Review paper

Atlantic Cod (*Gadus morhua*) benefits from the availability of seagrass (*Zostera marina*) nursery habitat

Richard J. Lilley [a], Richard K.F. Unsworth [b,*]

[a] *Sustainable Places Research Institute, Cardiff University, UK*
[b] *Seagrass Ecosystem Research Group, College of Science, Wallace Building, Swansea University SA2 8PP, UK*

HIGHLIGHTS

- Ocean scale assessment of the nursery role of eelgrass (*Zostera marina*) supporting Atlantic cod.
- Juvenile Atlantic cod in high density in eelgrass throughout its range growing faster as a result.
- Density of Juvenile Atlantic cod commonly higher in eelgrass relative to alternative habitats.
- Juvenile Atlantic cod select eelgrass habitat, consequently they have higher survival chances.
- We provide strong evidence that eelgrass is of significant importance to Atlantic cod stocks.

ARTICLE INFO

ABSTRACT

The Atlantic cod (*Gadus morhua*) is a species of significant economic and historic importance but infamous for its decline. Apart from overfishing, the causes of this decline and its subsequent lack of recovery remain largely unresolved. Indeed, the degree to which specific habitats are important for this species remains unquantified at the scale of North Atlantic. Here, the literature on the role of eelgrass meadows (*Zostera marina*) as valuable nursery habitat for the Atlantic cod is reviewed and synthesized. Evidence is presented on relative densities of Atlantic cod in shallow water environments and in eelgrass meadows in comparison to alternative habitats. In addition, evidence pertaining to the 'viability gains' attributed to the use of eelgrass meadows as nursery habitat (growth and survival) by juvenile Atlantic cod is analyzed. Although juvenile Atlantic cod use of *Z. marina* is found to be facultative, when possible, available literatures indicates that they may select *Z. marina* as a nursery habitat where they are found in high density (average of at least 246 ha^{-1}). From their use of *Z. marina* habitat the juvenile Atlantic cod receives viability benefits from it, improving their chances of reaching maturation. This paper provides strong evidence that eelgrass meadows are of significant importance to contributing to Atlantic cod stocks.

Contents

* Corresponding author. Tel.: +44 01792 602133.
  E-mail address: r.k.f.unsworth@swansea.ac.uk (R.K.F. Unsworth).

1. Introduction

The diminished status of fisheries for species such as the Atlantic cod (*Gadus morhua*) does not align with the needs of the region or the planet as a whole. To meet the needs of the predicted human population of 2050, an additional 75 million tons of protein from fish and aquatic invertebrates will be required, representing a 50% increase in current supply (Rice and Garcia, 2011). This will require supporting marine and coastal ecosystems (e.g. nursery habitats such as seagrass) to be resilient to future environmental change and maximize fisheries productivity. To direct fisheries management actions towards the conservation of supporting systems requires knowledge of the clear links between fisheries productivity and supporting services such as nursery habitat value (Jackson et al., 2001). One such potential nursery habitat is that created by seagrass (Heck et al., 2003).

Zostera marina is the dominant seagrass in the North Atlantic (Green and Short, 2003) forming one of a number of potential nursery habitats (Sundblad et al., 2013). It spans a distribution broadly similar (but exclusively in shallow waters) to that of Atlantic cod which is widely distributed across the continental shelves of the North Atlantic (Cannon, 1997; Froese and Pauly, 2013). *Z. marina* has been degraded, and significant areas lost throughout its range (Short and Wyllie-Echeverria, 1996; Baden et al., 2003; Hanson, 2004; Waycott et al., 2009). Preventing further degradation and loss of seagrass, and developing strategies to restore these habitats requires greater recognition for their value in supporting economically important fishing industries and regional food security (Unsworth and Cullen, 2010; Cullen-Unsworth and Unsworth, 2013).

The management of these systems (local conservation) and their links to human well-being are often disconnected from the end users (fishermen and consumers) of the products they help support (Cullen-Unsworth et al., 2014), and as a result there is a mismatch between biodiversity conservation needs and fisheries management (Rice and Garcia, 2011; Salomon et al., 2011).

Despite the assertion that seagrass meadows support world fisheries and global food security through the provision of juvenile habitat (Beck et al., 2001; Jackson et al., 2001; Heck et al., 2003; Gillanders, 2006; Bertelli and Unsworth, 2014), the role they play in supporting fisheries in many areas of the world remains poorly recognized and often unclear (Jackson et al., 2001; Gillanders, 2006; Unsworth et al., 2014). A specific case of this is the cod fishery throughout the North Atlantic basin. Evidence that *Z. marina* acts as valuable nursery habitat for Atlantic cod is available in some localities and at a local scale (Seitz et al., 2013), but this is not available at a basin scale. For example studies in Norway to conclude that intact juvenile habitat is essential for healthy Atlantic cod stocks (Løversen, 1946; Dannevig, 1954), and more recently, *Z. marina* expansion has been correlated with increased juvenile Atlantic cod density in Newfoundland (Warren et al., 2010). Although there is a plethora of literature examining *Z. marina*—Atlantic cod interactions at a local scale, there exists no examination of this relationship at an ocean basin scale and with respect to spatial differences. It is not currently possible to make broad statements about the nursery habitats of Atlantic cod across its complete range and use these to develop strategies that might impact the long-term recovery of this fishery.

The juvenile period is a critical life stage for any species. It is a time when an individual is at its most vulnerable and key priorities are likely to be shelter, food and protection from predation (Heck et al., 2003). It is at this point that the optimal habitat provides these attributes. Such habitats are often termed nurseries. There has been recent discourse in the literature surrounding the concept of what constitutes a juvenile or nursery habitat for fish and invertebrates (Beck et al., 2001; Dahlgren et al., 2006; Layman et al., 2006; Sheaves et al., 2006; Nagelkerken et al., 2013), not least that the habitat must act as a source and not a sink of juveniles (Pulliman, 1988). How such habitats are defined is critical, since the definition will have permutations as to the application of juvenile habitats in stock management, and to their perceived value.

In this study we use the concept of a Valuable Nursery Habitat and investigate whether *Z. marina* can be defined as being Valuable Nursery Habitat for Atlantic cod across its range. A habitat is a valuable nursery habitat for juveniles of a particular

species, if its contribution to the biological fitness of individuals that recruit and breed in adult populations is greater, on average, than the mean level contributed by all habitats used by juveniles, regardless of area coverage (see Methods).

Our study is a meta-analysis of the academic literature in order to: (1) determine whether their exists unequivocal evidence of juvenile Atlantic cod being present in *Z. marina* meadows throughout the North Atlantic region (east and west), (2) determining whether juvenile Atlantic cod obtain improved viability benefits from inhabiting *Z. marina* meadows as opposed alternative habitat and (3) determining whether juvenile Atlantic cod that utilize *Z. marina* grow and develop and reach maturity to reproduce.

2. Materials and methods

2.1. Valuable Nursery Habitat concept

Literature was examined relative to the hypothesis that *Z. marina* provides Valuable Nursery Habitat by supporting its three key assumptions.

Assumption 1 (*Presence*)**.** A habitat is only Valuable Nursery Habitat to a species if the species as juveniles are found within that habitat.

Assumption 2 (*Viability*)**.** Individuals seek out those environments that maximize their viability. The rationale of this is that species will actively maximize gains from their local environment. They will therefore spend time in environments that maximize viability, and these gains will be quantifiable either by (i) the number of individuals that are present relative to other habitats (abundance), (ii) the quality of individuals that survive (their size and growth rate) or, (iii) the survival rate from predation.

Assumption 3 (*Source*)**.** Individuals can only make contributions to the next generation if they have access to mates. A population is only sustainable if its juveniles complete their ontogenetic movements into the breeding adult population (seagrass must not be a 'sink' of juveniles, where they have chosen to live whilst young but do not in fact make any contribution to the adult breeding stock).

As such evidence pertaining to 'Presence', 'Viability' and 'Source' was collated relative to the assertion that *Z. marina* is Valuable Nursery Habitat.

2.2. Juvenile Gadus morhua

G. morhua were defined as juvenile if they were <50 cm in length (SL) or referred to as 0–4-group (Froese and Pauly, 2013). Only post-settled juveniles were considered. 0-group fish were defined as <6 cm pre-settled, 6 cm+ post-settled. (Methven and Bajdik, 1994) unless otherwise specified within the paper. Age groupings follow previous published work (Dalley and Anderson, 1997; Anderson and Gregory, 2000).

Of particular focus to this study was the 'Young Of Year' fish: Age-0 fish, or those animals born within the past year; from transformation to juvenile, until January 1 in the Northern Hemisphere, which have not yet reached one year of age (hereafter YOY).

2.3. Literature search

Papers containing peer-reviewed information pertinent to the distribution of juvenile Atlantic cod throughout the entire North Atlantic were reviewed. Searching for research papers used the following terms both separately and in combination: Atlantic cod, *G. morhua*, cod, seagrass, *Z. marina*, eelgrass. Additionally these terms were searched with respect to individual geographic regions of the North Atlantic. All searches were able to be highly exhaustive given the relatively small body of literature available. Due to the complex chemical–physical environment of the Baltic that is unrepresentative of the wider North Atlantic, all papers on juvenile cod from the Baltic were excluded from the analysis. The area of the Baltic that was excluded from the literature search was that defined as the Baltic Large Marine Ecosystem (www.seasaroundus.org). Searching for papers was conducted using 'Google Scholar'. Web of Knowledge was used as a secondary check on our paper search. Google Scholar was seen as referential to the academic databases due to limited age restrictions on research papers (e.g. Web of Knowledge is limited to 1970). In addition the Norwegian Institute of Marine Research (Havforskningsinstituttet) historic peer-reviewed literature database named the 'Brage Bibsys IMR' was used for the search. This was used due to the known historic research conducted on cod at the Institute dating back to the early 1900s.

After developing an initial list of research papers, these were sifted to exclude those not relevant. Three guidelines were used to reduce initial pool of research papers. Studies had to consider 'post settled' juvenile cod e.g. non-pelagic 0-group longer than 6 cm (Methven and Bajdik, 1994). Second, they had to report on presence, viability or source outcomes specifically relating to eelgrass, or to likely eelgrass habitat and water depth <10 m. Third, studies had as much as possible
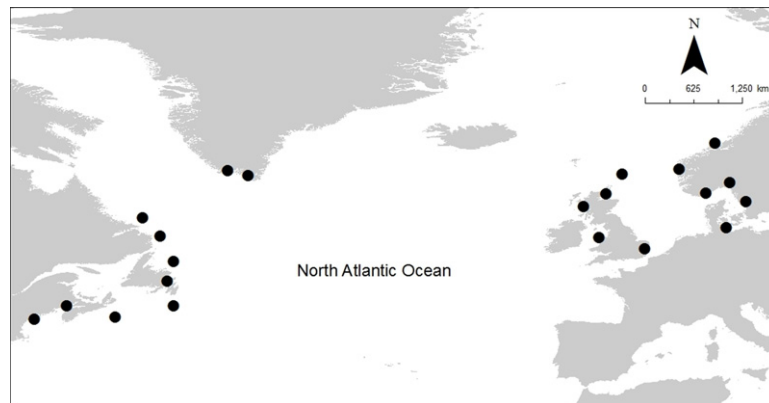
Fig. 1. Map of the North Atlantic showing in black the broad locations that were studied within the 50 data sources collated for analysis in the present study. Note the distribution of study areas is largely coastal with the exception of off-shore banks. The distribution of these studies approximates most of the broad extent of the known cod distribution (Watson et al., 2004).

to represent a geographical distribution of study sites across the North Atlantic, limiting the effect of study "Hot Spots" (Jackson et al., 2001).

Exclusion of certain papers to attempt an even geographic distribution was justified to endeavor to address the non-independence of data (Gurevitch et al., 1992) that occurs when a number of experiments or surveys are performed by the same investigator or research group in the same geographic area. For example many research studies from Newfoundland were excluded based on their repetition of existing research from the same locality. Through investigating potential commonalities among data that shared these characteristics, papers were limited to those that either involved new data, if data had been taken over consecutive years, or where the data came from different sites, and therefore could be considered independent. Furthermore, it was essential that the temporal and spatial scale of replication meant that different populations were being measured in each comparison.

2.4. Data analysis

Densities of juvenile cod per hectare were derived from the research papers. Densities were collated either directly from published figures, or calculated based upon raw catch data and area covered from seining. All mean summary statistics were calculated with their standard error.

Studies on juvenile cod identified in the literature search, were classified as investigating three key research themes: depth, age and habitat. Analysis on data extracted from these studies was then conducted. Geographical distributions of study areas were mapped and a size-depth chart was plotted to determine the depth related distribution of cod of different sizes. In order to determine the influence of sampling method upon reported densities, studies were compared relative to four sampling methods used (Underwater Visual Census UVC, 20 m beach seine, 30 m beach seine and trawl). Data sources available for purported viability gains were analyzed to determine the effect sizes of experiments. 'Cohen's d' as the Effect Size (ES) was calculated (Heck et al., 2003). Cohen's d is defined as the difference between the means divided by the pooled standard deviation (Cohen, 1988). The use of Cohen's d enabled all literature studies that report data on the presence of Atlantic cod in *Z. marina* as opposed to alternative habitat and the presence of juvenile fish in shallow waters <10 m to be compared on an equal basis.

3. Results

3.1. Presence of Atlantic cod in shallow nearshore Z. marina habitat

3.1.1. Spatial and temporal distribution of data sources

Data on the distribution of 0-group Atlantic cod has been collected for over a century. Fifty data sources documented the presence of juvenile cod in *Z. marina* in coastal shallow seas of the North Atlantic (≤4-group) (See Supplementary material, Appendix A), ranging from Cape Cod, USA in the West Atlantic to Trondheim, Norway in the East (Fig. 1). The data sources were evenly spatially distributed across the Atlantic although certain nations, notably Norway and Canada make the greatest contributions to the literature. Only 20% ($n = 10$) of individual data sources consisted of data from multiple coastal locations (multiple sites in one study).

Individual juvenile cod data sets could not always be pinpointed to specific individual *Z. marina* meadows based on a description within that specific study. Where secondary evidence was available to explicitly link the cod sampling to the presence of seagrass in that location, data was considered to be from a *Z. marina* meadow.
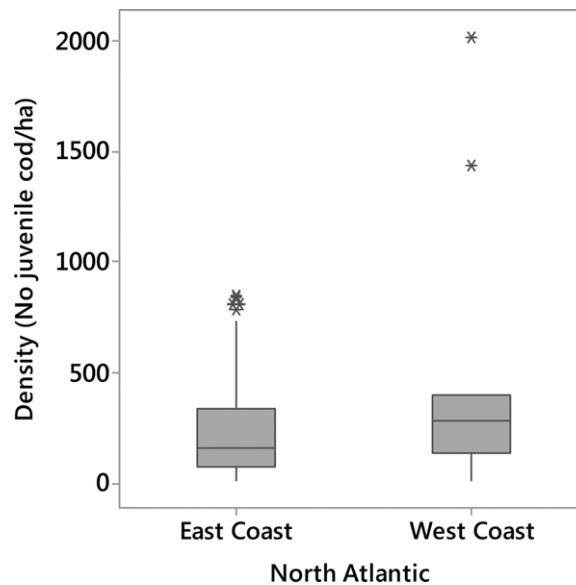
Fig. 2. Densities of juvenile Atlantic cod in the East Atlantic and the West Atlantic as derived from the sampled papers.

3.1.2. Preferences for Z. marina by juvenile G. morhua

Experimental field and laboratory studies provide conclusive evidence of a preference by juvenile Atlantic cod for vegetated habitats (including Fucus and Zostera habitats). These were conducted both sides of the Atlantic in Sweden, Norway and Newfoundland (Gjosaeter, 1987b,a; Borg et al., 1997; Gotceitas et al., 1997). Whether there exists an actual preference for *Z. marina* by juvenile Atlantic cod remains to be seen as other studies have even documented juvenile Atlantic cod preference for tall sponges (Gotceitas et al., 1997) and at artificial reef sites (Sargent et al., 2006). Other research using video systems have documented juvenile cod aggregations around pebble and gravel habitats on the Georges Bank (Lough and Bolz, 1989; Lough et al., 1989). Studies that have documented initial settlement rates of 0-group cod have also found no significant differences between habitat types (Tupper and Boutilier, 1995b).

3.2. Viability gains of Atlantic cod in Z. marina habitat

3.2.1. Abundance of Atlantic cod in Z. marina habitat

Density of surveyed juvenile cod (0-group) in the North West Atlantic is on average 1.4 times higher than mean density in the North East Atlantic (Fig. 2). On average there was $235.6 + 23.5$ juvenile cod. ha^{-1} in *Z. marina* of the North East Atlantic and 341.6 ± 116.4 juvenile cod. ha^{-1} in the North West Atlantic. The mean value from the North West Atlantic excludes one 'outlier' that records 2020 juvenile cod. ha^{-1}. All data was highly variable with densities in both east and west reaching only 10 juvenile cod. ha^{-1} in some localities. Caution must be shown in interpreting densities between the two coastlines due to the high variability in catch data within any one single paper—for example from 0 to 1300 fish/880 m^2 (Warren et al., 2010). Such differences are to be expected given the spatial and temporal differences between year strengths and the unbalanced use of survey methods between regions.

In the North East Atlantic juvenile cod were recorded in shallow nearshore waters in England, Wales, Scotland, Norway, Sweden and Germany. In the North West Atlantic juvenile cod were recorded in shallow nearshore waters in the USA, Canada and Greenland. Juvenile cod were also recorded in the West Atlantic in deeper waters on the Grand Banks. For example, surveys off Northeastern Newfoundland report distribution of age 0, 1, and 2 cod with respect to distance from shore, and hence depth. They found that 0-group cod were restricted to the coast, with ages 1 and 2 spread across the shelf to deeper water (Dalley and Anderson, 1997).

The densities of 0-group cod on the grand banks of Canada and the USA appear to be much lower than those found inshore, with figures reported between 0.49 and 7.12 cod/ha, although 'their abundance was patchy and at times strongly clustered' (Lough and Bolz, 1989).

Survey method can also be observed to have an effect on juvenile cod density data (Fig. 3). Cod were surveyed by Trawl, Gill Net, UVC and by 9, 14, 25, 30.5, 36, 38, and 40 m Seines. Density was not reported (or calculable) for 9 and 14 m Seine nets and other Seine net sizes have been collapsed into two categories. Trawl densities reported two orders of magnitude lower densities than those reported from UVC or Seining. This is likely a factor of the data coming from southern England and thus the southern boundary of the Atlantic cod's natural range, and from trawling being difficult over uneven or vegetated topography. Despite highly variable density levels, the three main survey methods report similar mean densities (trawl could not be included because it was an isolated data point).
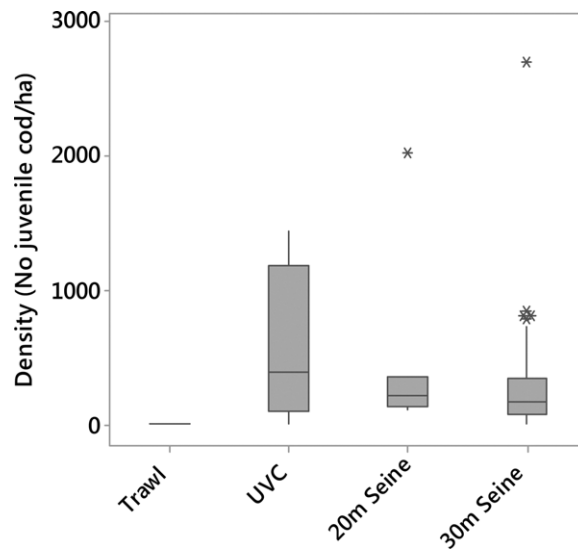
Fig. 3. Density of Atlantic cod by survey method as derived from sampled papers. Trawl data reported here is confounded by large survey areas at the limit of the Atlantic cod's natural range.

3.2.2. Viability gain through improved growth, foraging and survival

When growth of juvenile cod was compared in eelgrass relative to rocky reefs and cobble bottom habitats using visual assessments of marked individuals, growth in eelgrass was significantly higher (Tupper and Boutilier, 1995b). Similar increased growth rates were observed when cod were compared in eelgrass versus barren and open water habitats (Renkawitz et al., 2011), but these increases were only observed during spring and summer periods and not in the winter. Calculations of the relative costs of juvenile cod in Sweden utilizing different habitat types in terms of available prey density and foraging performance revealed that vegetated habitats were the most profitable to inhabit, but that bladderwrack habitat was a more profitable habitat than *Z. marina*. The authors do note that the differences were relatively small (Persson et al., 2012).

Predation rates on juvenile cod in *Z. marina* have been studied in a series of tethering experiments within seagrass relative to other habitat types (Linehan et al., 2001; Laurel et al., 2003; Gorman et al., 2009). This appears to be a function of fish size as well as being influenced by depth, time of day and habitat type. Predation was generally higher in un-vegetated compared to eelgrass sites during the day and dusk, but no difference could be observed at night (Linehan et al., 2001). Further studies in Newfoundland recorded predation rates on 0-group cod to be negatively correlated with eelgrass patch size, suggesting that larger patches reduce predator foraging ability (Laurel et al., 2003).

3.2.3. Viability gains in the West Atlantic

In Canada, surveys have caught 250–400 juvenile cod per seine in eelgrass in comparison to 0–20 per seine over sand (Linehan et al., 2001), these patterns have been confirmed both during daytime and nightime (Day: eelgrass 1.7 ± 0.7, sand 0.8 ± 0.5, Night: eelgrass 12.5 ± 3.7, sand 5.8 ± 1.9) (Anderson et al., 2007). Further south in the USA, CPUE of Atlantic cod was significantly higher in tows in *Z. marina* than adjacent habitats (Lazzari et al., 2003). Indeed, studies in Newfoundland found high densities of juvenile cod were found associated with eelgrass (Schneider et al., 2008) with one study reporting an 80% decline in fish abundance and biomass with *Z. marina* habitat loss (Morris et al., 2011). Studies have also reported increased density of 0-group juvenile Atlantic cod correlated with observed increase in eelgrass habitat (Warren et al., 2010; Morris et al., 2011). There exist further anecdotal evidence for the increased viability of individuals and populations in *Z. marina* within the West Atlantic, this evidence is summarized in Appendix 2 of the supplementary material.

3.2.4. Viability gains in the East Atlantic

In Scotland, high concentrations of juvenile Atlantic cod have been reported in St Andrews Bay (>100 cod. km^{-2}) and around Shetland (>1000 cod. km^{-2}) (Gibb et al., 2007). 99% of the total cod caught were found in depths less than 26 m (Gibb et al., 2007). Although not explicitly linked, both these areas are known to have extensive *Z. marina* meadows (Wilkie, 2012) and studies (from other localities) reveal how juvenile Atlantic cod typically migrate in and out of *Z. marina* with respect to time of day (Keats and Steele, 1992). In Sweden juvenile 0-group cod density was reduced by 96% at sites where *Z. marina* had disappeared (Pihl et al., 2006) and in Norway, the longest and most robust data set globally available reports that the rapid decrease of juvenile Atlantic cod during the 1920s was correlated with the disappearance of *Z. marina* meadows (Tveite, 1984). The only data available for juvenile Atlantic cod in *Z. marina* relative to other habitats within the Irish Sea comes from two studies on the North West coast of Wales, but densities in both are very low (Bertelli and Unsworth, 2014;

Table 1
The relative ES for multiple observations (i) Presence of Atlantic cod in *Z. marina* as opposed to alternative habitat, (ii) Presence of juvenile fish in shallow waters < 10 m.

Author	Country	Coast	Effect	Effect size
Hansen and Lehmann (1986)	Greenland	West	Presence < 10 m	0.51
Nygaard et al. (1989)	Greenland	West	Presence < 10 m	1.72
Ings et al. (1997)	Canada	West	0-group	1.01
Methven and Schneider (1998)	Canada	West	0-group	0.76
Linehan et al. (2001)	Canada	West	Presence in *Z. marina*	9.24
Laurel et al. (2003)	Canada	West	Presence in *Z. marina*	2.30
Lazzari et al. (2003)	USA	West	Presence in *Z. marina*	−0.92
Anderson et al. (2007)	Canada	West	Presence in *Z. marina*	0.41
Warren et al. (2010)	Canada	West	Presence in *Z. marina*	0.37
Fjøsne and Gjøsæter (1996)	Sweden	East	Presence in *Z. marina*	5.63
Borg et al. (1997)	Sweden	East	Presence in *Z. marina*	5.23
Pihl et al. (2006)	Sweden	East	Presence in *Z. marina*	1.70
Gibb et al. (2007)	Scotland	East	Presence < 10 m	1.80
Gibb et al. (2008)	Scotland	East	Presence < 10 m	2.00

Peters et al., in press; Unsworth et al., in press). Intertidal diel seine netting over multiple seasons at one site finds juvenile cod in *Z. marina* but not in adjacent sand, whilst comparative analysis between *Z. marina* and Kelp forests using Stereo BRUV systems again found similar results (Bertelli and Unsworth, 2014; Unsworth et al., in press). There exist further anecdotal evidence for the increased viability of individuals and populations in *Z. marina* within the East Atlantic, this evidence is summarized in Appendix 2 of the supplementary material.

3.2.5. Effect-size of viability gains for Atlantic cod in Z. marina habitat

The rational for 0-group Atlantic cod selecting shallow nearshore habitat and specifically exhibiting a preference for *Z. marina* is that there is a selective advantage in doing so. On this basis it should be expected that 0-group cod are more numerous in the ≦10 m depth range than 1–4 group cod, that there are a greater number of 0-group Atlantic Cod in the ≦10 m environment than in > 10 m deeper waters, and that there should be more 0-group Atlantic cod in *Z. marina* than in alternative habitats.

There exists higher abundance of 0-group juvenile Atlantic cod in shallow waters (< 10 m depth) and eelgrass in both the East and the West Atlantic (Table 1). The mean ES for finding 0-group Atlantic cod in < 10 m water as opposed to > 10 m is 1.9 (±0.1) in the East Atlantic and for densities of Atlantic cod in *Z. marina* as opposed alternative habitat 4.2 (±2.2). In the West Atlantic the mean ES for finding 0-group Atlantic Cod in < 10 m water as opposed to > 10 m is 1.1 (±0.9), for densities of Atlantic cod in *Z. marina* as opposed to alternative habitat is 3.5 (±5.2), and for finding 0-group fish as opposed to 1-group or greater fish is 0.9 (±0.2).

3.3. Shallow nearshore Z. marina habitat as a source of juveniles to form adult Atlantic cod

3.3.1. Evidence supporting the role of Z. marina habitat as a source of juveniles to adult populations of Atlantic cod

88% (n = 42) of the data sources recorded juvenile Atlantic cod within waters < 15 m and 86% (n = 36) of these reported fish were less than 25 cm in length; classifying them as 0-group and 1-group cod. The majority (80%) of data sources available for juvenile, 0-group, (≦10 cm) codlings find them to occur in the first 10 m of water.

The size of juvenile Atlantic cod was found to increase with depth in the marine environment (Fig. 4), indicating the ontogenetic migration of these individuals to deeper waters. 0-group Atlantic cod were additionally also found in a few studies on offshore banks at depths of approximately 80 m, but density was low and occurrences rare. There was a positive correlation between size and depth, which was statistically significant "($r_s = 0.480, p = 0.004$)" (Fig. 4). This is in accordance with Heinckes Law (Heincke, 1913).

Tagging studies from the West Coast of Sweden confirm such ontogenetic migrations of juvenile Atlantic cod into deeper waters to join adult stocks (Pihl and Ulmestrand, 1993; Svedang et al., 2007). Studies from the Gulf of St Laurence (Canada) also observe similar migration patterns of juvenile cod (Hansen and Lehmann, 1986). Although these studies do not specifically focus on the juvenile Atlantic cod from *Z. marina* they are conducted in locations where numerous studies have recorded high densities of juvenile Atlantic cod in extensive seagrass meadows. No genetic, isotopic or microchemical studies were available to specifically apportion individual juvenile cod in *Z. marina* to any one individual stock. Such evidence was also not found for any other single habitat (e.g. kelp, gravels) either.

4. Discussion

Here we demonstrate a valuable nursery role for *Z. marina* in supporting populations of Atlantic cod across its distribution. This is important as management of *Z. marina* meadows mostly happens at local levels and locally specific information on this link is not always available.
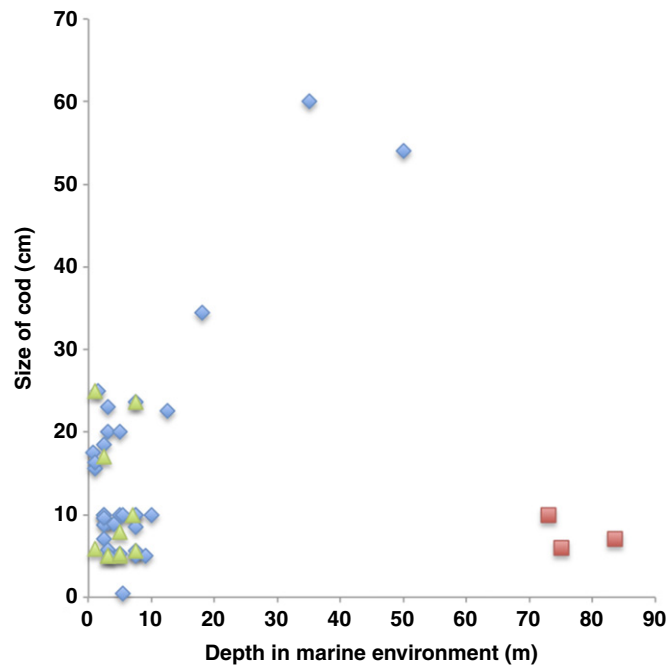
Fig. 4. Atlantic cod increases with depth in the marine environment ($n = 35$) in accordance with Heincke's Law (Heincke, 1913). Note the repeated presence of juvenile Atlantic cod (<10 cm, 0-group) nearshore (<10 m deep) in both *Z. marina* (▲) and other substrates (♦), but also their presence on deeper offshore banks e.g. Grand Banks (>20 m □).

Z. marina likely enhances growth and survival of Atlantic cod, increasing its viability and chances of reaching maturation. 0-group Atlantic cod occur are mostly found confined to shallow coastal areas containing habitats such as seagrass. A large volume of data is available to suggest that a significant proportion of these individuals using these coastal areas settle (where possible) in *Z. marina* habitat. Concentrated distributions of juvenile Atlantic cod have been reported on both sides of the North Atlantic in inshore waters. Studies in Scotland confirmed that the shallow and nearshore areas are the most important areas for juvenile Atlantic Cod (Gibb et al., 2007) with 99% of the total 0-group found in depths less than 26 m (Gibb et al., 2008).

0-group Atlantic cod can use multiple habitat types within coastal waters, particularly *Z. marina* and other 3D complex habitats on shallow banks. But there is strong evidence that 0-group Atlantic cod uses and favors *Z. marina*. Much of the evidence for this assertion comes from the West Atlantic based on targeted surveys within *Z. marina* conducted in Canada. This is in comparison to the east, which largely constitutes data from nearshore seagrass associated waters more broadly. Regardless of the variation in the data, the important conclusion to draw here is that average density of juvenile Atlantic cod in or in very close proximity to seagrass are at least 246 individuals. ha^{-1}.

A multitude of factors contribute to successful Atlantic cod recruitment (Runge et al., 2010) and this may be limiting to the population. Modeling indicates the influence of recruitment is probably outweighed by competition for limited resources, primarily living space as demersal juveniles (Iles and Beverton, 2000). Seasonal abundances of pelagic Atlantic cod juveniles are in some cases an order of magnitude higher in some years, but recruitment at age 1 being smaller; indicating a high mortality of juveniles at the demersal stage (Lough, 2010). Available juvenile habitat is therefore critical in reducing demersal mortality. If juvenile habitat is one of the major limiting factors restricting Atlantic cod recruitment, then the quality and availability of the habitat is of critical importance to stocks.

Logically the fittest individuals will be those that recruit successfully to the adult breeding stock. It is known that overwinter survival of temperate fishes is usually poorer for smaller individuals (Sogard, 1997) and thus recruitment to the 1-group will be dependent on the size of the 0-group Atlantic cod in the fall. The growth of 0-group Atlantic cod was significantly higher in *Z. marina* relative to barren, open water, cobble and rocky reef environments (Tupper and Boutilier, 1995a; Renkawitz et al., 2011). Atlantic cod growing faster and being biologically 'fitter' from developing in *Z. marina* meadows will be those that are more likely to spawn.

In a scenario of density-dependent competition it will be the biologically fittest individuals who prosper, and indeed a size-specific hierarchy is known to exist, with larger fish controlling larger territories (Tupper and Boutilier, 1995a,c). Survival after 1 month is highly correlated to available shelter and habitat complexity (Tupper and Boutilier, 1995b) and juvenile Atlantic cod actively choose such complex habitat (Gjosaeter, 1987a,b). If juvenile Atlantic cod are competing for shelter sites this would infer that shelter from predation is a critical limiting factor at this stage.

Studies provide evidence for the decreased level of predatory pressure present within large continuous seagrass meadows (Linehan et al., 2001; Laurel et al., 2003; Gorman et al., 2009). In incidences where juvenile Atlantic cod are found on sand bottoms they exhibit schooling behavior indicative of the need to seek protection. This may well occur because those individuals cannot compete for shelter sites (Tupper and Boutilier, 1995b,a). Support for post-settlement processes creating a carrying capacity for juvenile habitat is also supported by offshore observations from Georges Bank, where transitional pelagic juvenile Atlantic cod are widespread over the bank in June but by July the surviving demersal juveniles are found mainly on the more complex pebble–gravel meadows than the less complex substrates of the bank. This suggests that it is the availability of complex habitat that increases survival of demersal juveniles, and that complex habitat increases carrying capacity of juvenile Atlantic cod.

Complexity offers shelter from predation and subsequent reduced energy expenditure, but it is the nature of what creates the complexity that makes the habitat truly valuable. Higher growth rates of juvenile Atlantic cod in seagrass (Heck et al., 2003) have been attributed to greater prey densities (Tupper and Boutilier, 1995b). *Z. marina* is commonly found to harbor higher macro-invertebrate densities (such as crustaceans) than adjacent habitats (Sogard, 1992). This is striking since crustacea represent, at 81.6%, the largest portion of the diet of juvenile Atlantic cod (Bowman, 1981).

Whilst growth rate was highest in seagrass meadows, survival of juvenile Atlantic cod was highest on rocky reefs and cobble bottoms, representing a trade-off occurring between energy gain and predation risk (Heck et al., 1995; Frost et al., 1999; Heck et al., 2003), both at an individual and a population level. This is particularly important when the lower spatial extent of seagrass is considered against alternative habitats that are potentially widespread over shallow water banks. Alternative nursery habitats may not provide the viability benefits of *Z. marina* but the potential spatial extent of such habitats, particularly in the West Atlantic may result in population level benefits due to their high potential carrying capacity.

No evidence exists that directly links adult Atlantic cod to specific *Z. marina* meadows, and thus nothing to directly support the notion of seagrass as a 'source' of juveniles, as opposed to a 'sink' of juveniles (Pulliman, 1988). Although no direct evidence can be found, neither does any form of evidence refute any link. Importantly, no studies have directly linked adult Atlantic cod to any other specific habitat type either (e.g. kelp, rocky, sponge, or cobble) in any location.

In spite of the limited direct evidence, indirect evidence is available of the link between 0-group Atlantic cod and shallow nearshore environments containing extensive *Z. marina* meadows (Gibb et al., 2007; Maddock, 2008). Indeed, numerous studies show the ontogenetic migration of older, larger individuals to increasing depth allowing for the creation of generalized life-history patterns for Atlantic cod stocks in both the West and East Atlantic (Zeller and Pauly, 2001). This life-history pattern is endorsed by the present study which shows that there is a positive size-depth relationship seen in Atlantic cod where fish tend to move into deeper water as they grow bigger (Heincke, 1913). Importantly, the relative abundance of 0-group Atlantic cod reported in *Z. marina* meadows as opposed to alternative habitat suggest *Z. marina* may well be acting as a source of Atlantic cod that supplies the adult population.

Atlantic cod populations can exist without *Z. marina*, since juvenile Atlantic cod recruit from offshore nursery grounds without ever seeing a *Z. marina* meadow. There is also extensive data describing 0-group Cod present in habitats such as sand, cobble and sponge (Gotceitas and Brown, 1993; Lindholm et al., 1999) and data pertaining to high juvenile densities on scallop shell hash and sponge across the Scotian Self (Tupper, 1991). Thus, Atlantic cod use of *Z. marina* is facultative—they use it when they can. What is important is that it can be conclusively demonstrated that juvenile Atlantic cod intentionally select *Z. marina* as a nursery habitat and receive behavioral and fitness benefits from it (Gotceitas et al., 1997; Laurel et al., 2003), and that juvenile Atlantic cod density responds positively to the expansion of *Z. marina* cover (Warren et al., 2010), and negatively to its removal (Tveite, 1984).

In large areas of the North Atlantic fisheries management is mostly (e.g. EU Common Fisheries Policy) disconnected from nursery habitat management, and conservation of *Z. marina* habitat is largely restricted to being a biodiversity conservation concern. The present study provides evidence that in addition to the important role of seagrasses in supporting coastal biodiversity these productive habitats are of significant importance to sustaining the financially important Cod fisheries of the North Atlantic. Such fisheries contribute to the GDP of many nations and employ thousands of people. Atlantic Cod is only one of a number of commercially important species that may utilize seagrass meadows as nursery habitat (e.g. Pollock, Plaice and Herring) in the North Atlantic (Jackson et al., 2001; Bertelli and Unsworth, 2014) suggesting the value of seagrass in supporting commercial fisheries is largely undervalued.

While our literature search finds clear evidence of the selective choice of Atlantic cod for seagrass, the viability benefits of such a choice and the overwhelming abundance of these juvenile fish in seagrass their remains considerable spatial gaps in the knowledge and limited repetition of studies (e.g. choices and viability gains). Although we feel our conclusions are valid across the scale of the North Atlantic we recognize that more experimental information is needed to tease out the intricacies of these relationships.

In conclusion, this paper supports the notion that *Z. marina* provides Valuable Nursery Habitat for Atlantic cod. These productive habitats are therefore of significant importance to contributing to Atlantic cod. With the current poor state of Atlantic cod stocks, and in light of the evidence collated in this meta-analysis greater emphasis within fisheries management should be placed on protecting and rehabilitating Valuable Nursery Habitat such as *Z. marina*. Given that large areas of *Z. marina* have been lost throughout the 20th and 21st centuries the available evidence suggests that environmental renewal will enhance the long-term productivity of the Cod fishery by enhancing its breeding stock.

Acknowledgment

Appendix A. Supplementary data

Supplementary material related to this article can be found online at http://dx.doi.org/10.1016/j.gecco.2014.10.002.

References

Anderson, J.T., Gregory, R.S., 2000. Factors regulating survival of northern cod (NAFO 2J3KL) during their first 3 years of life. ICES J. Mar. Sci. 57, 349–359.

Anderson, J.L., Laurel, B.J., Brown, J.A., 2007. Diel changes in behaviour and habitat use by age-0 Atlantic cod (*Gadus morhua* L.) in the laboratory and field. J. Exp. Mar. Biol. Ecol. 351, 267–275.

Baden, S., Gullstrom, M., Lunden, B., Pihl, L., Rosenberg, R., 2003. Vanishing seagrass (Zostera marina, L.) in Swedish coastal waters. Ambio 32, 374–377.

Beck, M.W., Heck Jr., K.L., Able, K.W., Childers, D.L., Eggleston, D.B., Gillanders, B.M., Halpern, B., Hays, C.G., Hoshino, K., Minello, T.J., 2001. The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. BioScience 51, 633–641.

Bertelli, C.M., Unsworth, R.K.F., 2014. Protecting the hand that feeds us: seagrass (*Zostera marina*) serves as commercial juvenile fish habitat. Mar. Pollut. Bull 83 (2), 425–429. http://dx.doi.org/10.1016/j.marpolbul.2013.08.011.

Borg, Å., Pihl, L., Wennhage, H., 1997. Habitat choice by juvenile cod (Gadus morhua L.) on sandy soft bottoms with different vegetation types. Helgol. Meeresunters. 51, 197–212.

Bowman, R.E., 1981. Food of 10 species of Northwest Atlantic juvenile groundfish. Fish. Bull. 79, 200–206.

Cannon, J., 1997. Northeast Atlantic FAO, Review of the State of World Fishery Resources: Marine Fisheries. FAO, Rome, Italy.

Cohen, J., 1988. Statistical Power Analysis for the Behavioral Sciences. Lawrence Erlbaum Associates, New Jersey.

Cullen-Unsworth, L.C., Nordlund, L.M., Paddock, J., Baker, S., McKenzie, L.J., Unsworth, R.K.F., 2014. Seagrass meadows globally as a coupled social–ecological system: implications for human wellbeing. Mar. Pollut. Bull. 83, 387–397.

Cullen-Unsworth, L.C., Unsworth, R.K.F., 2013. Seagrass meadows, ecosystem services, and sustainability. Environment 55, 14–27.

Dahlgren, C.P., Kellison, G.T., Adams, A.J., Gillanders, B.M., Kendall, M.S., Layman, C.A., Ley, J.A., Nagelkerken, I., Serafy, J.E., 2006. Marine nurseries and effective juvenile habitats: concepts and applications. Mar. Ecol. Prog. Ser. 312, 291–295.

Dalley, E.L., Anderson, J.T., 1997. Age dependent distribution of demersal juvenile cod (*Gadus morhua*) in inshore/offshore northeast Newfoundland. Can. J. Fish. Aquat. Sci. 54, 168–176.

Dannevig, A., 1954. The littoral cod of the Norwegian Skagerrak coast, Rapports et procès-verbaux des réunions, In: Conseil permanent international pour l'exploration de la mer, vol. 136, pp. 7–14.

Fjøsne, K., Gjøsæter, J., 1996. Dietary composition and the potential of food competition between 0-group cod (*Gadus morhua L.*) and some other fish species in the littoral zone. ICES J. Mar. Sci. 53, 757–770.

Froese, R., Pauly, D.E., 2013. FishBase. World Wide Web electronic publication, version (09/2013).

Frost, M.T., Rowden, A.A., Attrill, M.J., 1999. Effect of habitat fragmentation on the macroinvertebrate infaunal communities associated with the seagrass Zostera marina L. Aq. Cons. Mar. Fr. Ecos. 9, 255–263.

Gibb, F.M., Gibb, I.M., Wright, P.J., 2007. Isolation of Atlantic cod (Gadus morhua) nursery areas. Mar. Biol. Lett. 151, 1185–1194.

Gibb, I.M., Wright, P.J., Campbell, R., 2008. Identifying critical spawning and nursery areas for North Sea Cod; improving the basis for cod management. Scottish Industry/Science Partenrship (SISP).

Gillanders, B.M., 2006. Seagrasses, fish, and fisheries. In: Larkum, A.W., Orth, R.J., Duarte, C.M. (Eds.), Seagrasses: Biology, Ecology and Conservation. Springer, pp. 503–536.

Gjosaeter, J., 1987a. Habitat selection of juvenile cod (Gadus morhua), whiting (Merlangus merlangius) and some littoral fish in an aquarium. Flød. Rapp. 1, 17–26.

Gjosaeter, J., 1987b. Habitat selection and inter year class interaction in young cod (*Gadus morhua*) in aquaria. Flød. Rapp. 1, 27–36.

Gorman, A.M., Gregory, R.S., Schneider, D.C., 2009. Eelgrass patch size and proximity to the patch edge affect predation risk of recently settled age 0 cod (Gadus). J. Exp. Mar. Biol. Ecol. 371, 1–9.

Gotceitas, V., Brown, J., 1993. Substrate selection by juvenile Atlantic cod (Gadus morhua): effects of predation risk. Oecologia 93, 31–37.

Gotceitas, V., Fraser, S., Brown, J.A., 1997. Use of eelgrass beds (Zostera marina) by juvenile Atlantic cod (Gadus morhua). Can. J. Fish. Aquat. Sci. 54, 1306–1319.

Green, E.P., Short, F.T., 2003. World Atlas of Seagrasses. University of California Press, Berkley, USA.

Gurevitch, J., Morrow, L.L., Wallace, A., Walsh, J.S., 1992. A meta-analysis of competiton in field experiments. Am. Nat. 140, 539–572.

Hansen, H., Lehmann, K., 1986. Distribution of Young Cod in coastal regions of West Greenland, 1985. Northwest Atlantic Fisheries Organisation Scientific Council Studies.

Hanson, A.R., 2004. Status and conservation of eelgrass (Zostera marina) in Eastern Canada. Final Report. Australian Fisheries Management Authority Repor. R99/1546. Technical Report Series Canadian Wildlife Service. Atlantic Region. viii. +, p. 40.

Heck, K.L., Able, K.W., Roman, C.T., Fahay, M.P., 1995. Composition, abundance, biomass, and production of macrofauna in a New-England estuary—comparisons among eelgrass meadows and other nursery habitats. Estuaries 18, 379–389.

Heck, K., Hays, G., Orth, R., 2003. Critical evaluation of the nursery role hypothesis for seagrass meadows. Mar. Ecol. Prog. Ser. 253, 123–136.

Heincke, F., 1913. Untersuchungen über die Scholle-Generalbericht I. Schollenfischerei und Schonmassregeln. Vorlaeufige kurze Uebersicht über die wichtigsten Ergebnisse des Berichts. Rapp. Proc. Verb. Réun. ICES 16, 1–70.

Iles, T.C., Beverton, R.J.H., 2000. The concentration hypothesis: the statistical evidence. ICES J. Mar. Sci. 57, 216–227.

Ings, D.W., Schneider, D.C., Methven, D.A., 1997. Detection of a recruitment signal in juvenile Atlantic Cod (*Gadus morhua*) in coastal nursery areas. Can. J. Fish. Aquat. Sci. 54, 25–29.

Jackson, E.L., Rowden, A.A., Attrill, M.J., Bossey, S., Jones, M., 2001. The importance of seagrass beds as a habitat for fishery species. Oceanogr. Mar. Biol. 39, 269–304.

Keats, D.W., Steele, D.H., 1992. Diurnal feeding of juvenile cod (*Gadus morhua*) which migrate into shallow water at night in Eastern Newfoundland. J. Northwest Atl. Fish. Sci. 13, 7–14.

Laurel, B.J., Gregory, R.S., Brown, J.A., 2003. Predator distribution and habitat patch area determine predation rates on Age-0 juvenile cod Gadus spp. Mar. Ecol. Prog. Ser. 251, 245–254.

Layman, C.A., Dahlgren, C.P., Kellison, G.T., Adams, A.J., Gillanders, B.M., Kendall, M.S., Ley, J.A., Nagelkerken, I., Serafy, J.E., 2006. Marine nurseries and effective juvenile habitats. Mar. Ecol. Prog. Ser. 318, 307–308.

Lazzari, M.A., Sherman, S., Kanwit, J.K., 2003. Nursery use of shallow habitats by epibenthic fishes in Maine nearshore waters. Estuar. Coast. Shelf Sci. 56, 73–84.

Lindholm, J.B., Auster, P.J., Kaufman, L.S., 1999. Habitat-mediated survivorship of juvenile (0-year) Atlantic cod Gadus morhua. Mar. Ecol. Prog. Ser. 180, 247–255.

Linehan, J.E., Gregory, R.S., Schneider, D.C., 2001. Predation risk of age-0 cod (Gadus) relative to depth and substrate in coastal waters. J. Exp. Mar. Biol. Ecol. 263, 25–44.

Lough, R.G., 2010. Juvenile cod (Gadus morhua) mortality and the importance of bottom sediment type to recruitment on Georges Bank. Fish. Oceanogr. 19, 159–181.

Lough, R.G., Bolz, G.R., 1989. The movement of cod and haddock larvae onto the shoals of Georges Bank. J. Fish Biol. 35, 71–79.

Lough, R.G., Valentine, P.C., Potter, D.C., Auditore, P.J., Bolz, G.P., Neilson, J.D., Perry, R.I., 1989. Ecology and distribution of juvenile cod and haddock in relation to sediment type and bottom currents on eastern Georges Bank. Mar. Ecol. Prog. Ser. 56, 1–12.

Løversen, R., 1946. Torskens vekst og vandringer påSørlandet. Fiskerid. Skrif. Ser. Havunders. 8, 1–34.

Maddock, A., 2008. Priority habitat descriptions: UK biodiversity action plan. UK Government.

Methven, D.A., Bajdik, C., 1994. Temporal variation in size and abundance of juvenile atlantic cod (*Gadus morhua*) at an inshore site off eastern Newfoundland. Can. J. Fish. Aquat. Sci. 51, 78–90.

Methven, D.A., Schneider, D.C., 1998. Gear-independent patterns of variation in catch of juvenile Atlantic cod (*Gadus morhua*) in coastal habitats. Can. J. Fish. Aquat. Sci. 55, 1430–1442.

Morris, C.J., Gregory, R.S., Laurel, B.J., Methven, D.A., Warren, M.A., 2011. Potential effect of eelgrass (*Zostera marina*) loss on nearshore Newfoundland fish communities, due to invasive green crab (Carcinus maenas). Canadian Science Advisory Secretariat Research Document, Fisheries and Oceans Canada.

Nagelkerken, I., Sheaves, M., Baker, R., Connolly, R.M., 2013. The seascape nursery: a novel spatial approach to identify and manage nurseries for coastal marine fauna. Fish Fisheries.

Nygaard, K., Lehmann, K., Hovgård, H., 1989. Young cod distribution and abundance in West Greenland Inshore Areas, 1988. In: Northwest Atlantic Fisheries Organisation Scientific Council Studies.

Persson, A., Ljungberg, P., Andersson, M., Gotzman, E., Nilsson, P.A., 2012. Foraging performance of juvenile Atlantic cod Gadus morhua and profitability of coastal habitats. Mar. Ecol. Prog. Ser. 456, 245–253.

Peters, J.R., McCloskey, R.M., Hinder, S.L., Unsworth, R.K.F., 2014. Motile fauna of sub-tidal Zostera marina meadows in England and Wales. Mar. Biodivers. 1–8. http://dx.doi.org/10.1007/s12526-014-0264-x. in press.

Pihl, L., Baden, S., Kautsky, N., Ronnback, P., Soderqvist, T., Troell, M., Wennhage, H., 2006. Shift in fish assemblage structure due to loss of seagrass Zostera marina habitats in Sweden. Estuar. Coast. Shelf Sci. 67, 123–132.

Pihl, L., Ulmestrand, M., 1993. Migration pattern of juvenile cod (Gadus morhua) on the Swedish west-coast. ICES J. Mar. Sci. 50, 63–70.

Pulliman, H.R., 1988. Sources, sinks and population regulations. Am. Nat. 132, 652–661.

Renkawitz, M.D., Gregory, R.S., Schneider, D.C., 2011. Habitat dependant growth of three species of bottom settling fish in a coastal fjord. J. Exp. Mar. Biol. Ecol. 409, 79–88.

Rice, J.C., Garcia, S.M., 2011. Fisheries, food security, climate change, and biodiversity: characteristics of the sector and perspectives on emerging issues. ICES J. Mar. Sci. 68, 1343–1353.

Runge, J.A., Kovach, A.I., Churchill, J.H., Kerr, L.A., Morrison, J.R., Beardsley, R.C., Berlinsky, D.L., Chen, C.S., Cadrin, S.X., Davis, C.S., Ford, K.H., Grabowski, J.H., Howell, W.H., Ji, R.B., Jones, R.J., Pershing, A.J., Record, N.R., Thomas, A.C., Sherwood, G.D., Tallack, S.M.L., Townsend, D.W., 2010. Understanding climate impacts on recruitment and spatial dynamics of Atlantic cod in the Gulf of Maine: integration of observations and modeling. Prog. Oceanogr. 87, 251–263.

Salomon, A.K., Gaichas, S.K., Jensen, O.P., Agostini, V.N., Sloan, N.A., Rice, J., McClanahan, T.R., Ruckelshaus, M.H., Levin, P.S., Dulvy, N.K., Babcock, E.A., 2011. Bridging the divide between fisheries and marine conservation science. Bull. Mar. Sci. 87, 251–274.

Sargent, P.S., Gregory, R.S., Schneider, D.C., 2006. Density responses of subarctic coastal marine fish and crabs to artificial reefs. Trans. Am. Fish. Soc. 135, 348–360.

Schneider, D.C., Norris, M.J., Gregory, R.S., 2008. Predictive analysis of scale-dependent habitat association: juvenile cod (Gadus spp.) in eastern Newfoundland. Estuar. Coast. Shelf Sci. 79, 71–78.

Seitz, R.D., Wennhage, H., Bergström, U., Lipcius, R.N., Ysebaert, T., 2013. Ecological value of coastal habitats for commercially and ecologically important species. ICES J. Mar. Sci. Journal du Conseil.

Sheaves, M., Baker, R., Johnston, R., 2006. Marine nurseries and effective juvenile habitats: an alternative view. Mar. Ecol. Prog. Ser. 318, 303–306.

Short, F.T., Wyllie-Echeverria, S., 1996. Natural and human-induced disturbance of seagrasses. Environ. Conserv. 23, 17–27.

Sogard, S.M., 1992. Variability in growth rates of juvenile fishes in different estuarine habitats. Mar. Ecol. Prog. Ser. 85, 35–53.

Sogard, S.M., 1997. Size-selective mortality in the juvenile stage of teleost fishes: a review. Bull. Mar. Sci. Gulf Carribean 60, 1129–1157.

Sundblad, G., Bergström, U., Sandström, A., Eklöv, P., 2013. Nursery habitat availability limits adult stock sizes of predatory coastal fish. ICES J. Mar. Sci. Journal du Conseil.

Svedang, H., Righton, D., Jonsson, P., 2007. Migratory behaviour of Atlantic cod Gadus morhua: natal homing is the prime stock-separating mechanism. Mar. Ecol. Prog. Ser. 345, 1–12.

Tupper, M., 1991. Unpublished data collected aboard the Fisheries and Oceans Canada research vessel MV Lady Hammond.

Tupper, M., Boutilier, R.G., 1995a. Size and priority affect growth and competitive success of newly settled Atlantic cod. Mar. Ecol. Prog. Ser. 118, 295–300.

Tupper, M., Boutilier, R.G., 1995b. Effects of habitat on settlement, growth, and postsettlement survival of Atlantic cod (Gadus morhua). Can. J. Fish. Aquat. Sci. 52, 1834–1841.

Tupper, M., Boutilier, R.G., 1995c. Effects of conspecific density on settlement, growth and post-settlment survival of a temperate reef fish. J. Exp. Mar. Biol. Ecol. 191, 209–222.

Tveite, S., 1984. 0-Group Cod investigations on the Norwegian Skagerrak coast. Flød. Rapp. 1, 581–590.

Unsworth, R.K.F., Cullen, L.C., 2010. Recognising the necessity for Indo-Pacific seagrass conservation. Conserv. Lett. 3, 63–73.

Unsworth, R.K.F., Hinder, S.L., Bodger, O.G., Cullen-Unsworth, L.C., 2014. Food supply depends on seagrass meadows in the coral triangle. Environ. Res. Lett. 9, 094005.

Unsworth, R.K.F., Peters, J.R., Mccloskey, R.M., Hinder, S.L., 2014. Optimising stereo baited underwater video for sampling fish and invertebrates in temperate coastal habitats. Estuar. Coast. Shelf Sci. http://dx.doi.org/10.1016/j.ecss.2014.03.020. in press.

Warren, M.A., Gregory, R.S., Laurel, B.J., Snelgrove, P.V.R., 2010. Increasing density of juvenile Atlantic (Gadus morhua) and Greenland cod (G. ogac) in association with spatial expansion and recovery of eelgrass (Zostera marina) in a coastal nursery habitat. J. Exp. Mar. Biol. Ecol. 394, 154–160.

Watson, R., Kitchingman, A., Gelchu, A., Pauly, D., 2004. Mapping global fisheries: sharpening our focus. Fish Fisheries 5, 168–177.

Waycott, M., Duarte, C.M., Carruthers, T.J.B., Orth, R.J., Dennison, W.C., Olyarnik, S., Calladine, A., Fourqurean, J.W., Heck, K.L., Hughes, A.R., Kendrick, G.A., Kenworthy, W.J., Short, F.T., Williams, S.L., 2009. Accelerating loss of seagrasses across the globe threatens coastal ecosystems. Proc. Natl. Acad. Sci. USA 106, 12377–12381.

Wilkie, L., 2012. The role of intertidal seagrass Zostera spp. in sediment deposition and coastal stability in the Tay Estuary, Scotland. University of St Andrews.

Zeller, D., Pauly, D., 2001. Visualization of standardized life-history patterns. Fish Fisheries 2, 344–355.