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The range of juvenile movements of estuarine and coastal nursery dependent flatfishes: estimation from a meta-analytical approach



Olivier Le Pape, Noriane Cognez

AGROCAMPUS OUEST, UMR985 ESE Ecologie et santé des écosystèmes, F-35042 Rennes, France

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ABSTRACT

The juvenile pleuronectiforms need specific feeding and sheltering conditions in order to succeed in the critical period following their metamorphosis. This dependence to restricted nurseries grounds is the reason why movements are limited along this stage of flatfish development relative to the larval planktonic stage. However, a controversy remains about the home range of young-of-the-year coastal and estuarine-dependent flatfishes: both a limited home range and the capacity of considerable movements are alternatively reported. In the present meta-analysis based on a review of existing literature on pleuronectiforms, we gathered information about young-of-the-year flatfish movements, in order to better understand the scale of their dependence to local habitat (i.e., whether and at which scale they move between different habitats of a nursery area). For this meta-analysis, two different methods were retained to estimate the range of movements: the daily maximal distance of displacement and the minimal distance of segregation between distinct pools of flatfishes (contrasted patterns in natural tracers, growth, and fitness). We analysed patterns in daily movements and distances of segregation with respect to habitat features and to fish life history, accounting for discrepancies linked to methods of estimation. The scale of movements depends on both semi-passive tidal transport, linked to tidal amplitude, and the ability of individuals to move, which is related to body length of the group-0 flatfishes, but remains limited (few 100 s meters without tidal cyclic migration). These moderate movements lead to segregation among patches of juvenile fish at small scales in upstream–downstream estuarine gradients (5 km), and of moderate scales along the coastline (10 km). This meta-analytical approach allowed for the resolution of strong dependence of young of the year flatfishes upon local nursery habitats.

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1. Introduction

Most marine fish species are mobile and undertake quite large migrations (Harden, 1968). Especially, marine fish have dispersive drifting planktonic larval stages and migrate at the adult stage for spawning. In contrast, the requirements of juvenile fishes differ from those of larvae, sub-adults, and adults (Adams et al., 2004) and, for many species, juveniles have relatively small home ranges (Peterson, 2003; White and Brown, 2013). Especially, for pleuronectiforms (Gibson, 2005), the influence of hydrodynamics and larval vertical movements may lead to important transport during the egg and larval stages (Savina et al., 2010). After metamorphosis, the postsettlement juvenile benthic life leads to dramatically lower movements and, for a large proportion of flatfish species, concentration of individuals within coastal and estuarine-limited habitats (e.g., Rochette et al., 2010; Trimoreau et al., 2013). Older juveniles (Furey et al., 2013), subadults, and adult flatfish then realize ontogenetic migrations to wider areas (Dorel et al., 1991; Gibson, 2005); they tend to be distributed over broader spatial and temporal scales with a positive relationship between size-related ontogenetic shifts and depth (Heinke's law; Dorel et al., 1991; Gibson, 2005;

Vasconcelos et al., 2014). Adults have potentially large spawning migrations (Darnaude and Hunter, 2006).

However limited, juvenile fish movements are important for determining habitat selection (Fox et al., 2006; Ramzi et al., 2001; Sluka et al., 2001). Juvenile fish must choose habitat with regards to individual requirements and spatial and temporal variations in environmental conditions, and their ability to realize this choice is related to their capacities for movement (White and Brown, 2013). Indeed, fish habitat relationships depend on habitat requirements on the spatial scale over which individuals integrate those habitats (Thrush et al., 2002). At the juvenile stage, two mechanisms are commonly invoked: the ability of fishes to forage and escape predation (Adams et al., 2004; Fulford et al., 2011; Thrush et al., 2002). Surprisingly, the feeding (Nunn et al., 2012) and sheltering ecology of juvenile fish is poorly understood and there is insufficient information to estimate individual movements and define spatial scales associated with juvenile fish habitat dependence (Thrush et al., 2002).

As described in the concentration hypothesis (Iles and Beverton, 2000), dependence upon habitat is especially sensitive for juvenile flatfishes, with large density-dependent effects (Archambault et al.,

Table 1
Indicators used to evidence spatial segregation.

Méthod*	Category	Integration period	References
Stable isotopes in muscle	Tracer	Week to month	Vinagre et al., 2008; Fodrie and Herzka, 2013
Otolith geochemistry	Tracer	1 day to few days	Gillanders, 2005; Fodrie and Herzka, 2013
Body length	Growth	1 day to few days	Haynes et al., 2012
Otolith microstructure	Growth	1 day	Sogard and Able, 1992
Body condition	Fitness	1 day	De Raedemaeker et al., 2011; Meyer et al., 2012
RNA/DNA	Fitness	<1 day	Meyer et al., 2012; Ciotti et al., 2013b

* This table present approaches used in the references selected to estimate segregation distances in Table 3 only, not all the potential ones.

2014) related to carrying capacity (food limitation hypothesis, Le Pape and Bonhommeau, in press) and to the structure (Johnson, 2007) of the nursery habitat. However, the home ranges and spatial utilization patterns of juvenile flatfishes remain controversial. This controversy can be illustrated by the especially well-studied Young-of-the-Year (YoY) plaice (*Pleuronectes platessa*, L.): Burrows et al. (2004) state that YoY plaice have a very high probability of remaining within a restricted (<100 m) zone over periods of at least one day, and this can lead to small-scale contrasts in growth patterns (De Raedemaeker et al., 2011). However, YoY plaice appear to be an unlikely candidate for showing strong site fidelity and homing behaviour. Once in the water column, YoY plaice can swim for considerable distances (Gibson, 2005) and large daily migrations (>1 km) have been reported (Kuipers, 1973).

Knowing whether juvenile flatfish remain in the same location or move is important in order to understand the scale of their dependence to nursery habitats (Saucerman and Deegan, 1991). The primary aim of this meta-analytic review was to synthesize the available information, so as to shed light on the question of the range of daily movements that juvenile flatfish display during their strongly habitat-dependent life in coastal and estuarine nursery grounds. The first year of the juvenile phase has been demonstrated to be critical for juvenile flatfishes (Le Pape and Bonhommeau, in press; Miller et al. 1988), large size-selective mortality linked to nursery-habitat suitability being mainly restricted to YoY (Van der Veer et al., 1994). In order to focus on the critical first juvenile stages, and to standardize our approach, we thus restricted the current analysis to YoY flatfish while resident in their primary nursery areas (Ross, 2003; Vasconcelos et al., 2014). This meta-analytical approach aims at addressing: (i) general patterns regarding the extent of flatfish YoY daily movements (scale and direction); (ii) previously suggested hypotheses concerning factors influencing the range of those movements, i.e., consequences of semi-passive tidal migrations (Kuipers, 1973) and size-related movement abilities (Gibson, 2005); (iii) consequences for the management of coastal and estuarine essential flatfish habitat management.

2. Material and method

2.1. Estimating YoY flatfish movements from the literature

We carried out this synthesis using literature review. We searched for studies that could be used to evaluate the range of daily movements of YoY flatfishes in shallow (less than 20 m depth; Trimoreau et al., 2013) coastal (few km from the coastline) and estuarine nursery areas. Two different kinds of information based on observational studies, with or without manipulative experimentation, were considered:

–Direct estimates of juvenile flatfish movements from *in situ* observations. This included studies in which the maximal daily distance travelled by juveniles had been estimated from direct (*de visu* or video) observations; from the tracking of individuals (tagging catch-recapture or tracking using active and passive telemetry; Able and Grothues, 2007); or from short term variation in the distribution of juveniles with regards to diel and/or tidal cycle (short-term sampling showing variation in distribution and density gradient, or distance

from the position of juvenile capture to the limit of water extent at low tide).

–Evidence of spatial segregation, from several approaches (Table 1) including footprint tracers and individual performance measures (growth and body condition indices). Except for short term spatial density variations representative of fish movements, density patterns were not taken into account. We consider these measures to be indicative of habitat suitability (Le Pape et al., 2003a), but not representative of spatial segregation (Scharf, 2000).

Two different metrics were calculated for the two aforementioned categories of segregation data: maximum daily movements, estimated from tracking or temporal gradients of population density; and the minimum distance between pools of individuals that could be separated using natural tracers, growth, or individual fitness, which can be considered as proxies of non-overlap distance. For minimum distance of segregation, we limited the analysis by removing information indicating a distance higher than 40 km, because a lack of such large-scale movements of YoY flatfish has been previously demonstrated (Coggan and Dando, 1988).

2.2. Search strategy and study inclusion criteria

We searched for references by combining different methods in order to collate literature. First, we selected relevant papers from a systematic search of Thomson Reuters Web of Knowledge. This search was conducted on October, 2013 using the Web of Science, with the keywords “flatfish”, “juvenile”, and “movement” as topics. We then enlarged this collection using: >2000 references from a personal database that collated a bibliography of flatfish juvenile-ecology manuscripts published since the 1990s; from an exhaustive search of related papers from the eight International Flatfish Symposia that were convened from 1990–2011; from the “flatfish book” (Gibson, 2005); from a previous review on plaice growth (Table 3 in Ciotti et al., 2014); and from an exhaustive check of papers published in more than 50 ISI journals, either generalist or focused on ecology and marine sciences, spanning from 2012 to 2014. Lastly, we collated the relevant papers listed as references within all of the sources that had been selected using the methods detailed above.

The references returned by these various searches were evaluated for inclusion in our study. This screening process aimed to identify the studies that were relevant to our review question. We evaluated the abstracts of the selected references, then the full text of the studies that had been retained. To be finally retained, a study had to focus on coastal and estuarine nursery dependent flatfish species and to provide, or to allow for the calculation of range of movements or distances of segregation for YoY juvenile. Estimated distances were alternatively taken from the text, recalculated from scaled maps or geographic positions, or obtained directly from authors. However, because many distances were estimated on maps from figures, without geolocations, a large proportion of both ranges of movements and distances between segregated pools of YoY flatfish were estimated with important estimation error. We also collated the direction of observed movements and distances of segregation, separating movements or pools of fish distributed along the coastline (parallel, PAR) from those that were positioned

Table 2

Estimates of age 0 flatfish movements from literature review and associated information, marine zone (NEA, Northeast Atlantic; NEP, Northeast Pacific; NWA, Northwest Atlantic; SWP, Southwest Pacific); Tidal range, local tidal range at sampling time; direction of the segregation (PAR, parallel; PER, perpendicular to the coastline); Length, average body length of sampled juveniles; method of observation (VAR, short term variation during the tidal or diel cycle; TRA, tracked movement of individuals); scale, the maximal distance covered by juvenile movements.

Species	Location	Marine zone	Tidal range (m)	Direction	Length (mm)	Method of observation category	Insights	Scale* (m)	Reference
<i>Pleuronectes platessa</i>	Bay of Mt St Michel	NEA	8.64	PER	89.9	Distance to the sea at low tide	VAR Tidal migrations	5000	Beillois et al. (1979)
<i>Solea solea</i>	Bay of Mt St Michel	NEA	8.64	PER	78.8	Distance to the sea at low tide	VAR Tidal migrations	5000	Beillois et al. (1979)
<i>Pleuronectes platessa</i>	Bay of Veys	NEA	4.41	PER	91.6	Distance to the sea at low tide	VAR Tidal migrations	3000	Beillois et al. (1979)
<i>Solea solea</i>	Bay of Veys	NEA	4.41	PER	81.1	Distance to the sea at low tide	VAR Tidal migrations	3000	Beillois et al. (1979)
<i>Pleuronectes platessa</i>	Wadden Sea	NEA	3.64	PAR	46.1	Average variation of distribution	VAR Tidal/diel migrations	1000	Berghahn (1986)
<i>Pleuronectes platessa</i>	Wadden Sea	NEA	3.20	PER	16.9	Average variation of distribution	VAR Tidal migrations	500	Berghahn (1987)
<i>Pleuronectes platessa</i>	Wadden Sea	NEA	3.36	PAR	NA	Variation in density gradient	VAR Diel migrations	100	Berghahn (2001)
<i>Limanda limanda</i>	Western Scotland	NEA	2.26	PER	NA	Video	VAR Tidal/diel migration	100	Burrows et al. (1994)
<i>Pleuronectes platessa</i>	Western Scotland	NEA	2.26	PER	NA	Video	VAR Tidal/diel migration	100	Burrows et al. (1994)
<i>Pleuronectes platessa</i>	Western Scotland	NEA	3.41	PAR	55.0	Mark-recapture	TRA Alongshore migrations	100	Burrows et al. (2004)
<i>Pleuronectes platessa</i>	Northern Scotland	NEA	4.05	PER	17.1	Distance to the sea at low tide	VAR Tidal migration	200	Edwards and Steele (1968)
<i>Pleuronectes platessa</i>	West Sweden	NEA	0.23	PER	39.7	Video	VAR Diel migration	100	Gibson et al. (1998)
<i>Pleuronectes platessa</i>	Western Scotland	NEA	2.78	PER	33.6	Visual	VAR Tidal migrations	100	Gibson (1973, 1980)
<i>Paralichthys californicus</i>	Southern California	NEP	0.78	PER	142.3	Mark-recapture	TRA Estuarine migrations	700	Herzka et al. (2009)
<i>Hypsopsetta guttulata</i>	Southern California	NEP	0.78	PER	126.5	Mark-recapture	TRA Estuarine migrations	700	Herzka et al. (2009)
<i>Pleuronectes platessa</i>	Wadden Sea	NEA	1.56	PER	80.0	Distance to the sea at low tide	VAR Tidal migrations	1000	Kuipers (1973)
<i>Pleuronectes platessa</i>	Bay of St Brieuc	NEA	8.40	PER	59.0	Distance to the sea at low tide	VAR Tidal migrations	2000	Leluharne (in review)
<i>Rhombosolea leporina</i>	Western New Zealand	SWP	2.89	PER	65.4	Distance to the sea at low tide	VAR Tidal/diel migration	1000	Morrison et al. (2002)
<i>Rhombosolea plebeia</i>	Western New Zealand	SWP	2.89	PER	68.6	Distance to the sea at low tide	VAR Tidal/diel migration	1000	Morrison et al. (2002)
<i>Platichthys flesus</i>	Eastern Scotland	NEA	3.84	PER	85.0	Distance to the sea at low tide	TRA Tidal migration	100	Raffaelli et al. (1990)
<i>Pleuronectes platessa</i>	Wales	NEA	4.09	PAR	57.5	Mark-recapture	TRA Local movements	450	Riley (1973)
<i>Pleuronectes platessa</i>	Wales	NEA	4.09	PAR	57.5	Mark-recapture	TRA Alongshore migrations	300	Riley (1973)
<i>Pleuronectes platessa</i>	Wales	NEA	4.09	PAR	57.5	Mark-recapture	TRA Inshore migrations	4000	Riley (1973)
<i>Pseudopleuronectes americanus</i>	Massachusetts	NWA	0.39	PER	47.5	Mark-recapture	TRA Local movements	100	Saucerman and Deegan (1991)
<i>Paralichthys dentatus</i>	New Jersey	NWA	1.01	PER	59.9	Ultrasonic tagging	TRA Tidal migrations	1000	Szedlmayer and Able (1993)
<i>Pseudopleuronectes americanus</i>	Bay of Fundy	NWA	5.58	PER	70.0	Video	VAR Tidal/diel migration	200	Tyler (1971)
<i>Pleuronectes platessa</i>	Wadden Sea	NEA	1.62	PER	37.5	Variation in density gradient	VAR Tidal migration	1000	van der Veer and Bergman (1986)
<i>Solea senegalensis</i>	West Portugal	NEA	2.36	PER	34.4	Distance to the sea at low tide	VAR Tidal/diel migration	300	Vinagre et al. 2006

* Ranges of movements are estimated with important associated variability and estimation error, they have to be considered as order of magnitudes only

along upstream–downstream or tidal gradients (i.e., perpendicular to the coastline, PER).

Among the selected papers, a few instances were found in which more than one reference reported on the same study. In order to avoid including the same data more than once, when the information from these references was similar, we selected the study that presented the data most fully and clearly; thus, removing redundancy. Alternatively, when one reference estimated movements, and another the distance of segregation between pools of fish, data from both studies were retained. As few ($n = 7$) references contained data for more than one

species, the information from each studied species was considered as distinct data.

2.3. Description of collected data from selected studies, and methods of analysis

In addition to the estimates of the scale and the direction of movements or distances of segregation for YoY flatfish species, we collated information on the methods that were applied in each paper, and subsequently retained to estimate distances. Methods that allowed for

Table 3
Minimal distance of segregation between distinct patches of age 0 flatfish, estimated from literature review, and associated information, marine zone (NEA, Northeast Atlantic; NEP, Northeast Pacific; NWA, Northwest Atlantic; SWP, Southwest Pacific); Tidal range, local tidal range at sampling time; Direction of the segregation (PAR, parallel; PER, perpendicular to the coastal line); Length, average body length of sampled juveniles; Method (GRO, growth variations; FIT, variation in fitness measures; TRA, variation in tracers signatures), Scale, the minimum distance between segregated patches.

Species	Location	Marine zone	Tidal range (m)	Direction	Length (mm)	Method used to prove the segregation category	Insight	Scale* (m)	Reference
<i>Pleuronectes platessa</i>	Wadden Sea	NEA	2.80	PAR	53.9	Otolith microstructure	GRO Tidal gradient	5000	Berghahn et al. (1995)
<i>Pleuronectes vetulus</i>	Northern California	NEP	0.80	PER	NA	Otolith geochemistry	TRA Inshore gradient	8000	Brown, 2006
<i>Citharichthys stigmaeus</i>	Northern California	NEP	0.80	PER	NA	Otolith geochemistry	TRA Inshore gradient	8000	Brown, 2006
<i>Pleuronectes platessa</i>	Western Scotland	NEA	2.42	PAR	55.1	Rna/Dna ratios	FIT Differences between beaches	10,000	Ciotti et al. (2013a)
<i>Pleuronectes platessa</i>	Western Scotland	NEA	2.02	PAR	50.7	Rna/Dna ratios	FIT Differences between parts of beaches	500	Ciotti et al. (2013b)
<i>Pleuronectes platessa</i>	Irish Sea	NEA	3.25	PAR	80.3	Otolith microstructure	GRO Differences between beaches	30,000	De Raedemaeker et al. (2011)
<i>Pleuronectes platessa</i>	Irish Sea	NEA	3.25	PAR	79.3	Body condition	FIT Differences between parts of beaches	600	De Raedemaeker et al. (2011)
<i>Limanda limanda</i>	Irish Sea	NEA	3.19	PAR	37.5	Body condition	FIT Differences between beaches	8000	De Raedemaeker et al. (2012)
<i>Solea solea</i>	Bay of Biscay	NEA	3.52	PAR	69.4	Body length	GRO Local patterns	5000	Durieux et al. (2010)
<i>Solea solea</i>	Bay of Biscay	NEA	3.56	PAR	45.7	Body condition	FIT Local patterns	7000	Durieux et al. (2010)
<i>Paralichthys californicus</i>	Southern California	NEP	0.94	PER	90.5	Otolith geochemistry	TRA Estuarine gradient	3000	Fodrie and Herzka (2013)
<i>Solea solea</i>	English Channel	NEA	5.02	PAR	113.6	Otolith microstructure	GRO Differences between coastal areas	40,000	Gilliers et al. (2004)
<i>Pleuronectes platessa</i>	English Channel	NEA	5.02	PAR	113.1	Rna/Dna ratios	FIT Differences between coastal areas	40,000	Gilliers et al. (2004)
<i>Limanda limanda</i>	English Channel	NEA	5.02	PAR	82.4	Rna/Dna ratios	FIT Differences between coastal areas	40,000	Gilliers et al. (2004)
<i>Solea solea</i>	Bay of Biscay	NEA	3.78	PAR	10.8	Rna/Dna ratios	FIT Differences between coastal areas	25,000	Gilliers et al. (2006)
<i>Solea solea</i>	English Channel	NEA	5.70	PER	107.5	Recent growth	GRO Estuarine gradient	10,000	Gilliers (2004)
<i>Paralichthys lethostigma</i>	Southern USA	NWA	0.38	PAR	17.3	Rna/Dna ratios	FIT Differences between coastal areas	35,000	Glass et al. (2008)
<i>Pleuronectes platessa</i>	Irish Sea	NEA	3.45	PAR	70.1	Body length	GRO Differences between beaches	25,000	Haynes et al. (2012)
<i>Paralichthys californicus</i>	Southern California	NEP	0.78	PER	83.1	Length distribution	GRO Estuarine gradient	2500	Herzka et al. (2009)
<i>Rhombosolea tapirina</i>	Southern Australia	SEI	0.85	PAR	10.5	Otolith microstructure	GRO Differences between subparts of a bay	35,000	Jenkins et al. (1993)
<i>Pleuronectes platessa</i>	Wadden Sea	NEA	3.57	PAR	25.5	Otolith microstructure	GRO Tidal gradient	5000	Karakiri et al. (1989)
<i>Pleuronectes platessa</i>	Wadden Sea	NEA	2.08	PAR	83.5	Otolith microstructure	GRO Tidal gradient	40,000	Karakiri et al. (1991)
<i>Solea solea</i>	Bay of Biscay	NEA	3.41	PER	NA	Stable isotopes	TRA Estuarine gradient	10,000	Kostecki et al. (2010)
<i>Solea solea</i>	Gulf of Lions	MED	0.15	PAR	168.3	Otolith geochemistry	TRA Differences between coastal and estuarine areas	30,000	Morat et al. (2014)
<i>Solea solea</i>	Bay of Biscay	NEA	3.28	PER	106.4	Stable isotopes	TRA Estuarine gradient	25,000	Pasquaud et al. (2008)
<i>Pleuronectes platessa</i>	Clyde Sea	NEA	2.37	PAR	30.0	Body length	GRO Differences between coastal areas	15,000	Poxton et al. (1983)
<i>Limanda limanda</i>	Clyde Sea	NEA	2.92	PAR	60.0	Body length	GRO Differences between coastal areas	15,000	Poxton et al. (1983)
<i>Pleuronectes platessa</i>	Wadden Sea	NEA	3.05	PAR	95.9	Otolith microstructure	GRO Tidal gradients	35,000	Rauck (1974)
<i>Pseudopleuronectes americanus</i>	New Jersey	NWA	0.71	PAR	47.1	Otolith microstructure	GRO Differences between coastal areas	35,000	Sogard and Able (1992)
<i>Pleuronectes platessa</i>	Wadden Sea	NEA	2.37	PAR	30.0	Body length	GRO Tidal gradients	5000	van der Veer and Witte (1993)
<i>Solea senegalensis</i>	West Portugal	NEA	2.40	PER	76.0	Stable isotopes	TRA Differences between estuarine areas	15,000	Vinagre et al. (2008)
<i>Solea solea</i>	West Portugal	NEA	2.37	PER	80.9	Stable isotopes	TRA Differences between estuarine areas	3000	Tanner et al. (2013)
<i>Solea solea</i>	West Portugal	NEA	1.85	PER	70.5	Body condition	FIT Estuarine gradient	8000	Vasconcelos et al. (2009)
<i>Platichthys flesus</i>	West Portugal	NEA	2.14	PER	85.4	Body length	GRO Estuarine gradient	2000	Souza et al. (2013)

* Ranges of movements are estimated with important associated variability and estimation error, they have to be considered as order of magnitudes only.

estimating daily distance travelled were split into two categories: the tracking of individual movements (MOV; by direct *de visu* or video observations, mark recapture, or ultrasonic tagging); or, the consideration

of short-term variation in distribution (VAR; by density gradients or distance to water limit at low tide). Methods that highlighted segregation between pools of juveniles were split into three categories: differences

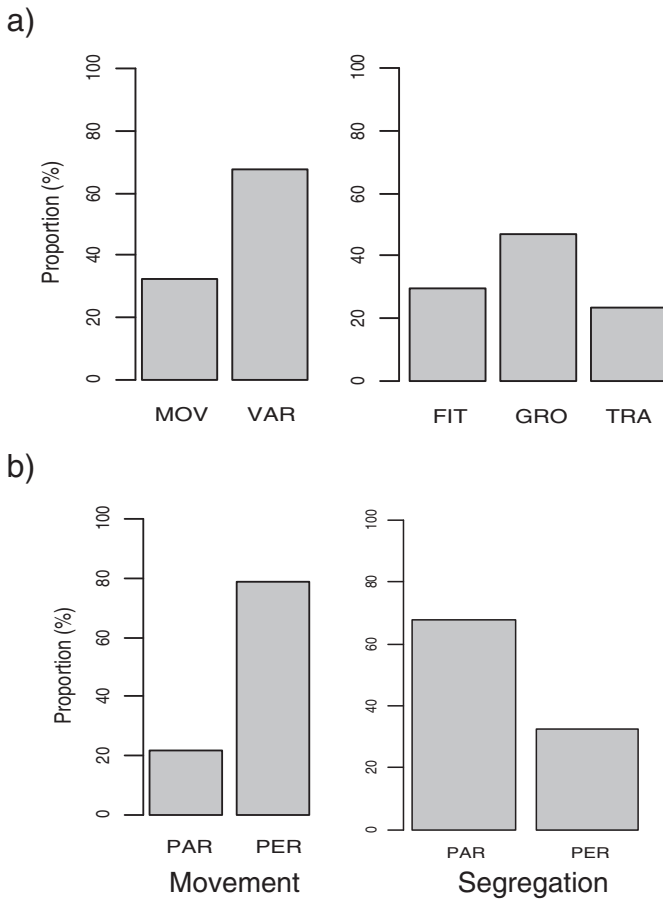


Fig. 1. Proportions (in %) of the estimated distance of movement (n = 28) on the left side and distance of segregation (n = 34) on the right side in the retained data related to a) the different methods used to estimate the distance (MOV, tracked movement of individuals; VAR, short term variations during the tidal or diel cycle; FIT, difference in fitness performance; GRO, difference in growth rate; TRA, difference in tracers) and b) the type of gradient, parallel (PAR) or perpendicular (PER) to the coastline.

in (i) growth (GRO, determined by otolith microstructure, somatic growth, or length distribution); (ii) fitness performances (FIT, determined by body condition or RNA/DNA ratios), or; (iii) footprint tracers (TRA, determined by otolith geochemistry or stable isotope).

We also compiled information on the location of each study sector, the local tidal range at time of sampling, and average YoY flatfish size. Locations were grouped into six marine zones: Northeast Atlantic Ocean (NEA), Northeast Pacific Ocean (NEP), Northwest Atlantic Ocean (NWA), Southwest Pacific Ocean (SWP), Southeast Indian

Ocean (SEI) and Mediterranean Sea (MED). The tidal range for each study was calculated from local tide calendars, mainly found on the websites mobilegeographics.com and shom.fr. The mean size of individual flatfish was either provided by the authors or calculated from the tables and figures of the related paper.

We analysed the collated data from general linear models (least square criterion). Estimates of YoY movement or distances of segregation were used as response variables and additional information (i.e., method, species, marine zone, direction relative to the coastline, mean body length, tidal range) as explanatory factors or covariates. The application conditions of linear models were verified in preliminary analyses and data log-transformation was used when necessary. A level of significance of 0.05 was retained. Statistical analyses were conducted with R software. In cases of transformed data, a correction (Laurent, 1963) was applied to chart unbiased relations with log-transformed variables. By doing so, accounting for discrepancies among methods, we analysed the patterns in the scales of movements and distances of segregation, and the effects of potential explanatory parameters. Especially, we consider differences in the range of movements with respect to: (i) fish length, as body size influences swimming speed (generally measured in body length.s⁻¹; Gibson, 2005) and the capacity to realize long daily migration; (ii) tidal amplitude, as flatfish movements are frequently related to tide cycle (Gibson, 2005); (iii) the type of gradient of segregation, parallel or perpendicular to the coastline; (iv) species or species groups, and; (v) locations.

3. Results

3.1. Main features of retained data

Only 47 references allowing for quantitative estimates of scale of movements of YoY flatfish were retained, after the multiple criteria selection, despite a primary selection of many more scientific papers. A large number of references that focused on older juvenile fish were rejected because they presented no measured patterns of spatial segregation or because they did not use appropriate methods (e.g., used caging experiments to measure differences in individual performance without demonstrating segregation), or did not provide sufficient data to calculate distances. However, our approach of cross-checking and pooling references during their systematic review prevented us from generating reliable statistics regarding the rate at which relevant references were selected.

Here, in order to estimate juvenile flatfish movements, we separate the data with regards to the two main approaches: i.e., measures of movement and distances between segregated groups. The selected references were quite equally distributed between these two categories, with 28 and 34 data collated from measured distance (Table 2) and segregation (Table 3), respectively. Two thirds of the estimates of distances of movement were estimated (Fig. 1a) from short term variation in spatial distribution linked to tidal or diel cycle (VAR); the last third by direct observation of fish movements (MOV). Nearly half of the estimated distances of segregation were determined (Fig. 1a) from differences in growth rate (GRO); and the other half (approximately 25% each) from differences in fitness (FIT) and tracers (TRA).

Most (80%) of observed movements were perpendicular to the coast (Fig. 1b), with most of these (19 of 22) being linked to tidal inshore-offshore cyclic migrations. In contrast, two thirds of the distances of segregation (Table 3) were associated with a gradient parallel (PAR) to the coastline (Fig. 1b) and the last third (perpendicular, PER) were associated mainly to upstream-downstream estuarine gradients.

Retained data were focused (Table 4) on a limited number of species (15) belonging to three families of Pleuronectiforms only (i.e., Pleuronectidae, Soleidae, Paralichthyidae), and were collated in a limited number of locations from around the world. Indeed, among all of the estimated distances retained in the current analysis, two thirds concerns common plaice (*Pleuronectes platessa*; n = 28 lines in Tables 2

Table 4 Proportions (in % of data in the summed Tables 1 and 2, n = 62) of the different a) taxa and b) marine zones.

a) Taxon: family and species (%)					
Pleuronectidae	70	Paralichthyidae	10		
<i>Hypsopsetta guttulata</i>	2	<i>Citharichthys stigmaeus</i>	2		
<i>Limanda limanda</i>	67	<i>Paralichthys californicus</i>	5		
<i>Platichthys flesus</i>	3	<i>Paralichthys dentatus</i>	2		
<i>Pleuronectes platessa</i>	45	<i>Paralichthys lethostigma</i>	2		
<i>Pseudopleuronectes americanus</i>	2	Soleidae	23		
<i>Rhombosolea plebeia</i>	2	<i>Solea senegalensis</i>	3		
<i>Rhombosolea tapirina</i>	2	<i>Solea solea</i>	19		
b) Marine zone (%)					
Northeast Atlantic	75	Northwest Atlantic	9	Southeast Indian	2
Northeast Pacific	9	Southwest Pacific	3	Mediterranean Sea	2

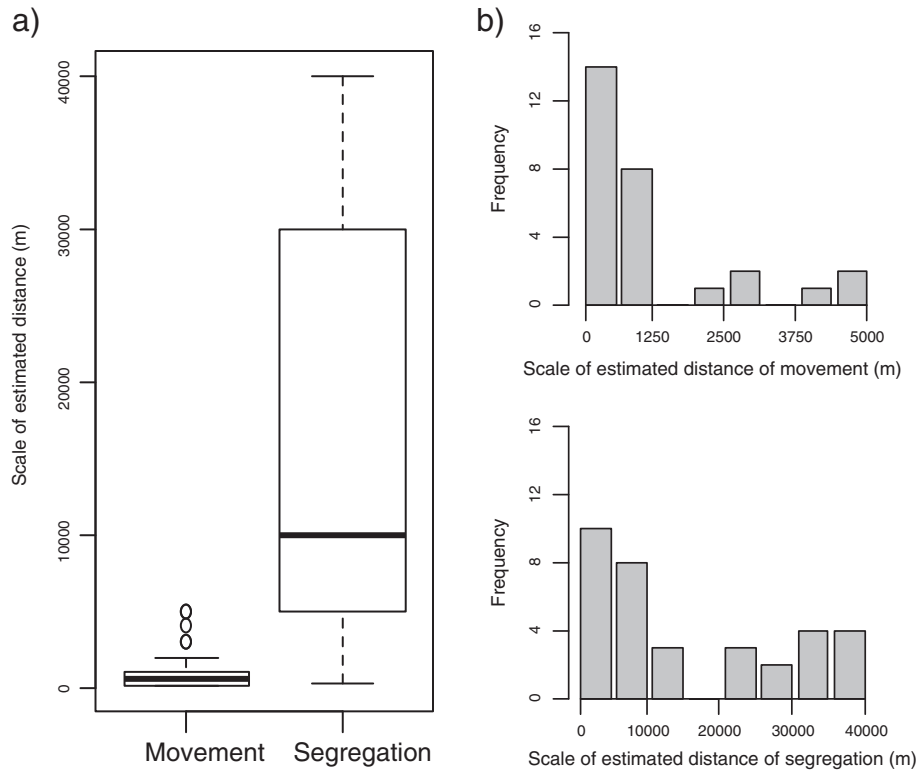


Fig. 2. Distribution of estimated movements and distance of segregation a) boxplots (thick line; median; box, from the 0.25 quartile to the 0.75 quartile; whiskers, 1.5 times the distance between the quartiles; circles, outlier values) and b) distribution in frequency (number of data).

& 3) and common sole (*Solea solea*; $n = 12$), both of which are distributed in the Northeast Atlantic, from which three quarters of the data were collated (Table 4). This lack of contrasts in the dataset prevents clear patterns related to species or family, or to study area, to be resolved. However, a large range of YoY flatfish body lengths (from 10 to 168 mm; mean = 67, $sd = 32$) and of tidal amplitudes (from 0.15 to 8.6 m; mean = 3, $sd = 1.9$) were accounted for.

3.2. Outcomes and discrepancies among estimation methods

Home range of 0-group flatfishes (Fig. 2), estimated from measured movements (Table 2; mean = 1150 m, $sd = 1480$), was significantly smaller (Wilcoxon test: $W = 51$, $p < 0.001$) than the estimated distance of segregation (Table 3; mean = 17,100 m, $sd = 14,000$). This difference prevented us from pooling these two datasets into a common analysis, thus requiring the two metrics (i.e., Tables 2 and 3) to be treated separately. Data on measured movements (Table 2) contained a high proportion of low values, with a cluster at very low distances. Indeed, the distribution (Fig. 2) of the data in Table 2 suggests log transformation of estimated distances of movement prior to general linear models analyses. After data transformation, application conditions of linear model were verified without contra-indication. Distances of segregation were more equally distributed and data could be analysed with linear models without contra-indications. However 62% of estimates were $\leq 15,000$ m; the 38% of larger distances being linked to alongshore gradients.

3.3. Factors influencing the maximal daily movements of the juveniles

Reported maximal daily movements are in the hundred-to-thousand meters scale and didn't exceed five kilometers, with only 5/28 of the data indicating movements up to 1 km. The method of estimation was a structuring driver (Fig. 3a, Table 5a), direct estimates of movements (MOV) being significantly lower than estimates from short-term

gradients in distribution (VAR). No significant difference in estimated distances was found with regard to the direction of the observed gradient relative to the coastline (Fig. 3b).

Linear modelling highlights the significant effect of juvenile length on maximal daily movement (Table 5a, Fig. 4): the distance of movement dramatically increases with the body length of the individuals. The scale of movements also increased with tidal range (Fig. 5, Table 5b). Indeed, distances were dramatically lower (few hundreds of meters) when tidal migrations were excluded, in such cases never exceeding 700 m (Table 2).

3.4. Factors influencing the minimal distance between segregated groups of juveniles

Average minimal distance between segregated groups of 0-group flatfishes reached as great as 17 km; but, this average strongly depended upon the 40 km upper limit that our methods imposed upon the analysis. More than 50% of the 34 studies reported distances of segregation below 10 km, and 30% < 5 km. Methods used to estimate distance of segregation (i.e., gradients in fitness, growth, or tracers) did not lead to significantly different estimates (Fig. 3a). On the other hand, the direction of the gradient was a structuring driver for distance of segregation (Fig. 3b, Table 5c), with shorter distances segregating pools of fish along upstream-downstream gradients, and greater distances segregating fish along the coastline. No significant effect was found for the other explanatory variables, and especially not for juvenile body length nor for tidal range.

When a subsample considering only distances < 15 km (shift in distribution, Fig. 2b) was reanalysed, thereby removing 38% of data consisting in alongshore gradients, the significant effect of the direction of the gradient was eliminated. However, except for two very short distances evidenced from gradients in fitness among sections of beaches, all of the segregation distances < 5 km remained linked to estuarine

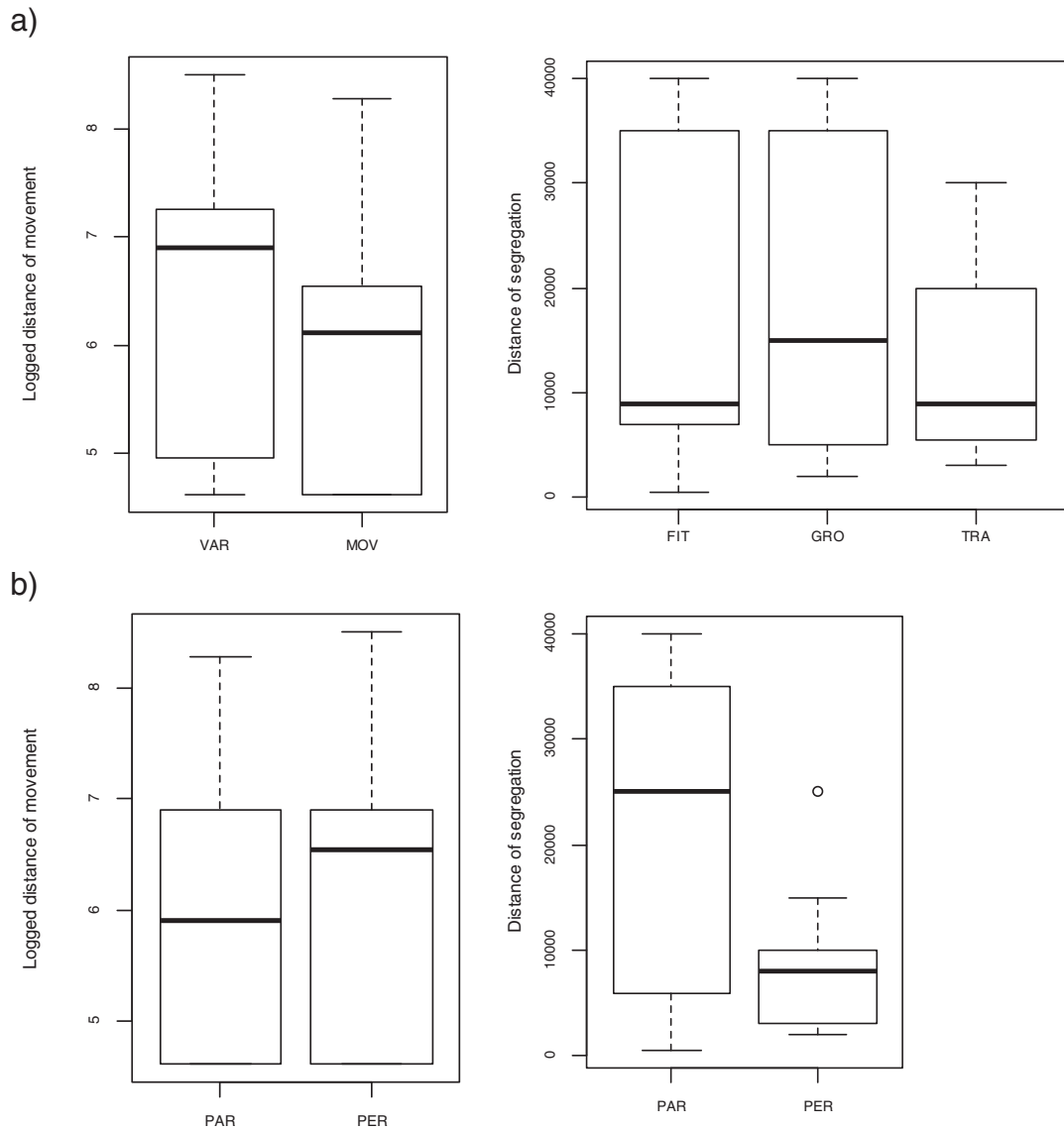


Fig. 3. Scale of distance of movement on the left side and of segregation on the right side relates to a) the method used to estimate the distance (MOV, tracked movement of individuals; VAR, short term variations during the tidal or diel cycle; FIT, fitness performance; GRO, growth rate; TRA, tracers) and b) the type of gradient, parallel (PAR) or perpendicular (PER) to the coastline (thick line, median; box, from the 0.25 quartile to the 0.75 quartile; whiskers, 1.5 times the distance between the quartiles; circle, outlier value).

gradients. This selection did not lead to significant patterns linked to methods of observation, fish length, nor tidal range.

4. Discussion

4.1. Possible limits: discrepancies linked to review procedure and estimation methods

Few studies allowing for the quantification YoY flatfish movements, or distance of segregation, were retained in the present meta-analysis. This limited amount of references, focused on a low number of species and locations, and using heterogeneous methods, raises questions regarding the representativeness of this approach. These will be discussed in the following subsections.

4.1.1. Robustness of the references selected for estimating range of movements

One possible limitation of our analysis arises from our reference-selection procedure, which likely led to the analysis of a dataset that was incomplete with regards to the existing body of knowledge on

juvenile flatfish movements. Especially, a large proportion of the retained literature (i.e., most of the references in Table 3) was not focused on juvenile flatfish movements, but instead appeared useful for estimating distances of segregation. Indeed, as the current review's topic was not the focus of many of the papers that allowed for estimation of spatial segregation, it was difficult to identify all relevant references from a systematic keyword research on academic search services. Instead, the systematic review was completed using other references, especially from the eight prior International Flatfish Symposia, the flatfish book (Gibson, 2005), previous reviews (e.g., Ciotti et al., 2014), a personal database, and papers listed as references in the selected sources. We have no reason to believe that the identified spatial patterns are likely to be biased through the restrictions on the search procedure.

4.1.2. Discrepancies between estimates from measured movements and distance of segregation

Reported maximal daily movements were dramatically lower than were the average minimal distances between segregated groups of 0-group flatfishes. Two main reasons could explain this large gap:

Table 5

Outputs of linear models analysing scale of movements and distance of segregation, a) Logged distance of movement as a function of body length and estimation method, b) Logged distance of movement as a function of tidal range, c) Distance of segregation as a function of its direction (perpendicular or parallel to the coastline).

Resp: Logged distance of movement									
a) Expl					b) Expl				
	Estimate	t	p		Estimate	t	p		
Intercept	5.438	9.867	<0.001	Intercept	5.224	12.626	<0.001		
Method	-1.120	-2.230	0.0363	Tidal range	0.297	2.923	0.0070		
Length	0.022	-2.637	0.0151						
n	df	R ² (%)	F	p	n	df	R ² (%)	F	p
28	25	29	4.53	0.0225	28	26	25	8.55	0.0070

Resp: Distance of segregation				
c) Expl				
	Estimate	t	p	
Intercept	21135	7.877	<0.001	
Direction	-12544	-2.651	0.0121	
n	df	R ² (%)	F	p
34	32	18	7.07	0.0121

Symbols:

Resp = response variable

Expl = explicative variables

t = Student score, p = p-value

n = sample size, df = degrees of freedom

R²(%) = fraction of explained variance

F = Fisher score

- (i) The estimation method. Segregation among pools of moving fish is observable at a less fine scale than their observed movements. Indeed, we estimated, on one side, the maximal distance travelled daily by juveniles, but the minimal distance of segregation on the other. Undersampling linked to measurement limits led to underestimation of the travelled distance in the first case; but, in the latter, to overestimation of the minimum distance of segregation.
- (ii) The different meaning of these two metrics. Movement behaviour affects the distribution of fish, but outcomes depend on interactions between movement patterns and local habitat structure and heterogeneity (Fulford et al., 2011; Hanski, 1998; Palmer et al., 2014). Movements and dispersal abilities are key ecological processes determining connectivity, and dispersal distances could be used to derive segregation between patches (Hanski, 1998; Palmer et al., 2014). However, distance of segregation provides information on the storage (over a given duration of the species' life history, depending upon the tracers that are used; Table 1) of separate pools, due to the lack of dispersal patterns

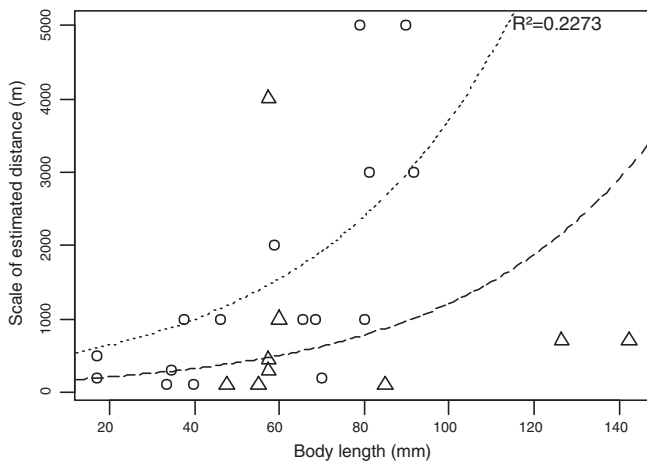


Fig. 4. Evolution of the scale of estimated distance of movements as function of the body length of the juvenile flatfishes, related to the estimation method (circles and dotted line, short term variations during the tidal or diel cycle; triangles and dashed line, tracked movements of individuals).

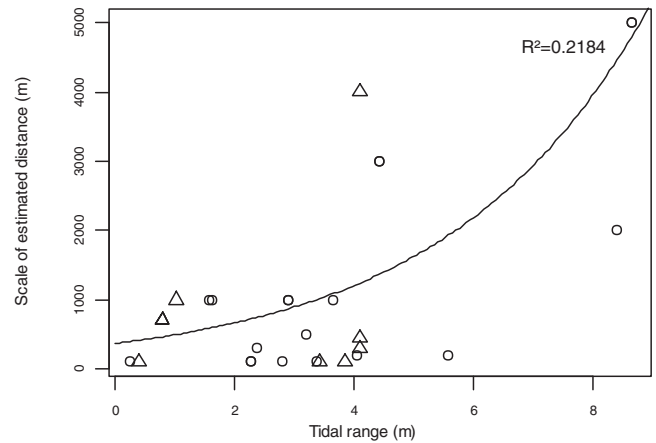


Fig. 5. Evolution of the scale of estimated distance of movements as function of the tidal range (circles, short term variations during the tidal or diel cycle; triangles, tracked movement of individual).

across habitats (Secor and Rooker, 2005); i.e., an obvious dramatic overestimation of the home range. Distance of segregation is an alternative measure that focuses on the lack of exchange of individuals over longer time steps.

Accordingly, observed patterns, analysed separately, were different from the two approaches. In this study, neither the 40 km limit nor a shorter alternative distance (i.e., 15 km), allowed for showing any effects of the body length of flatfish, nor the tidal range, on the distance between segregated groups; whereas, we were able to assess the effects of those factors on maximal daily distance of movement. Indeed, drivers of daily movements are not similar to drivers of segregation.

4.1.3. Measuring movement: the gap between direct observations and variations in spatial distribution

Daily movements appear larger when they are estimated by short-term variations in distribution than when they are determined by tracking the movement of individuals. As short-term variations are frequently analysed in tidal systems, where partly-passive movements linked to tidal movements may be important (Gibson, 2005), this can lead to higher estimates of movement than in non-tidal systems, especially where high tidal range leads to long distances travelled.

4.1.4. Estimating spatial segregation: different approaches, gradients, and levels of resolution

Various methods used for identifying segregation suggest differences in spatial resolution, in relation to their time scales of storage and to gradients in habitat footprint.

Distances of segregation appear partly linked to the integration period of the indicators that are used to detect them (Table 1). As daily movements are lower than scales of segregation based on the storage of separated pools (Secor and Rooker, 2005), the duration of the storage period influences its spatial resolution. This could explain why indices related to short-term responses to feeding conditions (Meyer et al., 2012; Table 1), i.e., body condition (De Raedemaeker et al., 2011), and RNA/DNA (Ciotti et al., 2013b), provide evidence of smaller-scale segregation (i.e., the two outlier distances, <1 km, in Table 3) relative to other estimates.

Distances between segregated groups are smaller along environmental gradients (especially upstream–downstream in estuarine gradients) than they are among separate regions of the coast, along the coastline. Indeed, environmental gradients induce patterns in many of the natural tracers (carbon stable isotopes $\delta^{13}\text{C}$; Le Pape et al., 2013;

otolith geochemistry (Sr/Ca ratio); de Pontual et al., 2003; Gillanders, 2005) that are used to identify segregation. Fish otolith microchemistry (Brown, 2006; Fodrie and Herzka, 2013) and stable isotopes (Kostecki et al., 2010; Morat et al., 2014; Woodland and Secor, 2011) are reliable methods for tracing upstream–downstream gradients and for distinguishing between the use of estuarine and coastal habitat. Along the coastline, otolith geochemistry can also discriminate nursery areas at the mesoscale (Dierking et al., 2012; Tanner et al., 2013); but the lack of small-scale patterns in habitat signature prevents geochemical tracers, and also stable isotopes, from discriminating finer-scale segregation (Hanson et al., 2004). Even if they do not rely on tracers of estuarine footprint, contrasts in growth rate (body length; Le Pape et al., 2003b; Souza et al., 2013; otolith microstructure; Gilliers, 2004; Brown, 2006; Herzka et al., 2009) and body condition (Vasconcelos et al., 2009) are also resolvable at finer scales in estuarine gradients, in relation to natural patterns in habitat suitability (Meng et al., 2005).

Genetic studies may provide insights on population structuring; e.g., at mesoscale for estuarine resident species (Selkoe et al., 2008). However, even spatially-structured marine populations (Smedbol et al., 2002; Ward et al., 1994), including flatfish (Exadactylos et al., 2003; Rolland et al., 2007), may display no genetic differentiation. To our knowledge no significant segregation gradient has been demonstrated from genetic approaches for YoY flatfish, at finer than mesoscale. Although xenobiotics (Loizeau, IFREMER, France, pers. com.) and parasite signatures (Durieux et al., 2010) might display spatial patterns in YoY flatfish, the lack of any demonstrated segregation in these indicators prevented these approaches from being retained as discriminant in the current analysis.

4.2. The moderate displacements at first juvenile stages and their driving factors

4.2.1. Tidal influence

The first insight from daily movement data concerns the large influence of tidal circulation on periodic movements along depth gradients. For juvenile flatfish living in tidal areas, movements are dominated by a tendency to follow the rise and fall of the tides (Gibson, 1973), for a mean distance of 1500 m, to make periodic use of intertidal habitats (Rountree and Able, 1992). The tidal amplitude significantly increases the scale of observed daily movements (Fig. 5). YoY flatfishes congregate in tidal channels, or below the low tide inshore limit, and migrate onto the flats with the rising tide (Burrows et al., 2004; Kuipers, 1973). The tidal half-day cycle takes fishes from hundreds of meters to several kilometers across tidal flats from drainage channels (Berghahn, 1987) or into tidal creeks (Szedlmayer and Able, 1993; Wirjoatmodjo and Pitcher, 1984); the distance covered depends upon the length of the intertidal area, which is linked to the tidal amplitude. Tidal migrations (Gibson, 1973; Kuipers, 1973) consist of selective passive tidal transport (De Veen, 1978), based on synchronization between off-bottom behaviour and the flooding tide (Burrows et al., 1994; Gibson, 1980), thereby minimizing energy costs (Tupper and Able, 2000) while maximizing food access (Berghahn, 1987). Such wide-ranging movement ought to diminish any affinity for a particular locality. Intertidal soft-bottom habitat is relatively homogenous and often turbid, and offers few obvious cues as to specific location (Burrows et al., 1994). As these migrations are cyclic and do not result in selection of specific locations within these temporary habitats, they do not lead to YoY flatfish segregation. Accordingly, distances of segregation do not present any tidally-related patterns.

The general depth distribution of juvenile flatfishes (e.g., Dorel et al., 1991) is based on Jeincke's law: the smaller the shallower (Berghahn, 1987; Gibson, 1973; Gibson et al., 2002). Tidal migrations, in which larger juvenile individuals conduct larger migrations and display shallower distribution at high tide, represent a reversal of Jeincke's law at small spatial and temporal scales.

4.2.2. Limited size-dependent active movements

When tide is negligible, or when the related cyclic movements are not accounted for, daily migrations appear very limited, reaching only 360 m on average (i.e., four times less than tidal movements). Diel movements occur in combination with tidal movements or alone (Gibson, 2005). YoY flatfish move into deeper water in the early morning and return to the shallows at dusk (Burrows et al., 1994). Numerous ecological reasons, especially foraging and avoiding predation, explain the circadian diel cycle (Gibson, 1973; Hurst and Duffy, 2005). Juveniles limit high predation risk (Ansell and Gibson, 1993) by remaining in shallow water at night (Burrows et al., 1994; Gibson et al., 1998). However, the scale of this diel cycle remains limited without “passive” swimming that is linked to tidal cycles. Size-related abilities have a considerable influence on capacity to realize active daily migration (Gibson, 2005; Barbour et al., 2014; Fig. 4) and species-specific differences in feeding behaviour (diurnal vs nocturnal, vision vs olfaction; Nunn et al., 2012) or sheltering strategy also lead to limit the “passive” diel cycle scheme.

4.2.3. A significant estuarine segregation

The current review allowed for the demonstration of both limited upstream–downstream YoY flatfish movements and segregation of patches of juveniles along estuarine gradients. Local connectivity can decrease for juvenile flatfish (Vinagre et al., 2008), as for other estuarine nursery-dependent species (Fuji et al., 2011), in estuarine zones because of site fidelity to local habitat.

4.2.4. Segregation of patches along the coastline

With regards to inshore movements, little is known about the rates of alongshore dispersal in juvenile flatfishes (Burrows et al., 2004; Riley, 1973). The present approach estimates that these lateral movements reach 200 m on average, in accordance with Burrows et al. (2004) who highlighted a hundred-meters scale for correlations between food availability and juvenile density. Mesoscale (10 s km) migration of YoY juvenile flatfish between nursery sectors appear unlikely (Pihl et al., 2000) in spite of important tidal residual drifts in some locations. When transplanted laterally, fish have even been shown to display a tendency to move toward the site of their original capture (Burrows et al., 2004). Spatial segregation estimated from natural tracers confirms that juvenile flatfishes present site fidelity in conjunction with moderate alongshore dispersal. However, the lack of small-scale patterns in habitat signature of the tracers themselves, along the coastline, may prevent the detection of small-scale segregation; it is possible that patches of YoY flatfish segregated at low scale could not be separated using such tracers, and that the present dataset therefore overestimates minimum alongshore distances of segregation.

4.2.5. Ecological meaning of limited movements and scales of segregation

The present review estimates a maximal home range of 5 km·day⁻¹ for YoY flatfish and dramatically less when passive tidal swimming is not included; the scale of displacement linked to swimming abilities alone reaches not more than a few hundred meters. Indeed, YoY flatfish present important site fidelity and behave as specialists of their local habitat (White and Brown, 2013). Such site fidelity is widespread in many groups of fishes, and individuals of many species remain within a limited home area during the juvenile stage (Cerutti-Pereyra et al., 2014). If homing is the rule in heterogeneous habitat; e.g., in coral or rocky reefs (Pittman et al., 2014), mangroves (Gannon et al., 2015) or seagrass beds (Adams et al., 2004), small home range has also been verified for fish species living in more homogeneous habitats (e.g., soft bottom flatfish nursery grounds). Indeed, site fidelity also concerns juvenile fish that conduct important tidal migrations, with juveniles returning to particular tidal creeks, across tidal channels, after displacement (White and Brown, 2013). Even if passive drift and cyclic migrations are substantial, YoY flatfish can rely on local habitats at specific

stages of both the tidal and diel cycles, such that site fidelity may act over relatively small distances (Burrows et al., 2004).

The ability to use connected habitats could be crucial for juvenile fish (Sheaves, 2009). Connectivity links habitats in space and time and facilitates many life-history functions related to flatfish nursery utilization, as providing tradeoffs between shelter from predation (Burrows et al., 2001; Manderson et al., 2000; Van der Veer and Bergman, 1987) and the availability of prey (Le Pape et al., 2007; Nicolas et al., 2007). The small home range of YoY flatfish emphasizes the importance of site fidelity, indicating that limited movements can have beneficial impacts on individual's fitness (White and Brown, 2013). The cost of searching on a small scale for the highest quality patch is low because juvenile fish do not stray too far from cover, especially during the day, when they remain in deeper water to limit predation pressure. The consequences of a poor choice are low compared to the selection of an inappropriate large-scale habitat (Peterson, 2003). At this small scale, juvenile flatfish are able to locate high quality food or better shelter without large energy expenditure nor increased risks of predation (DeCesare et al., 2014). A larger-scale search for optimal habitats would require leaving shelter and travelling through poor quality habitats (Peterson, 2003). This site fidelity is coupled with temporary tidal/night inshore migration, which increases foraging area with limited energy cost or predation risk.

4.3. Consequences for flatfish population dynamics and insights for coastal management

Evidence is growing regarding the links between nursery habitat quality, juvenile fitness (Ohlberger et al., 2012) and related fish populations (Levin and Stunz, 2005; Thrush et al., 2002; Vasconcelos et al., 2014). The juvenile life history stages need to be emphasized because fish-habitat interactions are the strongest for these stages (Diaz et al., 2003), especially for flatfishes (Iles and Beverton, 2000) and even more so for YoY (Le Pape and Bonhommeau, in press). Accounting for flatfish ecology has important implications for coastal and estuarine management, considering their vulnerability and their dependence upon these nursery habitats; i.e., small-scale processes affecting juvenile flatfish result in large-scale outcomes for related populations.

Juvenile flatfish remain in a limited area and effects of nursery habitat suitability operate on this small scale of dispersal, with a strong dependence to local conditions (Burrows et al., 2001). The small home range reinforces juvenile flatfish sensitivity to local environmental changes. As individual juvenile fish may be relatively tolerant to local water and habitat quality degradation, disturbed habitats may appear beneficial, despite anthropogenic pressures (Le Pape et al., 2003b; Meng et al., 2002; Whitfield and Elliot, 2002). This lack of perception of anthropogenic disturbances and the low scale of displacement of juvenile flatfish render them especially sensitive to local habitat degradation and selection of degraded habitat can conduct to lower survival and fitness (DeCesare et al., 2014). Juvenile flatfish do not move in order to avoid unfavourable conditions linked to anthropogenic disturbances, such as oxygen depletion and hypoxic conditions (Dalla via et al., 1998; Meng et al., 2005) or exposure to contaminated water and sediments (Moles et al., 1994). Thus, degradation alters individual fitness (Saucerman and Deegan, 1991), besides negatively affecting recruitment (Gibson, 1994).

Understanding whether or not there are high levels of site fidelity has important implications for habitat conservation and the design of management measures (Green et al., 2012). As movements of juvenile flatfish are limited, the functional role of coastal and estuarine nurseries must be addressed within a fine-grained framework (Ciotti et al., 2013b; Peterson, 2003; Saucerman and Deegan, 1991). To that aim, coastal and estuarine Marine Protected Areas could efficiently allow for the protection of essential nursery habitats (Mesnildrey et al., 2013). MPAs where nursery habitats are the focus of important restrictions (Le Pape et al., 2014) may be more efficient than regulating fishing efforts

and landings to maintain flatfish stocks (van de Wolfshaar et al., 2011) and associated fisheries. Considering the moderate home range of juvenile flatfish, even small coastal and estuarine MPAs may protect juvenile flatfish individuals while allowing for moderate levels of spillover (Abecasis et al., 2014; Grüss et al., 2011; Pittman et al., 2014) before the adult stage.

As many species present both a similar dependence to coastal and estuarine nursery grounds (Seitz et al., 2014) and a moderate dispersion along the life cycle (Pittman et al., 2014), these insights from flatfish case studies could be considered of more general interest and significance across fish taxa.

4.4. Suggestions for future research

This review identified a number of knowledge gaps on the daily movements of YoY flatfishes. Range of movement is studied for few species in few locations and the perception and reaction of juvenile flatfish to the structure of their environment, the determinism of their movements, and the level of their habitat dependence remain poorly understood. Our findings provide a number of insights on methods that ought to be considered to improve knowledge of juvenile flatfish movements and habitat dependence.

4.4.1. From direct estimates of juvenile fish movement

Although video observations could provide reliable information (Spencer et al., 2005), they remain limited to relatively low-turbidity areas and conditions (Stoner et al., 2007), far from the norm in coastal and estuarine flatfish nursery grounds. Recent progress in tagging techniques and acoustic telemetry (e.g., Passive Integrated Transponder (PIT) tags) may represent fruitful options for measuring fish movements (Barbour and Adams, 2012; Rudershausen et al., 2014). With recent technological advances, movements of animals can be tracked with high resolution (Benhamou, 2014). Many recent references, rejected in the current review because they were focused on older-age flatfishes, evidence the interest of these approaches (Fairchild et al., 2009; Furey et al., 2013; Sackett et al., 2008). However, in spite of their rapid miniaturization, the size of available tags is still too large to be used on small and fragile YoY flatfish, and these approaches are still focused on larger individuals; i.e., 1-year olds and lengths > 10 cm (Barbour and Adams, 2012; Rudershausen et al., 2014).

4.4.2. From distances of segregation

Innovative approaches provide opportunities to estimate distance of segregation at finer resolution in the near future. Stable isotope signatures in liver have shorter times of response than signatures in muscle, and could provide evidence of refined segregation patterns. Analysis of stable isotopes in otoliths could be a powerful tool for tracking the movement of fishes across isoscapes (McMahon et al., 2011; Trueman et al., 2012); although they require the existence of patterns in habitat signature of the tracers, which are often not obvious along the coastline. Adaptive genetic markers show promise (Diopere et al., 2013). However, as the signal of discriminance is relatively weak for marine fish (Selkoe et al., 2010), approaches integrating several methods appear to be the most relevant for future research, as illustrated by various recent works (e.g., tags, otolith geochemistry and genetic molecular tools; Selkoe et al., 2008; otolith geochemistry and stable isotopes, Fodrie and Herzka, 2013; several genetic markers, Cuveliers et al., 2012; capture-recapture and diffusion models; Lagrange et al., 2014).

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References

- Abecasis, D., Afonso, P., Erzini, K., 2014. Can small MPAs protect local populations of a coastal flatfish, *Solea senegalensis*? *Fish. Manag. Ecol.* 21 (3), 175–185.
- Able, K.W., Grothues, T.M., 2007. Diversity of estuarine movements of striped bass (*Morone saxatilis*): a synoptic examination of an estuarine system in southern New Jersey. *Fish. Bull.* 105, 426–435.
- Adams, A.J., Locascio, J.V., Robbins, B.D., 2004. Microhabitat use by a post-settlement stage estuarine fish: evidence from relative abundance and predation among habitats. *J. Exp. Mar. Biol. Ecol.* 299, 17–33.
- Ansell, A.D., Gibson, R.N., 1993. The effect of sand and light on predation of juvenile plaice (*Pleuronectes platessa*) by fishes and crustaceans. *J. Fish Biol.* 43, 837–845.
- Archambault, B., Le Pape, O., Rivot, E., 2014. Density dependence can be revealed by modeling the variance in the stock-recruitment process. An application to flatfishes. *ICES J. Mar. Sci.* 71, 2127–2140.
- Barbour, A.B., Adams, A.J., 2012. Biologging to examine multiple life stages of an estuarine dependent fish. *Mar. Ecol. Prog. Ser.* 457, 241–250.
- Barbour, A.B., Aaron, J.A., Lorenzen, K., 2014. Size-based, seasonal, and multidirectional movements of an estuarine fish species in a habitat mosaic. *Mar. Ecol. Prog. Ser.* 5107, 263–276.
- Beilouis, P., Desaunay, Y., Dorel, D., Lemoine, M., 1979. Nurseries littorales de la Baie du Mont St Michel et du Cotentin-est. *ISTPM Nantes, France* (115 pp).
- Benhamou, S., 2014. Of scales and stationarity in animal movements. *Ecol. Lett.* 17 (3), 261–272.
- Berghahn, R., 1986. Determining abundance, distribution and mortality of 0-group plaice (*Pleuronectes platessa* L.) in the Wadden Sea. *J. Appl. Ichthyol.* 2, 11–22.
- Berghahn, R., 1987. Effects of tidal migration on growth of 0-group plaice (*Pleuronectes platessa* L.) in the North Frisian Wadden Sea. *Meeresforschungen* 31 (3–4), 209–226.
- Berghahn, R., 2001. Estimated intensity needed for sampling flatfish assemblages in reference areas of tidal mud flats systems may be disproportionately costly and deleterious. *J. Sea Res.* 45, 281–291.
- Berghahn, R., Lüdemann, K., Ruth, M., 1995. Differences in individual growth of newly settled 0-group plaice (*Pleuronectes platessa* L.) in the intertidal of neighbouring Wadden Sea areas. *Neth. J. Sea Res.* 34, 131–138.
- Brown, J.A., 2006. Classification of juvenile flatfishes to estuarine and coastal habitats based on the elemental composition of otoliths. *Estuarine, Coastal and Shelf Science* 66, 594–611.
- Burrows, M.T., Gibson, R.N., Robb, L., Comely, C.A., 1994. Temporal patterns of movement in juvenile flatfish and their predators: underwater television observations. *J. Exp. Mar. Biol. Ecol.* 177, 251–268.
- Burrows, J., Euchner, T., Baccante, N., 2001. Bull trout movement patterns: Halfway River and Peace River progress. In: Brewin, M.K., Paul, A.J., Monita, M. (Eds.), *Bull trout II conference proceedings*. Trout Unlimited Canada, Calgary, Alberta, pp. 153–157.
- Burrows, J.F., Horwood, J.W., Pitchford, J.W., 2004. Variable variability: difficulties in estimation and consequences for fisheries management. *Fish. Fish.* 14, 205–212.
- Cerutti-Pereyra, F., Thums, M., Austin, C.M., Bradshaw, C.J.A., Stevens, J.D., Babcock, R.C., Pillans, R.D., Meekan, M.G., 2014. Restricted movements of juvenile rays in the lagoon of Ningaloo Reef, Western Australia — evidence for the existence of a nursery. *Environ. Biol. Fish.* 97 (4), 371–383.
- Ciotti, B.J., Targett, T.E., Burrows, M.T., 2013a. Decline in growth rate of juvenile European plaice (*Pleuronectes platessa*) during summer at nursery beaches along the west coast of Scotland. *Can. J. Fish. Aquat. Sci.* 70 (5), 720–734.
- Ciotti, B.J., Targett, T.E., Burrows, M.T., 2013b. Spatial variation in growth rate of early juvenile European plaice *Pleuronectes platessa*. *Mar. Ecol. Prog. Ser.* 475, 213–232.
- Ciotti, B.J., Targett, T.E., Nash, R.D.M., Geffen, A.J., 2014. Growth dynamics of European plaice *Pleuronectes platessa* L. in nursery areas: a review. *J. Sea Res.* 90, 64–82.
- Coggan, R.A., Dando, P.R., 1988. Movements of juvenile Dover sole, *Solea solea* (L.), in the Tamar estuary, south western England. *J. Fish Biol.* 33, 177–184.
- Cuveliers, E., Larmuseau, M., Hellemans, B., Verherstraeten, S., Volckaert, F., Maes, G., 2012. Multi-marker estimate of genetic connectivity of sole (*Solea solea*) in the North-East Atlantic Ocean. *Mar. Biol.* 159 (6), 1239–1253.
- Dalla Via, J., Van den Thillart, G., Cattani, O., Cortesi, P., 1998. Behavioural responses and biochemical correlates in *Solea solea* to gradual hypoxic exposure. *Can. J. Zool.* 76, 2108–2113.
- Darnaude, A.M., Hunter, E., 2006. Linking natural and electronic data records to assess population dispersal and lifetime migration in North Sea Plaice. *J. Fish Biol.* 69 (230–230).
- De Pontual, H., Lagardere, F., Amara, R., Bohn, M., Ogor, A., 2003. Influence of ontogenetic and environmental changes in the otolith microchemistry of juvenile sole (*Solea solea*). *J. Sea Res.* 50, 199–210.
- De Raedemaeker, F., Keating, J., Brophy, D., O'Connor, I., Mc Grath, D., 2011. Spatial variability in diet, condition and growth of juvenile plaice (*Pleuronectes platessa*) at sandy beach nursery grounds on the south-west coast of Ireland. *J. Mar. Biol. Assoc. UK* 91, 1215–1223.
- De Raedemaeker, F., Brophy, D., O'Connor, I., O'Neill, B., 2012. Dependence of RNA:DNA ratios and Fulton's K condition indices on environmental characteristics of plaice and dab nursery grounds. *Estuar. Coast. Shelf Sci.* 98, 60–70.
- De Veen, J.F., 1978. On selective tidal transport in the migration of North Sea plaice (*Pleuronectes platessa*) and other flatfish species. *Neth. J. Sea Res.* 12, 115–147.
- DeCesare, N.J., Hebblewhite, M., Bradley, M., Hervieux, D., Neufeld, L., Musiani, M., 2014. Linking habitat selection and predation risk to spatial variation in survival. *J. Anim. Ecol.* 83, 343–352.
- Diaz, R.J., Cutter, G.R., Able, K.W., 2003. The importance of physical and biogenic structure to juvenile fishes on the shallow inner continental shelf. *Estuaries* 26 (1), 12–20.
- Dierking, J., Morat, F., Letourneur, Y., Harmelin-Vivien, M., 2012. Fingerprints of lagoonal life: migration of the marine flatfish *Solea solea* assessed by stable isotopes and otolith microchemistry. *Estuar. Coast. Shelf Sci.* 104–105, 23–32.
- Diopere, E., Hellemans, B., Volckaert, F., Maes, G., 2013. Identification and validation of single nucleotide polymorphisms in growth- and maturation-related candidate genes in sole (*Solea solea* L.). *Mar. Genomics* 9, 33–38.
- Dorel, D., Koutsikopoulos, C., Desaunay, Y., Marchand, J., 1991. Seasonal distribution of young sole (*Solea solea* (L.)) in the nursery ground of the Bay of Vilaine (Northern Bay of Biscay). *Neth. J. Sea Res.* 27, 297–306.
- Durieux, E., Le Duigou, M., Millot, S., Sasal, P., Begout, M.L., 2010. Sedentary behaviour establishment in 0-group common sole *Solea solea*: a laboratory video-tracking study. *J. Mar. Biol. Assoc. U. K.* 90, 1257–1262.
- Edwards, R., Steele, J.H., 1968. The ecology of 0-group plaice and common dabs at Loch ewe. I Population and food. *J. Exp. Mar. Biol. Ecol.* 2, 215–238.
- Exadactylos, A., Geffen, A.J., Panagiotaki, P., Thorpe, J.P., 2003. Population structure of Dover sole *Solea solea*: RAPD and allozyme data indicate divergence in European stocks. *Mar. Ecol. Prog. Ser.* 246, 253–264.
- Fairchild, E.A., Rennels, N., Howell, H., 2009. Using telemetry to monitor movements and habitat use of cultured and wild juvenile winter flounder in a shallow estuary. *Rev. Methods Technol. Fish Biol. Fish.* 9, 5–22.
- Fodrie, J.F., Herzka, S.Z., 2013. A comparison of otolith geochemistry and stable isotope markers to track fish movement: describing estuarine ingress by larval and post-larval halibut. *Estuar. Coasts* 36, 906–917.
- Fox, C.J., McCloghrie, P., Young, E.F., Nash, R.D.M., 2006. The importance of individual behaviour for successful settlement of juvenile plaice (*Pleuronectes platessa* L.): a modelling and field study in the eastern Irish Sea. *Fish. Oceanogr.* 15, 301–313.
- Fuji, T., Kasai, A., Suzuki, K.W., Ueno, M., Yamashita, Y., 2011. Migration ecology of juvenile temperate seabass *Lateolabrax japonicus*: a carbon stable-isotope approach. *J. Fish Biol.* 78, 2010–2025.
- Fulford, R.S., Peterson, M.S., Grammer, P.O., 2011. An ecological model of the habitat mosaic in estuarine areas: part I — Interaction of dispersal theory and habitat variability in describing juvenile fish distribution. *Ecol. Model.* 17, 3203–3215.
- Furey, N.B., Dance, M.A., Rooker, J.R., 2013. Fine-scale movements and habitat use of juvenile southern flounder *Paralichthys lethostigma* in an estuarine seascape. *J. Fish Biol.* 82 (5), 1469–1483.
- Gannon, R., Payne, N., Suthers, I., Gray, C., van der Meulen, D., Taylor, M., 2015. Fine-scale movements, site fidelity and habitat use of an estuarine dependent sparid. *Environ. Biol. Fish.* 98, 1599–1609.
- Gibson, R.N., 1973. Tidal and circadian activity rhythms in juvenile plaice *Pleuronectes platessa*. *Mar. Biol.* 22, 379–386.
- Gibson, R.N., 1980. A quantitative description of the behaviour of wild juvenile plaice (*Pleuronectes platessa*). *Anim. Behav.* 28, 1202–1216.
- Gibson, R.N., 1994. Impact of habitat quality and quantity on the recruitment of juvenile flatfishes. *Neth. J. Sea Res.* 32 (2), 191–206.
- Gibson, R.N., 2005. Flatfishes: biology and exploitation. Blackwell Publishing, Oxford.
- Gibson, R.N., Pihl, L., Burrows, M.T., Modin, J., Wennhage, H., Nickell, L.A., 1998. Diel movements of juvenile plaice *Pleuronectes platessa* in relation to predators, competitors, food availability and abiotic factors on a microtidal nursery ground. *Mar. Ecol. Prog. Ser.* 165, 145–159.
- Gibson, R.N., Robb, L., Wennhage, H., Burrows, M.T., 2002. Ontogenetic changes in depth distribution of juvenile flatfishes in relation to predation risk and temperature on a shallow-water nursery ground. *Mar. Ecol. Prog. Ser.* 229, 233–244.
- Gillanders, B.M., 2005. Using elemental chemistry of fish otoliths to determine connectivity between estuarine and coastal habitats. *Estuar. Coast. Shelf Sci.* 64 (1), 47–57.
- Gilliers, C., 2004. Recherche des bioindicateurs de la qualité des écosystèmes côtiers. Application aux nourriceries côtières et estuariennes de poissons plats Thèse de doctorat (Ph.D.), spécialité «Sciences de la vie», Université du Littoral — Côte d'Opale (174 pp + appendix).
- Gilliers, C., Amara, R., Bergeron, J.P., Le Pape, O., 2004. Comparison of growth and condition indices flatfish in different coastal nursery grounds. *Environ. Biol. Fish.* 71, 189–198.
- Gilliers, C., Le Pape, O., Desaunay, Y., Bergeron, J.P., Schreiber, N., Guerault, D., Amara, R., 2006. Growth and condition of juvenile sole (*Solea solea* L.) as indicators of habitat quality in coastal and estuarine nurseries in the Bay of Biscay with a focus on sites exposed to the Erika oil spill. *Sci. Mar.* 70, 183–192.
- Glass, L.A., Rooker, J.R., Kraus, R.T., Holt, G.J., 2008. Distribution, condition, and growth of newly settled southern flounder (*Paralichthys lethostigma*) in the Galveston Bay Estuary, TX. *J. Sea Res.* 59, 259–268.
- Green, B.C., Smith, D.J., Grey, J., Underwood, G.J.C., 2012. High site fidelity and low site connectivity in temperate salt marsh fish populations: a stable isotope approach. *Oecologia* 168 (1), 245–255.
- Grüss, A., Kaplan, D., Guenette, S., Roberts, C.M., Botsford, L.W., 2011. Consequences of adults and juvenile movement for marine protected areas. *Biol. Conserv.* 144, 692–702.
- Hanski, I., 1998. Metapopulation dynamics. *Nature* 396, 41–49.
- Hanson, P.J., Koehn, C.C., Zdanowicz, V.S., 2004. Elemental composition of otoliths used to trace estuarine habitats of juvenile gag *Mycteroperca microlepis* along the west coast of Florida. *Mar. Ecol. Prog. Ser.* 267, 253–265.

- Harden, J., 1968. Fish migration. Edward Arnold, London, UK (325 pp).
- Haynes, P.S., Brophy, D., McGrath, D., 2012. Variability in the early life stages of juvenile plaice (*Pleuronectes platessa*) on west Ireland nursery grounds: 2000–2007. *J. Mar. Biol. Assoc. UK* 92, 395–406.
- Herzka, S.Z., Griffiths, R., Fodrie, F.J., McCarthy, I.D., 2009. Short-term size-specific distribution and movement patterns of juvenile flatfish in a Pacific estuary derived through length-frequency and mark-recapture data. *Cienc. Mar* 35 (1), 41–57.
- Hurst, T.P., Duffy, T.A., 2005. Activity patterns in northern rock sole are mediated by temperature and feeding history. *J. Exp. Mar. Biol. Ecol.* 325, 201–213.
- Iles, T.C., Beverton, R.J.H., 2000. The concentration hypothesis: the statistical evidence. *ICES J. Mar. Sci.* 57, 216–227.
- Jenkins, G.P., Shaw, M., Stewart, B.D., 1993. Spatial variation in food-limited growth of juvenile greenback flounder, *Rhombosolea tapirina*: evidence from otolith daily increments and otolith scaling. *Can. J. Fish. Aquat. Sci.* 50, 2558–2567.
- Johnson, D.W., 2007. Habitat complexity modifies post-settlement mortality and recruitment dynamics of marine fish. *Ecology* 88, 1716–1725.
- Karakiri, M., Berghahn, R., Von Westernhagen, H., 1989. Growth differences in 0-group plaice *Pleuronectes platessa* as revealed by otolith microstructure analysis. *Mar. Ecol. Prog. Ser.* 55, 15–22.
- Karakiri, M., Berghahn, R., van der Veer, H.W., 1991. Variations in settlement and growth of 0-group plaice (*Pleuronectes platessa* L.) in the Dutch Wadden Sea as determined by otolith microstructure analysis. *J. Sea Res.* 55, 15–22.
- Kostecki, C., Le Loc'h, F., Roussel, J.M., Desroy, N., Huteau, D., Le Bris, H., Le Pape, O., 2010. Dynamics of an estuarine nursery ground: the spatio-temporal relationship between the river flow and the food web of the juvenile common sole (*Solea solea*) as revealed by stable isotopes analysis. *J. Sea Res.* 64, 54–60.
- Kuipers, B., 1973. On the tidal migration of young plaice (*Pleuronectes platessa*) in the Wadden Sea. *Neth. J. Sea Res.* 6, 376–388.
- Lagrange, P., Pradel, R., Belisle, M., Gimenez, O., 2014. Estimating dispersal among numerous sites using capture-recapture data. *Ecology* 95, 2316–2323.
- Laurent, A.G., 1963. The log-normal distribution and the translation method: description and estimation problems. *J. Am. Stat. Assoc.* 58, 231–235.
- Le Luherne, E., Réveillac, E., Ponsoer, A., Sturbois, A., Ballu, S., Perdriau, M., Le Pape, O. (in review) Response of fish community to green tides in shallow estuarine and coastal areas. *Estuar. Coast. Shelf Sci.*
- Le Pape, O., Bonhommeau, S., 2015. The food limitation hypothesis for juvenile marine fish. *Fish. Fish.* <http://dx.doi.org/10.1111/faf.12063> (in press).
- Le Pape, O., Chauvet, F., Mahevas, S., Lazure, P., Guerault, D., Desaunay, Y., 2003a. Quantitative description of habitat suitability for the juvenile common sole (*Solea solea*, L.) in the Bay of Biscay (France) and the contribution of different habitats to the adult population. *J. Sea Res.* 50, 139–149.
- Le Pape, O., Holley, J., Guerault, D., Desaunay, Y., 2003b. Quality of coastal and estuarine fish habitats: estimations based on the size of juvenile common sole (*Solea solea* L.). *Estuar. Coast. Shelf Sci.* 58, 793–803.
- Le Pape, O., Baulier, L., Cloarec, A., Martin, J., Le Loc'h, F., Desaunay, Y., 2007. Habitat suitability for juvenile common sole (*Solea solea*, L.) in the Bay of Biscay (France): a quantitative description using indicators based on epibenthic fauna. *J. Sea Res.* 57, 126–136.
- Le Pape, O., Modéran, J., Beaunée, G., Riera, P., Nicolas, D., Savoye, N., Harmelin-Vivien, M., Darnaude, A.M., Brind'Amour, A., Le Bris, H., Cabral, H., Vinagre, C., Pasquaud, S., França, S., Kostecki, C., 2013. Sources of organic matter for flatfish juveniles in coastal and estuarine nursery grounds: a meta-analysis for the common sole (*Solea solea*) in contrasted systems of Western Europe. *J. Sea Res.* 75, 85–95.
- Le Pape, O., Delavenne, J., Vaz, S., 2014. Quantitative mapping of fish habitat: a useful tool to design spatialised management measures and Marine Protected Area with fishery objectives. *Ocean Coast. Manag.* 87, 8–19.
- Levin, P.S., Stunz, G.W., 2005. Habitat triage for exploited fishes: can we identify essential fish habitat? *Estuar. Coast. Shelf Sci.* 64, 70–78.
- Manderson, J.P., Phelan, B.A., Stoner, A.W., Hilbert, J., 2000. Predator prey relations between age-1 + summer flounder (*Paralichthys dentatus*, L.) and age 0 winter flounder (*Pseudopleuronectes americanus*, Walbaum): predator diets, prey selection, and effects of sediments and macrophytes. *J. Exp. Mar. Biol. Ecol.* 251, 17–39.
- McMahon, K.W., Fogel, M.L., Johnson, B.J., Houghton, L.A., Thorrold, S.R., 2011. A new method to reconstruct fish diet and movement patterns from $\delta^{13}C$ values in otolith amino acids. *Can. J. Fish. Aquat. Sci.* 68 (8), 1330–1340.
- Meng, L., Orphanides, C.D., Powell, J.C., 2002. Use of fish index to assess habitat quality in Narragansett Bay, Rhode Island. *Trans. Am. Fish. Soc.* 131, 731–742.
- Meng, L., Cicchetti, G., Raciti, S., 2005. Relationships between juvenile winter flounder and multiple scale habitat variation in Narragansett Bay, Rhode Island. *Trans. Am. Fish. Soc.* 134, 1509–1519.
- Mesnilidrey, L., Gascuel, D., Le Pape, O., 2013. Integrating Marine Protected Areas in fisheries management systems: some criteria for ecological efficiency. *Aquat. Living Resour.* 26, 159–170.
- Meyer, S., Caldaroni, E.M., Chicharo, M.A., Clemmesen, C., Faria, A.M., Faulk, C., Folkvord, A., Holt, G.J., Hoie, H., Kanstinger, P., Malzahn, A., Moran, D., Peteret, C., Stotttrup, J.G., Peck, M.A., 2012. On the edge of death: Rates of decline and lower thresholds of biogeochemical condition in food-deprived fish larvae and juveniles. *J. Mar. Syst.* 93, 11–24.
- Miller, T.J., Crowder, L.B., Rices, J.A., Marshall, E.A., 1988. Larval size and recruitment mechanisms in fishes: toward a conceptual framework. *Can. J. Fish. Aquat. Sci.* 45, 1657–1667.
- Moles, A., Rice, S., Norcross, B.L., 1994. Non-avoidance of hydrocarbon laden sediments by juvenile flatfishes. *Neth. J. Sea Res.* 32 (3/4), 361–367.
- Morat, F., Letourneur, Y., Dierking, J., Pécheyran, C., Bareille, G., Blamart, D., Harmelin-Vivien, M., 2014. The great melting pot. Common sole population connectivity assessed by otolith and water fingerprints. *PLoS ONE* 9 (1), e86585.
- Morrison, M., Francis, M., Hartill, B., Parkinson, D., 2002. Diurnal and tidal variation in the abundance of the fish fauna of a temperate tidal mudflat. *Estuar. Coast. Shelf Sci.* 54, 793–807.
- Nicolas, D., Le Loc'h, F., Désaunay, Y., Hamon, D., Blanchet, A., Le Pape, O., 2007. Relationship between benthic macrofauna and habitat suitability for juvenile common sole (*Solea solea*, L.) in the Vilaine estuary (Bay of Biscay, France) nursery ground. *Estuar. Coast. Shelf Sci.* 73, 639–650.
- Nunn, A.D., Tewson, L.H., Cowx, I.G., 2012. The foraging ecology of larval and juvenile fish. *Rev. Fish. Biol. Fish.* 22, 377–408.
- Ohlberger, J., Otero, J., Edeline, E., Winfield, I.J., Stenseth, N.C., Vollestad, L.A., 2012. Biotic and abiotic effects on cohort size distributions in fish. *Oikos* 122 (6), 835–844.
- Palmer, S.C.F., Coulon, A., Travis, J.M.J., 2014. Inter-individual variability in dispersal behaviour impacts connectivity estimates. *Oikos* 123, 923–932.
- Pasquaud, S., Elie, P., Jeantet, C., Billy, I., Martinez, P., Girardin, M., 2008. A preliminary investigation of the fish food web in the Gironde estuary, France, using dietary and stable isotope analyses. *Estuar. Coast. Shelf Sci.* 78, 267–279.
- Peterson, M., 2003. A conceptual view of environment-habitat-production linkages in tidal river estuaries. *Rev. Fish. Sci.* 11, 291–313.
- Pihl, L., Modin, J., Wennhage, H., 2000. Spatial distribution patterns of newly settled plaice (*Pleuronectes platessa* L.) along the Swedish Skagerrak archipelago. *J. Sea Res.* 44, 65–80.
- Pittman, S.J., Monaco, M.E., Friedlander, A.M., Legare, B., Nemeth, R.S., Kendall, M.S., Poti, M., Clark, R.D., Wedding, L.M., Caldwell, C., 2014. Fish with chips: tracking reef fish movements to evaluate size and connectivity of Caribbean marine protected areas. *PLoS ONE* 9 (5), e96028.
- Poxton, M.G., Eleftheriou, A., McIntyre, A.D., 1983. The food and growth of 0-group flatfish on nursery grounds in the Clydes Sea area. *Estuar. Coast. Shelf Sci.* 17, 319–337.
- Raffaelli, D., Richner, H., Summers, R., Northcott, S., 1990. Tidal migrations in the flounder (*Platichthys flesus*). *Mar. Behav. Physiol.* 16, 249–260.
- Ramzi, A., Arino, O., Koutsikopoulos, C., Boussouar, A., Lazure, P., 2001. Modelling and numerical simulations of larval migration of the sole (*Solea solea* (L.)) of the Bay of Biscay. Part 2: numerical simulations. *Oceanol. Acta* 24, 113–124.
- Rauck, G., 1974. The arrival of different groups of young plaice in the German Wadden Sea. *Berichte der Deutschen wissenschaftlichen Kommission für Meeresforschung* 23, 273–288.
- Riley, J.D., 1973. Movements of 0-group plaice *Pleuronectes platessa* L. as shown by latex tagging. *J. Fish Biol.* 5, 323–343.
- Rochette, S., Rivot, E., Morin, J., Mackinson, S., Riou, P., Le Pape, O., 2010. Effect of nursery habitat degradation on flatfish population: application to *Solea solea* in the Eastern Channel (Western Europe). *J. Sea Res.* 64, 34–44.
- Rolland, J.L., Bonhomme, F., Lagardere, F., Hassan, M., Guinand, B., 2007. Population structure of the common sole (*Solea solea*) in the Northeastern Atlantic and the Mediterranean Sea: revisiting the divide with EPIC markers. *Mar. Biol.* 151, 327–341.
- Ross, S.W., 2003. The relative value of different estuarine nursery areas in North Carolina for transient juvenile marine fishes. *Fish. Bull.* 101, 384–404.
- Rountree, R.A., Able, K.W., 1992. Foraging habits, growth, and temporal patterns of salt-marsh creek habitat use by young-of-the-year summer flounder in New Jersey. *Trans. Am. Fish. Soc.* 121, 765–776.
- Rudershausen, P.J., Buckel, J.A., Dubreuil, T., O'Donnell, M.J., Hightower, J.E., Poland, S.J., Letcher, B.H., 2014. Estimating movement and survival rates of a small saltwater fish using autonomous antenna receiver arrays and passive integrated transponder tags. *Mar. Ecol. Prog. Ser.* 499, 177–192.
- Sackett, D.K., Able, K.W., Grothues, T.M., 2008. Habitat dynamics of summer flounder *Paralichthys dentatus* within a shallow USA estuary based on multiple approaches using acoustic telemetry. *Mar. Ecol. Prog. Ser.* 364, 199–212.
- Saucerman, S.E., Deegan, L.A., 1991. Lateral and cross-channel movement of young-of-the-year winter flounder (*Pseudopleuronectes americanus*) in Waquoit Bay, Massachusetts. *Estuaries* 14, 440–446.
- Savina, M., Lacroix, G., Ruddick, K., 2010. Modelling the transport of common sole larvae in the Southern North Sea: Influence of hydrodynamics and larval vertical movements. *J. Mar. Syst.* 81, 86–98.
- Scharf, F.S., 2000. Patterns in abundance, growth, and mortality of juvenile red drum across estuaries on the Texas coast and implications for recruitment and stock enhancement. *Trans. Am. Fish. Soc.* 129, 1207–1222.
- Secor, H., Rooker, J.R., 2005. Connectivity in the life history of fishes that use estuaries. *Estuar. Coast. Shelf Sci.* 64 (1), 1–5.
- Seitz, R.D., Wennhage, H., Bergstrom, U., Lipcius, R.N., Ysebaert, T., 2014. Ecological value of coastal habitats for commercially and ecologically important species. *ICES J. Mar. Sci.* 71 (3), 648–655.
- Selkoe, K.A., Hinzler, C.M., Gaines, S.D., 2008. Seascape genetics and the spatial ecology of marine populations. *Fish. Fish.* 9, 363–377.
- Selkoe, K.A., Watson, J.R., White, C., Horin, T.B., Iacchei, M., Mitarai, S., Siegel, D.A., Gaines, S.D., Toonen, R.J., 2010. Taking the chaos out of genetic patchiness: seascape genetics reveals ecological and oceanographic drivers of genetic patterns in three temperate reef species. *Mol. Ecol.* 19, 3708–3726.
- Sheaves, M., 2009. Consequences of ecological connectivity: the coastal ecosystem mosaic. *Mar. Ecol. Prog. Ser.* 391, 107–115.
- Sluka, R.D., Chiappone, M., Sullivan Sealey, K.M., 2001. Influence of habitat on grouper abundance in the Florida Keys, U.S.A. *J. Fish Biol.* 58, 682–700.
- Smedbol, R.K., McPherson, A., Hansen, M.M., Kenchington, E., 2002. Myths and moderation in marine 'metapopulations'? *Fish. Fish.* 3, 20–35.
- Sogard, S.M., Able, K.W., 1992. Growth variation of newly settled winter flounder (*Pseudopleuronectes americanus*) in New Jersey estuaries as determined by otolith microstructure. *Neth. J. Sea Res.* 29 (1–3), 163–172.
- Souza, A.T., Dias, E., Nogueira, A., Campos, J., Marques, J.C., Martins, I., 2013. Population ecology and habitat preferences of juvenile flounder *Platichthys flesus* (Actinopterygii: Pleuronectidae) in a temperate estuary. *J. Sea Res.* 79, 60–69.

- Spencer, M.L., Stoner, A.W., Ryer, C.H., Munk, J.E., 2005. A towed camera sled for estimating abundance of juvenile flatfishes and habitat characteristics: comparison with beam trawls and divers. *Estuar. Coast. Shelf Sci.* 64, 497–503.
- Stoner, A., Spencer, M.L., Ryer, C.H., 2007. Flatfish-habitat associations in Alaska nursery grounds: use continuous video records for multiscale spatial analysis. *J. Sea Res.* 57 (2–3), 137–151.
- Szedlmayer, S.T., Able, K.W., 1993. Ultrasonic telemetry of age-0 summer flounder, *Paralichthys dentatus*, movements in a southern New Jersey estuary. *Copeia* 3, 728–736.
- Tanner, S.E., Reis-Santos, P., Vasconcelos, R., Thorrold, S.R., Cabral, H.N., 2013. Population connectivity of *Solea solea* and *Solea senegalensis* over time. *J. Sea Res.* 76, 82–88.
- Thrush, S., Schultz, D., Hewitt, J., Talley, D., 2002. Habitat structure in soft-sediment environments and abundance of juvenile snapper *Pagrus auratus*. *Mar. Ecol. Prog. Ser.* 245, 273–280.
- Trimoreau, E., Archambault, B., Brin D'Amour, A., Lepage, M., Guitton, J., Le Pape, O., 2013. A quantitative estimate of the function of soft-bottom sheltered coastal areas as essential flatfish nursery habitat. *Estuar. Coast. Shelf Sci.* 133, 193–205.
- Trueman, C.N., MacKenzie, K.M., Palmer, M.R., 2012. Identifying migrations in marine fishes through stable-isotope analysis. *J. Fish Biol.* 81 (2), 826–847.
- Tupper, M., Able, K.W., 2000. Movements and food habits of striped bass (*Marone saxatilis*) in Delaware Bay (USA) salt marshes: comparison of a restored and a reference marsh. *Mar. Biol.* 137, 1049–1058.
- Tyler, A.V., 1971. Surges of winter flounder, *Pseudopleuronectes americanus*, into the intertidal zone. *J. Fish. Res. Board Can.* 28, 1727–1732.
- Van de Wolfshaar, K.E., HilleRisLambers, R., Gardmark, A., 2011. Effect of habitat productivity and exploitation on populations with complex life cycles. *Mar. Ecol. Prog. Ser.* 438, 175–184.
- Van der Veer, H.W., Bergman, M.J.M., 1986. Development of tidally related behaviour of a newly settled 0-group plaice (*Pleuronectes platessa*) population in the western Wadden Sea. *Mar. Ecol. Prog. Ser.* 31, 121–129.
- Van der Veer, H.W., Bergman, M.J.N., 1987. Predation by crustaceans on a newly settled 0-group plaice *Pleuronectes platessa* population in the western Wadden Sea. *Mar. Ecol. Prog. Ser.* 35, 203–215.
- Van der Veer, H.W., Witte, J.I.J., 1993. The 'maximum growth/optimal food condition' hypothesis: a test for 0-group plaice *Pleuronectes platessa* in the Dutch Wadden Sea. *Mar. Ecol. Prog. Ser.* 101, 81–90.
- Van der Veer, H.W., Berghahn, R., Rijnsdorp, A.D., 1994. Impact of juvenile growth on recruitment in flatfish. *Neth. J. Sea Res.* 32, 153–173.
- Vasconcelos, R., Reis-Santos, P., Maia, A., Fonseca, V., Franca, S., Wouters, N., Costa, M.J., Cabral, H.N., 2009. Nursery use patterns of commercially important marine fish species in estuarine systems along the Portuguese coast. *Estuar. Coast. Shelf Sci.* 86, 613–624.
- Vasconcelos, R.P., Eggleston, D.B., Le Pape, O., Tulp, I., 2014. Patterns and processes of habitat-specific demographic variability in exploited marine species. *ICES J. Mar. Sci.* 71, 664–673.
- Vinagre, C., França, S., Cabral, H.N., 2006. Diel and semi-lunar patterns in the use of an intertidal mudflat by juveniles of Senegal sole, *Solea senegalensis*. *Estuar. Coast. Shelf Sci.* 69, 246–254.
- Vinagre, C., Salgado, J., Costa, M.J., Cabral, H.N., 2008. Nursery fidelity, food web interactions and primary sources of nutrition of the juveniles of *Solea solea* and *S. senegalensis* in the Tagus estuary (Portugal): A stable isotope approach. *Estuar. Coast. Shelf Sci.* 76, 255–264.
- Ward, R.D., Woodward, M., Skibinski, D.O.F., 1994. A comparison of genetic diversity levels in marine, freshwater and anadromous fish. *J. Fish Biol.* 44, 213–232.
- White, G.E., Brown, C., 2013. Site fidelity and homing behaviour in intertidal fishes. *Mar. Biol.* 160, 1365–1372.
- Whitfield, A.K., Elliot, M., 2002. Fishes as indicators of environmental and ecological changes within estuaries: a review of progress and some suggestions for the future. *J. Fish Biol.* 61 (A), 229–250.
- Wirjoatmodjo, S., Pitcher, T.J., 1984. Flounders follow the tides to feed: evidence from ultrasonic tracking in an estuary. *Estuar. Coast. Shelf Sci.* 19, 231–241.
- Woodland, R.J., Secor, D.H., 2011. Differences in juvenile trophic niche for two coastal fish species that use marine and estuarine nursery habitats. *Mar. Ecol. Prog. Ser.* 439, 241–254.