07/2018	surgeon 3	4	5	90	40	00:02:00	00:06:00
25155	35.7	Taw/Torridge	18/07/2018	surgeon 3	5	5	90	40	00:05:00	00:09:00
25154	39.6	Taw/Torridge	18/07/2018	surgeon 3	4	5	90	40	00:06:00	00:11:00
25135	44.4	Taw/Torridge	18/07/2018	surgeon 2	4	5	90	40	00:22:00	00:24:00
25148	28.8	Taw/Torridge	17/07/2018	surgeon 2	5	5	90	40	00:09:00	00:12:00
25147	28.4	Taw/Torridge	17/07/2018	surgeon 2	5	5	90	40	00:06:00	00:08:00
25146	27.2	Taw/Torridge	17/07/2018	surgeon 2	4	5	90	40	00:04:00	00:07:00
25145	25.5	Taw/Torridge	17/07/2018	surgeon 2	5	5	90	40	00:07:00	00:10:00
25130	31	Taw/Torridge	16/07/2018	surgeon 5	5	5	90	40	00:22:00	00:26:00
25129	27.3	Taw/Torridge	16/07/2018	surgeon 5	5	5	80	40	00:09:00	00:14:00
25128	25.7	Taw/Torridge	16/07/2018	surgeon 5	4	5	90	40	00:06:00	00:09:00
25141	32	Taw/Torridge	16/07/2018	surgeon 5	5	5	90	40	00:11:00	00:15:00
25140	26.8	Taw/Torridge	16/07/2018	surgeon 5	4	5	90	40	00:05:00	00:08:00
25139	27.4	Taw/Torridge	16/07/2018	surgeon 5	4	5	90	40	00:04:00	00:07:00
25138	25.2	Taw/Torridge	16/07/2018	surgeon 5	4	5	90	40	00:04:00	00:07:00
25137	25.8	Taw/Torridge	16/07/2018	surgeon 5	4	5	90	40	00:04:00	00:07:00
25136	60	Taw/Torridge	16/07/2018	surgeon 5	5	5	90	40	00:12:00	00:18:00
25168	28.3	Taw/Torridge	18/07/2018	surgeon 4	5	5	90	40	00:03:10	00:06:45
25167	32.2	Taw/Torridge	18/07/2018	surgeon 4	5	5	90	40	00:03:45	00:06:10
25166	32.9	Taw/Torridge	18/07/2018	surgeon 4	4	5	90	40	00:02:15	00:07:00
25165	29.7	Taw/Torridge	18/07/2018	surgeon 4	5	5	90	40	00:03:24	00:05:40
25164	28.4	Taw/Torridge	18/07/2018	surgeon 4	4	5	90	40	00:04:13	00:07:54
25159	28.9	Taw/Torridge	19/07/2018	surgeon 4	5	4	90	40	00:04:55	00:08:25
25158	34.5	Taw/Torridge	19/07/2018	surgeon 4	5	4	90	40	00:03:40	00:07:30
25157	39.3	Taw/Torridge	19/07/2018	surgeon 4	4	5	90	40	00:03:35	00:06:55
25156	26.2	Taw/Torridge	19/07/2018	surgeon 4	4	3	90	40	00:02:10	00:07:20
25169	30.6	Taw/Torridge	19/07/2018	surgeon 4	5	4	90	40	00:04:05	00:08:35
25163	28.9	Taw/Torridge	18/07/2018	surgeon 4	5	5	90	40	00:03:00	00:06:00

25170	25.3	Taw/Torridge	18/07/2018	surgeon 4	5	5	90	40	00:05:00	00:08:00
25171	26.7	Taw/Torridge	18/07/2018	surgeon 4	5	5	90	40	00:04:00	00:07:00
25172	35.3	Taw/Torridge	20/07/2018	surgeon 4	5	5	90	40	00:49:00	00:53:00
25173	29	Taw/Torridge	20/07/2018	surgeon 4	5	5	90	40	00:05:00	00:08:00
25174	26.1	Taw/Torridge	20/07/2018	surgeon 4	5	5	90	40	00:03:00	00:05:00
25175	27.2	Taw/Torridge	20/07/2018	surgeon 3	4	5	90	40	00:03:49	00:07:51
25176	27.9	Taw/Torridge	20/07/2018	surgeon 3	4	4	90	40	00:04:38	00:09:39
25177	39.9	Taw/Torridge	20/07/2018	surgeon 3	5	5	90	40	00:03:41	00:08:30
25178	37.9	Taw/Torridge	20/07/2018	surgeon 3	4	5	90	40	00:04:01	00:08:13
25150	28.7	Taw/Torridge	19/07/2018	surgeon 5	4	5	90	40	00:07:40	00:12:33
25149	25.7	Taw/Torridge	19/07/2018	surgeon 5	5	5	90	40	00:05:25	00:08:12
25162	26.7	Taw/Torridge	19/07/2018	surgeon 5	5	5	90	40	00:07:20	03:10:37
25161	27.9	Taw/Torridge	19/07/2018	surgeon 5	5	4	90	40	00:04:53	02:08:20
25160	27.1	Taw/Torridge	19/07/2018	surgeon 5	4	5	90	40	00:04:55	00:07:39
25206	29.8	Dart	10/08/2018	surgeon 5	5	5	80	40	00:10:30	00:14:36
25205	29.8	Dart	10/08/2018	surgeon 5	5	5	80	40	00:05:47	00:10:32
25199	29.3	Dart	10/08/2018	surgeon 5	5	5	80	40	00:09:37	00:12:37
25217	26	Dart	10/08/2018	surgeon 5	5	5	80	40	00:05:31	00:09:22
25198	52	Dart	10/08/2018	surgeon 5	5	5	80	40	00:12:14	00:17:21
25208	28.2	Dart	10/08/2018	surgeon 5	5	5	80	40	00:08:47	00:13:50
25207	27	Dart	10/08/2018	surgeon 5	5	5	80	40	00:10:20	00:14:22
25218	42	Dart	10/08/2018	surgeon 3	5	5	80	40	00:06:53	00:12:09
25209	41.2	Dart	10/08/2018	surgeon 3	5	5	90	40	00:09:45	00:17:18
25201	41.1	Dart	10/08/2018	surgeon 3	4	5	90	40	00:13:57	00:18:24
25193	33.5	Dart	10/08/2018	surgeon 3	5	5	90	40	00:08:04	00:12:26
25192	30.9	Dart	10/08/2018	surgeon 3	5	5	90	40	00:05:26	00:12:02
25191	26.8	Dart	10/08/2018	surgeon 3	5	4	100	40	00:06:58	03:06:06
25200	30.2	Dart	10/08/2018	surgeon 3	5	4	100	40	00:06:01	00:15:06
25203	49.4	Dart	10/08/2018	surgeon 5	5	5	80	40	00:07:16	00:11:57

25211	39	Dart	10/08/2018	surgeon 5	5	5	80	40	00:21:39	00:25:37
25202	35.8	Dart	10/08/2018	surgeon 5	5	5	90	40	00:24:14	00:28:52
25194	29.8	Dart	10/08/2018	surgeon 5	5	5	90	40	00:11:11	00:13:06
25210	33	Dart	10/08/2018	surgeon 5	5	5	90	40	00:05:07	00:08:24
25190	38.7	Dart	10/08/2018	surgeon 5	4	5	90	40	00:06:09	00:09:25
25197	42.5	Dart	10/08/2018	surgeon 5	5	5	90	40	00:11:58	00:15:39
25196	41.3	Dart	10/08/2018	surgeon 5	4	5	90	40	00:05:42	00:09:27
25195	26.6	Dart	10/08/2018	surgeon 5	5	5	90	40	00:09:09	00:12:50
25204	30.9	Dart	10/08/2018	surgeon 5	5	5	90	40	00:09:04	00:12:37
25184	39.2	Dart	10/08/2018	surgeon 5	4	5	90	40	00:07:40	00:10:45
25185	40.5	Dart	10/08/2018	surgeon 5	5	4	90	40	00:11:16	00:16:26
25186	32.9	Dart	10/08/2018	surgeon 5	4	5	90	40	00:09:08	00:12:25
25187	28.5	Dart	10/08/2018	surgeon 5	4	5	90	40	00:06:51	00:11:09
25188	30.8	Dart	10/08/2018	surgeon 5	4	5	90	40	00:11:43	00:16:04
25189	29.9	Dart	10/08/2018	surgeon 5	5	5	90	40	00:07:37	00:09:59
25216	27	Dart	10/08/2018	surgeon 5	5	5	80	40	00:05:48	00:09:08
25215	26.5	Dart	10/08/2018	surgeon 5	5	5	80	40	00:06:42	00:10:15
25214	28.2	Dart	10/08/2018	surgeon 5	5	5	80	40	00:09:30	00:12:46
25213	28.5	Dart	10/08/2018	surgeon 5	5	5	80	40	n/a	n/a
25212	29.2	Dart	10/08/2018	surgeon 5	5	5	80	40	00:06:38	00:10:00
25220	37.5	Dart	19/08/2018	surgeon 5	5	5	80	40	00:05:50	00:08:01
25219	30.9	Dart	19/08/2018	surgeon 5	5	5	80	40	00:06:25	00:09:15
25232	33.7	Dart	19/08/2018	surgeon 2	5	5	80	40	00:06:02	00:10:31
25231	32.4	Dart	19/08/2018	surgeon 5	5	5	80	40	00:05:08	00:08:06
25230	30.8	Dart	19/08/2018	surgeon 2	5	5	80	40	00:08:00	00:11:33
25225	34.5	Dart	19/08/2018	surgeon 5	5	5	80	40	00:04:11	00:07:03
25224	50.3	Dart	19/08/2018	surgeon 5	5	5	80	40	00:08:12	00:12:19
25223	42.1	Dart	19/08/2018	surgeon 5	4	5	80	40	00:05:42	00:10:40
25222	28.4	Dart	19/08/2018	surgeon 5	5	5	80	40	00:04:18	00:07:20

25221	28.6	Dart	19/08/2018	surgeon 5	5	5	80	40	00:07:00	00:10:29
25229	30.2	Dart	19/08/2018	surgeon 2	5	5	80	40	00:06:16	00:10:42
25228	32.4	Dart	19/08/2018	surgeon 2	5	5	80	40	00:06:30	00:09:54
25227	29	Dart	19/08/2018	surgeon 2	5	5	80	40	00:06:43	00:09:38
25226	29.8	Dart	19/08/2018	surgeon 2	5	5	80	40	00:06:50	00:09:56
25273	29.5	Dart	19/08/2018	surgeon 2	5	5	80	40	00:06:00	00:09:02
25181	32.4	Dart	19/08/2018	surgeon 2	5	5	80	40	00:06:55	00:10:19

A1.4.1 Post-operative survival

Post-operative mortality was suspected to occur for seven individuals, within Salcombe harbour five individuals where either not detected following release or the last detection occurred shortly after the procedure high into the system with no subsequent movement detected. Within the Taw/Torridge two individuals were not detected following receiver deployment (approximately 2 weeks following the tagging procedure). All fish within the Dart estuary were detected following receiver deployment.

Seven fish were detected immediately leaving Salcombe harbour following the tagging procedure, and were not subsequently re-detected. The remaining 132 fish were detected for extended periods of 24.2-371.2days. The success rate of the tagging procedure was therefore considered as 95.2%. Please note survival estimate includes the seven fish detected leaving Salcombe immediately following the tagging procedure.

A1.5 References

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Annex 2 – Supplementary figures

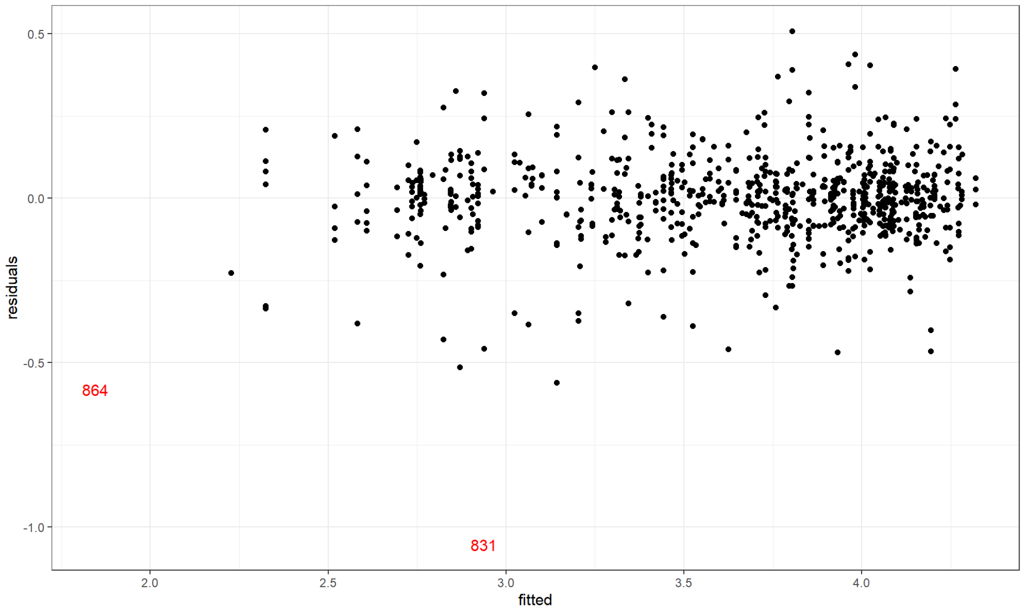

Figure A2. 1 - Residuals vs fitted plot for linear mixed effect model assessing seasonal water temperature within each nursery sites; Dart estuary, Salcombe harbour and Taw/Torridge estuaries. Data points 864 & 831 (highlighted in red) identified as outliers and removed from subsequent analysis

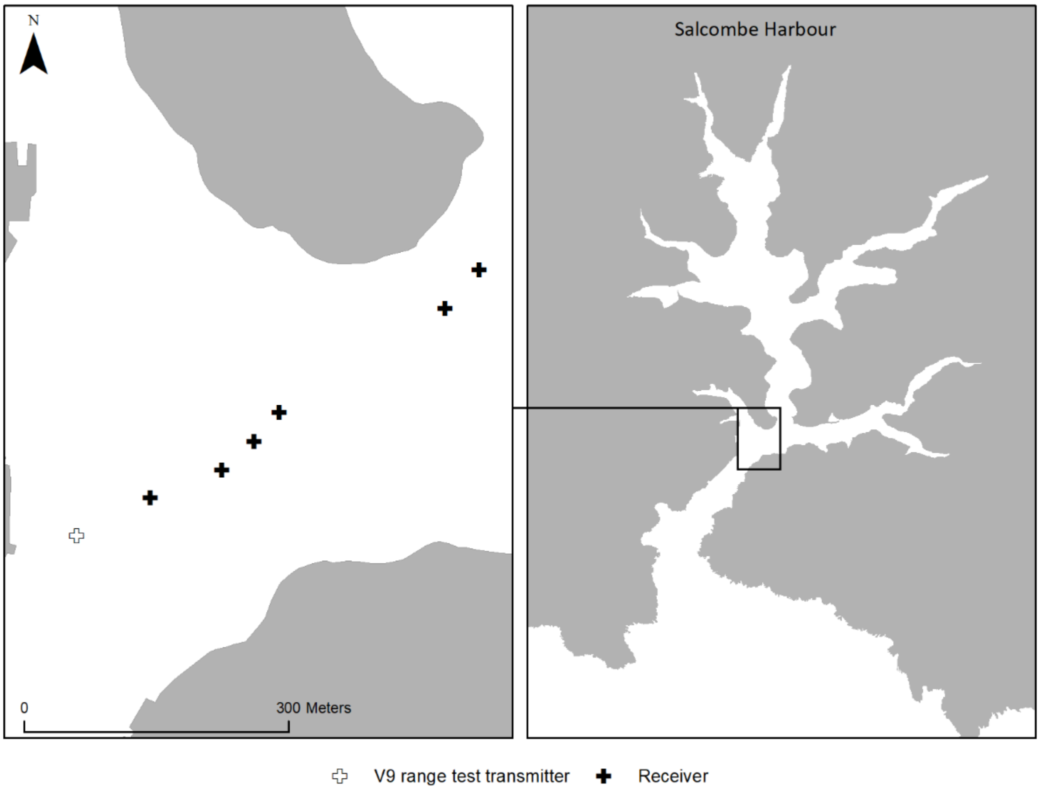

Figure A2. 2– Range testing configuration used to test detection efficiency of acoustic telemetry array within Salcombe harbour

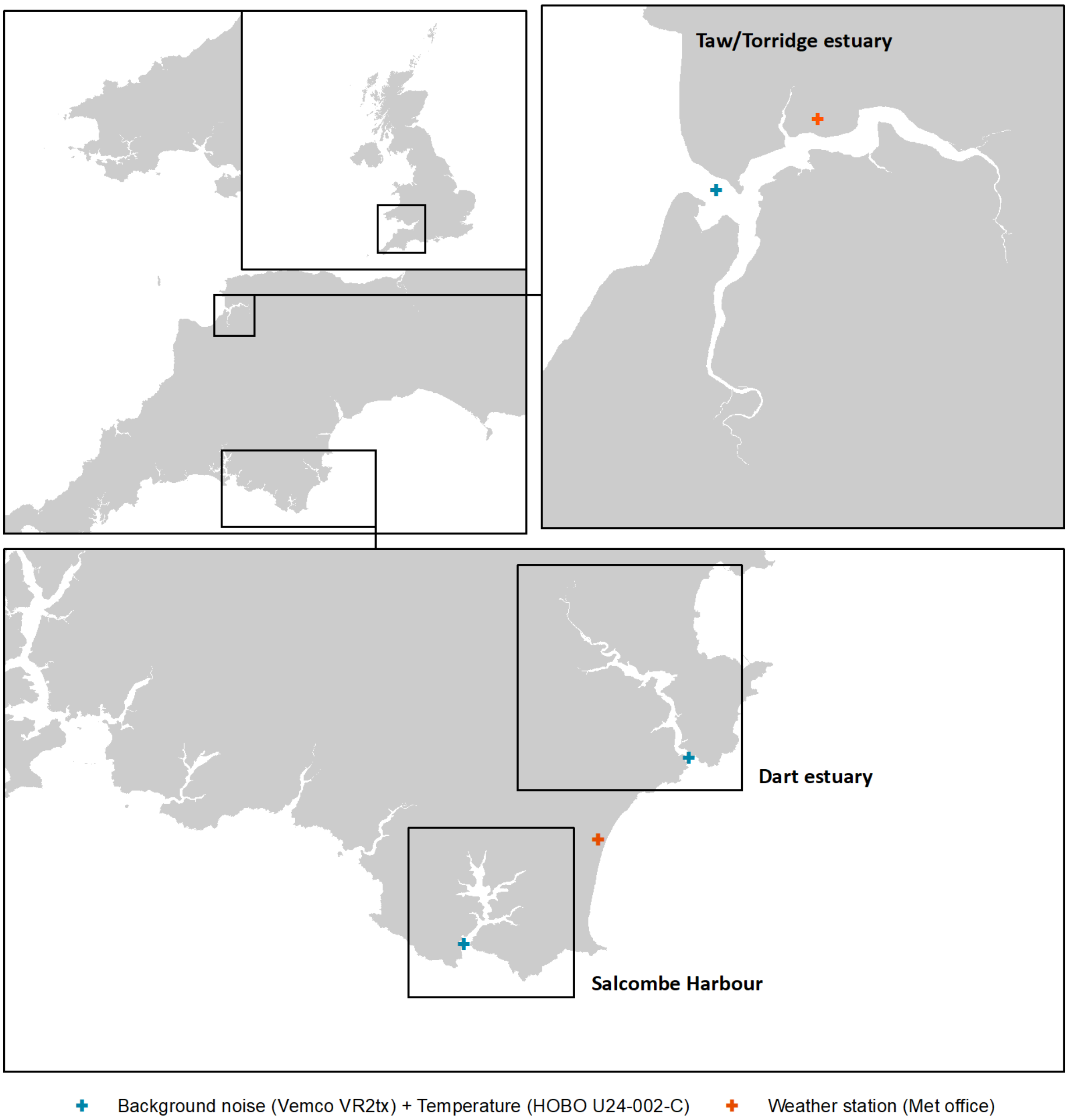

Figure A2. 3 – Location of background noise, temperature loggers and weather stations associated with; the Dart estuary, Salcombe Harbour and the Taw/Torridge estuary acoustic array. Due to geographic proximity Salcombe harbour and Dart estuary shared a weather station

Table A2. 1 – Average percentage detections of tagged European bass at each receiver station (Figure 6.2 & Table 6.2) in each tidal bin, n = number of tidal cycles for each receiver station

Sample site	Station	Tidal bin	Average % detections	n	Standard Deviation
Dart	D.1	1 (Low tide)	3.422	2384	15.131
Dart	D.1	2	2.319	2384	11.496
Dart	D.1	3	1.519	2384	8.551
Dart	D.1	4	2.5	2384	11.094
Dart	D.1	5	2.521	2384	11.839
Dart	D.1	6 (High tide)	3.158	2384	12.078
Dart	D.1	7	4.082	2384	14.113
Dart	D.1	8	4.101	2384	12.838
Dart	D.1	9	5.698	2384	16.605
Dart	D.1	10	4.779	2384	14.996
Dart	D.1	11	3.93	2376	14.202
Dart	D.1	12	4.279	2376	17.592
Dart	D.2	1 (Low tide)	1.896	2980	13.284
Dart	D.2	2	0.642	2980	6.777
Dart	D.2	3	0.467	2980	6.204
Dart	D.2	4	0.82	2980	8.403
Dart	D.2	5	0.895	2980	8.029
Dart	D.2	6 (High tide)	0.615	2980	6.731
Dart	D.2	7	0.746	2980	7.302
Dart	D.2	8	1.28	2980	9.554
Dart	D.2	9	1.647	2980	9.927
Dart	D.2	10	1.77	2980	10.896
Dart	D.2	11	1.684	2970	9.9
Dart	D.2	12	1.305	2970	8.665
Dart	D.3	1 (Low tide)	9.378	2682	20.037
Dart	D.3	2	6.723	2682	14.883
Dart	D.3	3	6.446	2682	15.445
Dart	D.3	4	4.572	2682	12.902
Dart	D.3	5	5.289	2682	13.748
Dart	D.3	6 (High tide)	7.878	2682	16.987
Dart	D.3	7	7.048	2682	13.558
Dart	D.3	8	7.266	2682	15.737
Dart	D.3	9	6.317	2682	11.848
Dart	D.3	10	6.979	2682	15.932
Dart	D.3	11	7.203	2673	15.514
Dart	D.3	12	7.162	2673	17.053
Dart	D.4	1 (Low tide)	3.339	4326	9.004
Dart	D.4	2	2.601	4326	6.159
Dart	D.4	3	2.44	4333	5.667
Dart	D.4	4	2.25	4333	5.954
Dart	D.4	5	2.29	4333	5.281
Dart	D.4	6 (High tide)	2.752	4333	5.95
Dart	D.4	7	2.893	4333	6.391

Dart	D.4	8	2.605	4326	5.684
Dart	D.4	9	3.31	4326	7.452
Dart	D.4	10	3.254	4326	7.113
Dart	D.4	11	2.699	4326	5.804
Dart	D.4	12	3.202	4326	8.293
Dart	D.5	1 (Low tide)	10.75	3708	14.437
Dart	D.5	2	8.475	3708	7.141
Dart	D.5	3	7.797	3714	6.083
Dart	D.5	4	7.183	3714	6.172
Dart	D.5	5	7.25	3714	6.235
Dart	D.5	6 (High tide)	7.137	3714	5.485
Dart	D.5	7	7.055	3714	7.195
Dart	D.5	8	6.171	3708	4.627
Dart	D.5	9	5.248	3708	3.819
Dart	D.5	10	6.312	3708	5.268
Dart	D.5	11	8.594	3708	7.252
Dart	D.5	12	10.919	3708	13.4
Dart	D.6	1 (Low tide)	6.974	3090	17.287
Dart	D.6	2	4.762	3090	13.188
Dart	D.6	3	3.077	3095	9.565
Dart	D.6	4	3.216	3095	10.705
Dart	D.6	5	3.611	3095	10.886
Dart	D.6	6 (High tide)	3.124	3095	12.344
Dart	D.6	7	1.874	3095	6.477
Dart	D.6	8	2.642	3090	9.197
Dart	D.6	9	2.847	3090	8.823
Dart	D.6	10	7.263	3090	16.279
Dart	D.6	11	7.976	3090	17.385
Dart	D.6	12	7.855	3090	19.296
Dart	D.7	1 (Low tide)	10.897	2472	12.919
Dart	D.7	2	9.642	2472	8.873
Dart	D.7	3	8.923	2476	8.72
Dart	D.7	4	7.315	2476	7.386
Dart	D.7	5	6.316	2476	5.955
Dart	D.7	6 (High tide)	6.036	2476	6.738
Dart	D.7	7	5.941	2476	5.571
Dart	D.7	8	6.154	2472	5.482
Dart	D.7	9	6.639	2472	7.49
Dart	D.7	10	7.702	2472	7.174
Dart	D.7	11	9.71	2472	8.903
Dart	D.7	12	11.831	2472	13.934
Dart	D.8	1 (Low tide)	4.102	1854	11.476
Dart	D.8	2	4.098	1854	9.36
Dart	D.8	3	4.994	1857	11.102
Dart	D.8	4	3.632	1857	7.824
Dart	D.8	5	3.06	1857	7.504
Dart	D.8	6 (High tide)	2.268	1857	5.77
Dart	D.8	7	2.563	1857	7.682

Dart	D.8	8	4.663	1854	12.478
Dart	D.8	9	3.868	1854	10.926
Dart	D.8	10	2.839	1854	7.656
Dart	D.8	11	3.968	1854	11.405
Dart	D.8	12	3.077	1854	10.366
Dart	D.9	1 (Low tide)	0.034	1236	0.504
Dart	D.9	2	0.196	1236	2.427
Dart	D.9	3	0.702	1238	5.366
Dart	D.9	4	1.94	1238	10.246
Dart	D.9	5	3.893	1238	14.237
Dart	D.9	6 (High tide)	4.931	1238	15.204
Dart	D.9	7	9.06	1238	22.337
Dart	D.9	8	5.879	1236	18.254
Dart	D.9	9	1.428	1236	8.975
Dart	D.9	10	0	1236	0
Dart	D.9	11	0	1236	0
Dart	D.9	12	0	1236	0
Dart	D.10	1 (Low tide)	2.097	618	6.903
Dart	D.10	2	2.43	618	5.715
Dart	D.10	3	3.63	619	8.144
Dart	D.10	4	4.428	619	8.308
Dart	D.10	5	4.981	619	8.804
Dart	D.10	6 (High tide)	5.456	619	9.912
Dart	D.10	7	5.144	619	9.589
Dart	D.10	8	3.86	618	7.601
Dart	D.10	9	2.709	618	5.8
Dart	D.10	10	1.715	618	4.166
Dart	D.10	11	1.277	618	3.914
Dart	D.10	12	1.952	618	9.316
Salcombe	S.1	1 (Low tide)	4.02	5019	9.243
Salcombe	S.1	2	3.235	5019	6.766
Salcombe	S.1	3	2.622	5019	5.361
Salcombe	S.1	4	2.724	5019	5.485
Salcombe	S.1	5	2.555	5019	5.096
Salcombe	S.1	6 (High tide)	2.581	5019	6.313
Salcombe	S.1	7	2.563	5019	6.68
Salcombe	S.1	8	2.54	5019	8.13
Salcombe	S.1	9	2.235	5019	6.845
Salcombe	S.1	10	2.744	5019	6.604
Salcombe	S.1	11	4.665	5019	10.559
Salcombe	S.1	12	5.318	5012	12.141
Salcombe	S.2	1 (Low tide)	9.74	5736	11.677
Salcombe	S.2	2	9.239	5736	11.651
Salcombe	S.2	3	8.985	5736	11.752
Salcombe	S.2	4	9.016	5736	8.741
Salcombe	S.2	5	9.259	5736	8.553
Salcombe	S.2	6 (High tide)	8.323	5736	9.783
Salcombe	S.2	7	5.65	5736	8.541

Salcombe	S.2	8	2.686	5736	6.343
Salcombe	S.2	9	2.204	5736	7.789
Salcombe	S.2	10	4.885	5736	8.648
Salcombe	S.2	11	9.666	5736	12.424
Salcombe	S.2	12	12.413	5728	15.605
Salcombe	S.3	1 (Low tide)	9.53	4302	12.865
Salcombe	S.3	2	6.784	4302	7.517
Salcombe	S.3	3	6.566	4302	6.712
Salcombe	S.3	4	7.401	4302	7.353
Salcombe	S.3	5	7.83	4302	7.597
Salcombe	S.3	6 (High tide)	8.7	4302	7.799
Salcombe	S.3	7	8.592	4302	8.682
Salcombe	S.3	8	6.934	4302	7.913
Salcombe	S.3	9	7.101	4302	9.332
Salcombe	S.3	10	9.77	4302	11.448
Salcombe	S.3	11	9.269	4302	9.415
Salcombe	S.3	12	8.884	4296	10.97
Salcombe	S.4	1 (Low tide)	9.501	3585	8.136
Salcombe	S.4	2	7.965	3585	6.712
Salcombe	S.4	3	6.057	3585	4.846
Salcombe	S.4	4	5.931	3585	5.206
Salcombe	S.4	5	6.47	3585	5.761
Salcombe	S.4	6 (High tide)	7.476	3585	5.917
Salcombe	S.4	7	7.557	3585	4.85
Salcombe	S.4	8	7.585	3585	4.502
Salcombe	S.4	9	8.406	3585	5.241
Salcombe	S.4	10	10.068	3585	7.544
Salcombe	S.4	11	11.087	3585	9.807
Salcombe	S.4	12	9.956	3580	7.583
Salcombe	S.5	1 (Low tide)	0	8	0
Salcombe	S.5	2	0	8	0
Salcombe	S.5	3	5.833	8	6.236
Salcombe	S.5	4	10	8	10.69
Salcombe	S.5	5	0	8	0
Salcombe	S.5	6 (High tide)	2.5	8	2.673
Salcombe	S.5	7	6.111	8	6.533
Salcombe	S.5	8	6.389	8	6.83
Salcombe	S.5	9	19.167	8	20.49
Salcombe	S.5	10	0	8	0
Salcombe	S.5	11	0	8	0
Salcombe	S.5	12	0	4	0
Salcombe	S.6	1 (Low tide)	5.73	1434	14.822
Salcombe	S.6	2	5.019	1434	10.496
Salcombe	S.6	3	7.26	1434	12.799
Salcombe	S.6	4	7.488	1434	11.68
Salcombe	S.6	5	7.464	1434	10.977
Salcombe	S.6	6 (High tide)	8.704	1434	14.564
Salcombe	S.6	7	7.96	1434	13.014

Salcombe	S.6	8	7.902	1434	12.52
Salcombe	S.6	9	4.786	1434	11.066
Salcombe	S.6	10	4.299	1434	10.065
Salcombe	S.6	11	4.219	1434	9.697
Salcombe	S.6	12	5.462	1432	13.362
Salcombe	S.7	1 (Low tide)	2.984	2151	11.451
Salcombe	S.7	2	2.567	2151	8.821
Salcombe	S.7	3	4.093	2151	12.354
Salcombe	S.7	4	4.146	2151	10.898
Salcombe	S.7	5	4.921	2151	12.286
Salcombe	S.7	6 (High tide)	5.857	2151	14.18
Salcombe	S.7	7	6.05	2151	14.408
Salcombe	S.7	8	5.733	2151	14.601
Salcombe	S.7	9	4.538	2151	13.419
Salcombe	S.7	10	2.816	2151	9.538
Salcombe	S.7	11	2.033	2151	7.886
Salcombe	S.7	12	3.214	2148	13.335
Salcombe	S.8	1 (Low tide)	1.166	645	9.004
Salcombe	S.8	2	1.656	645	9.317
Salcombe	S.8	3	1.888	645	8.264
Salcombe	S.8	4	5.485	645	15.072
Salcombe	S.8	5	10.774	645	21.172
Salcombe	S.8	6 (High tide)	10.712	645	21.634
Salcombe	S.8	7	6.111	645	15.457
Salcombe	S.8	8	2.812	646	12.358
Salcombe	S.8	9	0.895	646	6.726
Salcombe	S.8	10	0.611	646	5.937
Salcombe	S.8	11	0.083	646	2.119
Salcombe	S.8	12	0.436	645	6.005
Taw/Torridge	Ta.1	1 (Low tide)	11.763	4648	19.833
Taw/Torridge	Ta.1	2	8.606	4648	13.803
Taw/Torridge	Ta.1	3	5.02	4648	8.821
Taw/Torridge	Ta.1	4	4.094	4648	5.945
Taw/Torridge	Ta.1	5	15.985	4641	18.323
Taw/Torridge	Ta.1	6 (High tide)	12.568	4641	15.107
Taw/Torridge	Ta.1	7	7.199	4641	11.516
Taw/Torridge	Ta.1	8	3.668	4641	6.752
Taw/Torridge	Ta.1	9	2.67	4641	6.092
Taw/Torridge	Ta.1	10	2.716	4641	6.436
Taw/Torridge	Ta.1	11	6.483	4641	14.387
Taw/Torridge	Ta.1	12	12.372	4641	24.082
Taw/Torridge	Ta.2	1 (Low tide)	5.215	1998	18.046
Taw/Torridge	Ta.2	2	3.828	1998	13.579
Taw/Torridge	Ta.2	3	7.112	1998	18.253
Taw/Torridge	Ta.2	4	3.023	1995	10.047
Taw/Torridge	Ta.2	5	3.65	1995	12.473
Taw/Torridge	Ta.2	6 (High tide)	4.673	1995	13.672
Taw/Torridge	Ta.2	7	7.278	1995	17.602

Taw/Torridge	Ta.2	8	7.708	1995	19.235
Taw/Torridge	Ta.2	9	3.419	1995	11.219
Taw/Torridge	Ta.2	10	2.281	1995	10.788
Taw/Torridge	Ta.2	11	2.3	1995	10.868
Taw/Torridge	Ta.2	12	2.269	1995	10.055
Taw/Torridge	Ta.3	1 (Low tide)	0.99	1332	9.209
Taw/Torridge	Ta.3	2	0.425	1332	5.556
Taw/Torridge	Ta.3	3	0.058	1332	1.164
Taw/Torridge	Ta.3	4	0.012	1330	0.313
Taw/Torridge	Ta.3	5	0.057	1330	1.334
Taw/Torridge	Ta.3	6 (High tide)	0.019	1330	0.491
Taw/Torridge	Ta.3	7	0.006	1330	0.147
Taw/Torridge	Ta.3	8	0.004	1330	0.098
Taw/Torridge	Ta.3	9	0.002	1330	0.049
Taw/Torridge	Ta.3	10	0.058	1330	1.108
Taw/Torridge	Ta.3	11	1.307	1330	8.245
Taw/Torridge	Ta.3	12	3.376	1330	15.945
Taw/Torridge	Ta.4	1 (Low tide)	0.699	666	7.488
Taw/Torridge	Ta.4	2	0.212	666	2.317
Taw/Torridge	Ta.4	3	0.579	666	6.085
Taw/Torridge	Ta.4	4	0.574	665	5.576
Taw/Torridge	Ta.4	5	0.636	665	4.63
Taw/Torridge	Ta.4	6 (High tide)	1.678	665	11.152
Taw/Torridge	Ta.4	7	0.829	665	6.709
Taw/Torridge	Ta.4	8	0.416	665	4.419
Taw/Torridge	Ta.4	9	0.4	665	5.517
Taw/Torridge	Ta.4	10	0.17	665	1.601
Taw/Torridge	Ta.4	11	0.455	665	4.899
Taw/Torridge	Ta.4	12	1.318	665	10.709
Taw/Torridge	To.1	1 (Low tide)	2.915	5312	14.304
Taw/Torridge	To.1	2	2.591	5312	14.069
Taw/Torridge	To.1	3	3.405	5312	12.095
Taw/Torridge	To.1	4	5.862	5312	13.381
Taw/Torridge	To.1	5	9	5304	18.853
Taw/Torridge	To.1	6 (High tide)	7.687	5304	15.692
Taw/Torridge	To.1	7	4.415	5304	12.575
Taw/Torridge	To.1	8	3.577	5304	15.506
Taw/Torridge	To.1	9	1.237	5304	8.909
Taw/Torridge	To.1	10	1.924	5304	9.051
Taw/Torridge	To.1	11	3.84	5304	13.494
Taw/Torridge	To.1	12	4.356	5304	16.106
Taw/Torridge	To.2	1 (Low tide)	0.047	3984	1.22
Taw/Torridge	To.2	2	0.313	3984	5.488
Taw/Torridge	To.2	3	1.866	3984	13.361
Taw/Torridge	To.2	4	0.951	3984	9.182
Taw/Torridge	To.2	5	0.107	3978	2.508
Taw/Torridge	To.2	6 (High tide)	0.882	3978	7.776
Taw/Torridge	To.2	7	2.844	3978	15.57

Taw/Torridge	To.2	8	0.965	3978	9.36
Taw/Torridge	To.2	9	0.558	3978	7.034
Taw/Torridge	To.2	10	0.114	3978	1.831
Taw/Torridge	To.2	11	0.129	3978	2.823
Taw/Torridge	To.2	12	0.119	3978	2.234
Taw/Torridge	To.3	1 (Low tide)	0.06	3320	1.098
Taw/Torridge	To.3	2	0.288	3320	4.406
Taw/Torridge	To.3	3	1.879	3320	10.742
Taw/Torridge	To.3	4	2.409	3320	11.11
Taw/Torridge	To.3	5	1.691	3315	7.519
Taw/Torridge	To.3	6 (High tide)	2.857	3315	12.187
Taw/Torridge	To.3	7	1.926	3315	10.095
Taw/Torridge	To.3	8	0.976	3315	4.81
Taw/Torridge	To.3	9	0.749	3315	4.801
Taw/Torridge	To.3	10	0.434	3315	2.197
Taw/Torridge	To.3	11	0.121	3315	1.27
Taw/Torridge	To.3	12	0.178	3315	3.345
Taw/Torridge	To.4	1 (Low tide)	0	2656	0
Taw/Torridge	To.4	2	0	2656	0
Taw/Torridge	To.4	3	0.025	2656	0.646
Taw/Torridge	To.4	4	0.126	2656	3.232
Taw/Torridge	To.4	5	0.297	2652	4.564
Taw/Torridge	To.4	6 (High tide)	0.394	2652	5.173
Taw/Torridge	To.4	7	0.186	2652	3.562
Taw/Torridge	To.4	8	0.027	2652	0.706
Taw/Torridge	To.4	9	0	2652	0
Taw/Torridge	To.4	10	0	2652	0
Taw/Torridge	To.4	11	0	2652	0
Taw/Torridge	To.4	12	0	2652	0
Taw/Torridge	TT.1	1 (Low tide)	3.033	2639	15.118
Taw/Torridge	TT.1	2	1.124	2639	7.463
Taw/Torridge	TT.1	3	2.432	2639	12.959
Taw/Torridge	TT.1	4	4.794	2639	17.806
Taw/Torridge	TT.1	5	3.094	2639	12.031
Taw/Torridge	TT.1	6 (High tide)	6.655	2639	19.244
Taw/Torridge	TT.1	7	4.732	2639	13.75
Taw/Torridge	TT.1	8	5.594	2639	14.542
Taw/Torridge	TT.1	9	3.93	2639	13.767
Taw/Torridge	TT.1	10	2.763	2639	12.864
Taw/Torridge	TT.1	11	3.183	2626	13.071
Taw/Torridge	TT.1	12	3.032	2626	12.885
Taw/Torridge	TT.2	1 (Low tide)	1.599	7337	10.803
Taw/Torridge	TT.2	2	0.961	7337	8.261
Taw/Torridge	TT.2	3	0.69	7337	5.863
Taw/Torridge	TT.2	4	0.58	7337	5.845
Taw/Torridge	TT.2	5	0.907	7337	8.064
Taw/Torridge	TT.2	6 (High tide)	0.429	7337	5.268
Taw/Torridge	TT.2	7	0.438	7337	4.861

Taw/Torridge	TT.2	8	0.466	7337	5.59
Taw/Torridge	TT.2	9	0.735	7337	5.629
Taw/Torridge	TT.2	10	1.471	7337	9.605
Taw/Torridge	TT.2	11	1.878	7337	11.193
Taw/Torridge	TT.2	12	1.392	7337	9.407
Taw/Torridge	TT.3	1 (Low tide)	12.793	2436	19.926
Taw/Torridge	TT.3	2	7.732	2436	9.509
Taw/Torridge	TT.3	3	10.916	2436	13.591
Taw/Torridge	TT.3	4	5.893	2436	9.439
Taw/Torridge	TT.3	5	4.128	2436	11.225
Taw/Torridge	TT.3	6 (High tide)	2.254	2436	6.342
Taw/Torridge	TT.3	7	1.339	2436	4.055
Taw/Torridge	TT.3	8	1.938	2436	8.747
Taw/Torridge	TT.3	9	4.577	2436	10.859
Taw/Torridge	TT.3	10	9.816	2436	12.334
Taw/Torridge	TT.3	11	20.438	2424	19.704
Taw/Torridge	TT.3	12	16.095	2424	17.831
Taw/Torridge	TT.4	1 (Low tide)	10.583	6670	12.084
Taw/Torridge	TT.4	2	4.046	6670	4.753
Taw/Torridge	TT.4	3	2.351	6670	3.231
Taw/Torridge	TT.4	4	4.696	6670	5.021
Taw/Torridge	TT.4	5	13.936	6670	12.229
Taw/Torridge	TT.4	6 (High tide)	15.243	6670	13.324
Taw/Torridge	TT.4	7	10.161	6670	10.03
Taw/Torridge	TT.4	8	4.025	6670	4.541
Taw/Torridge	TT.4	9	1.989	6670	3.415
Taw/Torridge	TT.4	10	3.958	6670	4.807
Taw/Torridge	TT.4	11	11.496	6670	9.056
Taw/Torridge	TT.4	12	17.512	6670	13.066