
The food limitation hypothesis for juvenile marine fish

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Abstract:

Coastal zones are productive areas that serve as nursery grounds for a large number of marine species. However, the processes involved in survival success during the juvenile phase are not well-known. Some authors suggest that the availability of prey is important to support the production of pre-recruit fish whose fitness is enhanced through optimal feeding conditions. Accordingly, recruitment is limited by the carrying capacity of the nursery habitat. In contrast, other authors state that the carrying capacity of the nursery grounds is not fully exploited, suggesting that there is no effect of food limitation. This study combines an overview of the literature, focused on flatfish that are especially dependent on coastal and estuarine nursery grounds, an extension to other marine fishes and a modelling approach on growth and survival of juvenile fish to explore the controversy of food limitation in their nursery grounds. We demonstrate that the relative lack of growth limitation observed for young marine fishes at the individual scale is related to an observational bias: fish have been affected by size-selective mortality linked to food limitation, but only surviving individuals are observed. As the population is skewed towards the faster-growing juveniles, the growth of survivors remains close to optimal, even when food resources are limited. Food limitation is of major influence in determining the carrying capacity of the nursery habitat. To sustain marine fish populations and related fisheries, management action is needed to protect coastal and estuarine areas and maintain or restore nursery productivity.

Keywords: Estuaries and coasts ; food limitation ; habitat functionality ; juvenile fish growth ; size-dependent mortality ; trophic capacity of nursery habitat

1 **Introduction**

2 The life strategy of most marine teleost fish species is characterized by high fecundity, the
3 production of large amounts of small pelagic eggs and the lack of parental care (Juanes 2007).
4 This strategy leads to high mortality in early life stages (eggs, larvae and juveniles). Survival-
5 to-maturity rates as low as 1:100,000 are common in many marine fish populations (Table 1).
6 This low survival rate is specific to marine fish, as freshwater and anadromous species exhibit
7 higher likelihood of surviving from egg to adult (e.g., 1% survival for Atlantic salmon (*Salmo*
8 *salar*, *Salmonidae*) populations; Hutchings and Jones 1998). A life strategy with high and
9 highly variable mortality makes the survival of eggs, larvae (Houde 1987, 2008, Cushing
10 1995, Bakun 1996) and juveniles (Sogard 1997) strongly dependent on abiotic and biotic
11 environmental factors. This, in turn, results in high variability in the recruitment and mortality
12 of early life stages with dramatic influence on the abundance of fish populations (Gallego et
13 al. 2012). Most of the recruitment variability of marine fishes (10-fold interannually and 100-
14 fold in overall variability; Houde 2008) is explained by larval and juvenile survival rates
15 (Levin and Stunz 2005). These stages represent a bottleneck in the dynamics of fish
16 populations and small changes in the survival rates of these stages can cause large differences
17 in recruitment (Levin and Stunz, 2005; Daewel et al. 2011). Recruitment variability and the
18 associated large fluctuations in fish populations have been a focus of marine and fisheries
19 science since in the early 20th century (Hjort 1914) and continue to be important areas of
20 research (Sinclair 1997, Houde 2008, Gallego et al. 2012).

21 The egg and larvae stage and the juvenile stage both exhibit low survival and
22 contribute to the large recruitment variability:

23 - The variability-generating processes that occur at the egg and larval stages are of
24 critical importance to population levels (Hjort 1914, van der Veer et al. 2000a, Rochette et al.

1 2012; Table 1). During these life stages, complex and varied mechanisms influence both
2 growth and survival and are important determinants of recruitment success. These include the
3 drift of eggs and larvae, temperature control over early life dynamics (i.e., life stage duration,
4 growth and mortality), food availability for larvae and predation. These mechanisms interact
5 to generate recruitment variability that can fluctuate by an order of magnitude (Houde 2008).

6 - Mortality rates of the juvenile stage are also high (Table 1), though significantly
7 lower than the larval stage (van der Veer et al. 2000a). Processes occurring in the nursery
8 habitat are important determinants of population density (Holbrook et al. 2000). Minto et al.
9 (2008) investigated the link between survival variability and population density from stock
10 recruitment relationships using both a modelling approach and a meta-analysis of wild fish
11 populations. They show that the interannual variability of progeny survival increases at low
12 adult abundance. This pattern is consistent with density-dependent mortality in the juvenile
13 phase which follows stochastic density-independent mortality in the egg and larval stages.
14 Thus, density-independent and -dependent effects on settlement, growth and mortality in the
15 nursery habitat influence recruitment success and variability (van der Veer et al. 2000a,
16 Peterson et al. 2000, Peterson 2003, Levin and Stunz 2005, Fodrie et al. 2009) and are
17 important in regulating year-class strength (Scharf 2000, Stottrup and Sparrevojn 2007). As
18 described in the concentration hypothesis, recruitment variability is lower in populations with
19 large density-dependent effects (Iles and Beverton 2000) related to the capacity and features
20 of the nursery habitat (Johnson 2007). This is especially verified for flatfishes (Iles and
21 Beverton 2000, Le Pape et al. 2003c, Rooper et al. 2004). Thus, nursery habitats are
22 particularly important for many marine fish species (Peterson et al, 2000, Beck et al. 2001
23 Fulford et al. 2011) and can act as habitat bottlenecks.

24 Though growth limitation and mortality on nursery grounds are thought to contribute
25 to recruitment variability (Rauck and Zijlstra 1978, Karakiri et al. 1989, Cowan et al. 2000,

1 Grover et al. 2002, Duncan and Holland 2006), survival processes of the juvenile phase are
2 still not well known and remain controversial in regards to their contribution to recruitment
3 variability.

4 - According to many analyses, prey availability is important to sustain production of
5 pre-recruit fishes and juveniles. Coastal and estuarine (C&E) habitats (mudflats, salt marshes,
6 kelp forests, seagrass beds, mangroves, coral reefs, upwelling regions, etc; Vasconcelos et al.
7 in press), but also other productive habitats, serve as nursery grounds for many marine fish
8 species (Able et al. 1999, Elliott and Dewailly 1995, Holbrook et al. 2000, Grover et al. 2002,
9 Jones et al. 2002, Laegdsgaard and Johnson 2001, Peterson 2003, McLusky and Elliott 2004,
10 Elliott et al. 2007, Franco et al. 2008, Selleslagh and Amara, 2008), and especially flatfishes
11 (Gibson 1994, Meng et al. 2002, Le Pape et al. 2003b). Fishes aggregate in these productive
12 areas where their fitness is enhanced through optimal growth from better feeding conditions
13 (Blaber and Blaber 1980, Miller et al. 1984, Gibson 1994, Friedland et al. 1996, Beck et al.
14 2001, Houde 2008). The interannual distribution of food availability and juvenile fish biomass
15 are synchronous (Fujii and Noguchi 1995, Walsh 1996, Vinagre et al. 2005, Wouters and
16 Cabral 2009). Thus, food resources are often mentioned as a limiting factor in the capacity of
17 nursery habitats (van der Veer and Witte 1993, Gibson 1994, Craig et al. 2007, Nash and
18 Geffen 2000, Nash et al. 2007).

19 - Other studies show that juvenile growth is not affected by trophic conditions in
20 nursery habitats, indicating that there is no effect of food limitation (Curran and Able 2002,
21 Ross 2003, Hampel et al. 2005, Diaz et al. 2011; Selleslagh et al., 2012) and suggesting that
22 the carrying capacity of nursery areas is not reached (Rogers 1994, Shi et al. 1997, van der
23 Veer et al. 2000a, Vinagre and Cabral 2008). Van der Veer et al. (2000b) and Manderson et
24 al. (2000) propose predation as the main factor in the variability of juvenile mortality and
25 recruitment success, suggested for various species (McErlean et al. 1973, Blaber and Blaber

1 1980, Riley et al. 1981, Gibson 1994, Levin et al. 1997, Wennhage and Gibson 1998, Halpin
2 2000, Lewis 2001, Wennhage and Pihl 2001, Hixon and Jones 2005, Baker and Sheaves
3 2005, White and Caselles 2008, Sheaves 2009). Predators and their short-term response (Stier
4 et al. 2013) to juvenile fish densities generate density dependent mortality (Johnson 2007,
5 Juanes 2007), helping to explain why recruitment is dampened during the juvenile stage on
6 nursery grounds.

7 This controversy is illustrated (Table 2) by several well-studied cases of numerous
8 species of the juveniles of commercial flatfish off the Western coasts of Europe (Fig. 1) and
9 other temperate and subarctic areas. In many studies, measures of growth, nutritional
10 condition and body condition indicate almost no food limitation or links to prey availability of
11 the juveniles collected on C&E nursery grounds during the summer growth period. Moreover,
12 these juveniles appear to be protected from interspecific competition by the process of food
13 partitioning. However, for the same species, study areas and periods, other studies indicate (i)
14 nutritionally-limiting conditions during metamorphosis, (ii) a small decrease in growth, (iii)
15 an overlap between the juvenile distribution of benthic species and their potential prey and
16 synchronous spatio-temporal variations, (iv) a link between recruitment and food production
17 and (v) density-dependent distribution of juveniles, with an increased range into the open sea
18 for stronger year classes, related to the extension of enriched productive areas. As a
19 consequence, the influence of food limitation on juvenile fishes in their C&E nursery grounds
20 remains unanswered.

21 The primary aim of this synthesis is to shed light on this question by focusing on
22 temperate and subarctic flatfish (Table 2) that are especially dependent on C&E nursery
23 grounds (Iles and Beverton, 2000), and extending this focus to other marine fishes (pelagic,
24 demersal and reef associated round fish and sharks, from tropical to subarctic ecoregions). We
25 estimate the influence of trophic limitation on the density-dependent processes involved in

1 year-class regulation during the juvenile stage of marine fishes in their nursery grounds.
2 Solving this question has implications to understanding the main processes involved in the
3 renewal of fish stocks during the juvenile stage. If food resources are an important regulating
4 factor, the regulation of year-class strength during the juvenile stage depends, at least partly,
5 on the productivity of consumable resources and the related capacity of nursery habitats
6 (Hayes et al. 1996). In this case, maintaining the quality and productivity of essential nursery
7 habitat is critical for the renewal of sustainable fish populations.

8

9 **The question of food limitation in nursery grounds: the**
10 **controversy from individual to population scale**

11 Different and complementary approaches have been used to evaluate the impacts of food
12 limitation on the survival of juvenile fish, from laboratory experiments and mesocosms to *in*
13 *situ* gradients at different biological scales: individual (growth, condition), population size
14 (density and distribution) and multispecific scales. Differing results are observed when
15 comparing the different approaches used to analyze the effect of food limitation on nursery
16 grounds.

17 ***Experimental approach in the laboratory***

18 Laboratory experiments enables us to estimate the influence of abiotic factors (e.g.,
19 temperature and salinity; Fonds 1975) as well as biotic factors (e.g., the effect of food intake
20 on the growth of young flatfishes). These experiments allow us to develop models (e.g., the
21 metabolic scope for growth, Fonseca et al. 2010, or the Dynamic Energy Budget models,
22 Kooijman 2000, van der Veer et al. 2003) to estimate juvenile flatfish growth with regard to
23 the food supply (Table 2). These models are useful for further comparisons between *in situ*

1 growth and estimates of growth based on controlled conditions. The experimental approach
2 demonstrates that food quantity and quality affect juvenile flatfish growth. Limited food
3 resources reduce growth, energy storage and the condition of juvenile flatfish after a few
4 days, with important consequences on juvenile growth and survival, even for short-term
5 events. Accordingly, a meta-analysis of starvation-induced changes in the early stages of
6 fishes from laboratory-controlled experiments, including seven marine species (six round
7 fishes, one flatfish) showed a general rapid exponential decrease of biogeochemical
8 conditions with starvation, immediately followed by death (Meyer et al. 2012), thus extending
9 previous mentioned results to round fishes.

10 ***Field experiments***

11 Field experiments are less controlled experimental systems which provide favourable habitats
12 in terms of the main factors governing juvenile fish growth, i.e., hydrodynamic exposure,
13 food availability, predation and water temperature (Gibson 1994). They can serve to bridge
14 the gap between field studies with the inherent difficulties of control, and laboratory
15 experiments that can be standardized and replicated but suffer from a lack of environmental
16 realism (Laffargue et al. 2007). Similarly, caging experiments that consist of stocking fishes
17 in cages placed in the natural environment enables the comparison of growth rates in different
18 habitats and living conditions (Able et al. 1999, Ciotti et al. 2010). However, growth rates of
19 fishes in enclosures or from *in situ* experiments must be interpreted with caution, as fish
20 movements and the threat of predation may be influential but are not realistically represented
21 (Stunz et al. 2002).

22 Both types of field experiments demonstrate that patterns in food availability result in
23 differences in growth rates for juvenile fish. They also show competition for food to be the
24 underlying mechanism in determining juvenile growth and survival for various marine fish

1 species (Sogard 1992, Craig et al. 2007). In accordance with laboratory studies, field
2 experiments confirm that, in spite of a trade-off with other factors and especially the threat of
3 predation (Sogard 1992, Halpin 2000), food availability on the nursery ground is a primary
4 driver of habitat choice and juvenile fitness.

5 ***In situ analysis, individual scale***

6 Many field studies have analyzed growth limitation for juvenile wild fishes from individual
7 food intake, growth and individual condition with the primary objective to estimate habitat
8 quality and the link between food availability and living conditions. At this individual scale,
9 food limitation often appears to be of minimal importance for juvenile flatfishes (Table 2).
10 Measures of growth, nutritional condition and body condition indicate neither significant food
11 limitation, nor a link with prey availability or juvenile density. However, some limited signals
12 of limitation can be observed from gut content, recent condition, body condition and lipid
13 reserve, especially just after settlement, with advantages to the first-settled fishes. Juvenile
14 flatfishes appear to be not food limited and comparisons between experimental models and *in*
15 *situ* estimates show that coastal nurseries provide a maximal potential for food intake, without
16 negative density-dependent growth. Food limitation in the sense of starvation, individual
17 growth and consumption of the prey of juvenile flatfishes often suggests that the carrying
18 capacity of nursery areas is not reached (van der Veer et al. 1994). Concerning other fish
19 orders (i.e., round fishes), Diaz et al. (2011) provide evidence that the Argentinean anchovy
20 (*Engraulis anchoita*, *Engraulidae*) may not be food limited in any of their nursery grounds;
21 juvenile growth and condition do not differ between nursery habitats for two other round fish
22 species (Ross 2003) and individual consumption indicates no effect of food limitation on
23 European sea bass (*Dicentrarchus labrax*, *Moronidae*) (Hampel et al. 2005).

1 On the contrary, some authors reach opposite conclusions from *in situ* approaches at
2 the individual scale on local habitat. Indeed, significant differences in condition are observed
3 at small scales for juvenile plaice (Table 2). Concerning round fishes, Islam and Tanaka
4 (2005) use RNA:DNA ratios, total protein and growth rates to estimate the proportion of
5 starving juvenile Japanese sea bass (*Lateolabrax japonicas*, *Lateolabracidae*) and to show
6 their dependency on prey availability. The condition of juvenile sea bass was not equal
7 throughout the nursery grounds. Fishes in the upper river were in better condition than those
8 in the lower estuary. Juvenile fishes living on prey-impooverished habitats have significantly
9 higher metabolic costs, and thus higher foraging expenses (Goto and Wallace 2010). Lastly,
10 when considering juvenile hammerhead shark (*Sphyrna lewini*, *Sphyrnidae*), a non-teleost
11 species with parental care and much larger juvenile individuals, the link between starvation
12 and body condition, i.e., the effect of food limitation, is highly significant (Duncan and
13 Holland 2006).

14 ***In situ estimation, population scale***

15 Contrary to studies of individuals, population-scale *in situ* studies generally conclude
16 that growth limitation and density-dependent effects on abundance and distribution are linked
17 to competition and mortality related to food limitation. Firstly, limited effects are revealed
18 when flatfish growth is analyzed from the size of individuals in the population (Table 2). With
19 regard to model estimates based on laboratory experiments or to optimal conditions in
20 mesocosms, *in situ* observations show smaller sizes of flatfish juvenile during part of the
21 growing season in the nursery grounds, with a slight decrease in regards to optimal estimates.
22 A synthesis of Table 2 suggests growth rates that were close to experimental values after
23 settlement but food limitation in summer for large juveniles that had settled a few months
24 previously. These lower growth rates and the related density-dependent regulation suggest

1 competition for food during the summer growth period. Similarly, growth rates appear to be
2 positively related to food quantity and quality in space and time. Estuarine habitats offer
3 optimal opportunities for flatfish juvenile growth, at least partly due to higher food
4 availability, as growth varies annually with the most important food source in the nursery
5 ground. When considering juvenile round fishes, Phelan et al. (1999) demonstrated that the
6 growth of juvenile tautogs (*Tautoga onitis*, *Labridae*) is faster where prey availability is
7 higher. Moreover the average length of juvenile Atlantic cod (Lekve et al. 2002) and red drum
8 (*Sciaenops ocellatus*, *Sciaenidae*) (Scharf 2000) decrease with increased density, indicating
9 density-dependent effects. By coupling analyses of growth and density in different estuarine
10 habitats, Sogard (1992) concludes that juvenile fishes of various species are most abundant in
11 habitats that support faster growth.

12 Alternatively, studies which focus on spatial distribution and recruitment success also
13 point out a clear influence of bottom-up food limitation on juvenile flatfishes (Table 2).
14 Especially, a significant relationship is found between fluvial discharge and the abundance of
15 high densities of flatfish juveniles in ecosystems of freshwater influence. This indicates that
16 the freshwater supply helps sustain the ability of estuarine nurseries to support juveniles. The
17 freshwater particulate organic matter propagates up the food web to juvenile flatfish, showing
18 the role of river discharge and terrigenous subsidy input in the function of nurseries.
19 Richness in organic matter impacts the settling of benthic communities preyed upon by
20 juvenile flatfishes. The influence of terrestrial discharge on juvenile flatfish differs in
21 intensity and spatial extent between years with relation to river inputs and is correlated to the
22 seaward extent of high densities of these juveniles. High land-based run-off is favorable to the
23 productivity of invertebrate prey and consequently to the productivity of flatfish species.
24 Trophic enhancement related to river inputs at least partly influences recruitment. The
25 influence of estuarine organic matter supply for the development of a community that is

1 tolerant to low salinity and can provide suitable food for juvenile fish were confirmed for
2 round fish species (Costa and Bruxelles 1989, Pasquaud et al. 2008). Similarly, the density
3 dependent distribution of juvenile, from estuaries to open waters, was also verified for round
4 fishes (Bacheler et al. 2012). For instance, juveniles of filter-feeding Atlantic menhaden
5 (*Brevoortia tyrannus*, *Clupeidae*) are found to be associated with gradients of phytoplankton
6 biomass in their estuarine nurseries along the Eastern coast of the USA (Friedland et al.
7 1996). When densities of juveniles are pooled for all marine species, the maximum juvenile
8 density is observed in the middle mesohaline region of estuaries (Nicolas et al. 2010). The
9 amount of organic matter is the highest in these areas and conditions are particularly suitable
10 for the development of benthic invertebrate prey (Moore 1978, Elliott and Taylor 1989). This
11 high abundance of benthic prey leads to high fish density, especially of juvenile marine
12 species (Courrat et al. 2009). Accordingly, a human-induced limitation of the river flow that
13 lowered the primary production of the adjacent shelf is found to negatively impact the
14 recruitment of the European anchovy population in the Gulf of Cadiz (Ruiz et al. 2009).
15 Likewise, severe droughts can reduce primary productivity in estuaries, with cascading effects
16 on higher trophic levels, food availability and juvenile survival for various fish species (Wetz
17 et al. 2010).

18 The relationship between food availability and juvenile flatfish abundance (Table 2)
19 and distribution are also confirmed outside regions of freshwater influence. In coastal areas,
20 the migrations of juvenile flatfish demonstrate the influence of foraging opportunities on daily
21 movements. At larger (i.e., seasonal to annual) time scales, their distribution match the
22 distribution of their prey. Similarly, the interannual variation of abundance and distribution of
23 juvenile flatfish are synchronous with those of the macrobenthos (Table 2). The density-
24 dependent distribution of juveniles that extends to deeper water when abundance increases in

1 their C&E nurseries is also verified for Atlantic cod on North West Atlantic coast (Swain
2 1993).

3 For flatfishes, local population density is a trade-off between larval supply and high
4 mortality rates (Nash et al. 2007). Accordingly, competition for a limited food resource is one
5 of the main causes of restocking failure in coastal stock enhancement programs (Stottrup and
6 Sparrevojn 2007). The survival rate of hatchery-reared fish is first related to the number of
7 larvae released and then to the total (wild and hatchery-reared) recruitment intensity,
8 indicating that there are limits in the carrying capacity of nursery grounds (Goto 2006). White
9 and Cazelles (2008) examine the effect of density-dependent processes linked to larval supply
10 and habitat capacity on post-settlement interactions in juvenile reef fish. They estimate that
11 the abundance of juvenile fish is not limited by the larval supply at low densities of recruits,
12 but by density-dependent competition for food resources and shelter at high densities of
13 recruits. However, other studies that estimate total consumption in C&E nursery grounds
14 using growth, daily food consumption and density find that food is abundant enough to
15 sustain juvenile growth for flatfish (Table 2), suggesting that the carrying capacity of nursery
16 areas is not reached.

17 Thus, using population approaches, even if opposite conclusions are sometimes
18 reached, density-dependent growth and mortality related to food availability appear to be
19 major factors controlling recruitment success of juvenile stages (Juanes 2007).

20 ***In situ, interspecific competition***

21 Many studies of C&E flatfish nurseries demonstrate that if numerous species use the same
22 nursery area, they develop strategies of resource partitioning to avoid food limitation and
23 niche overlap. Species, but also different cohorts or age groups of a given species, had
24 specialized their feeding behavior, with only a moderate niche overlap. Differences in feeding

1 rhythms, habitat use, and food preference reduce food competition (Table 2). More generally,
2 when all fish species are considered, niche overlaps vary: they are higher between species of
3 the same family but remain limited (Pasquaud et al. 2010b). Juvenile fish of different species
4 avoid competing for food resources even if competition is observed between resident species
5 (Lafaille et al. 2000).

6 Resource partitioning, indicative of competition (Nunn et al. 2012), is a strategy to
7 optimize food availability and appears as an adaptation to limited food resources that allows
8 coexistence of species within the nursery zone. Such partitioning results from the long term
9 natural selection of a trophic strategy. Indeed, there is no need to avoid niche overlap if food
10 supply exceeds the need of the different species. This conclusion is reinforced by ontogenic
11 shifts from higher overlap in diets of larval fish, to lower overlap in diets of juvenile fish,
12 enabling competition avoidance between different size and age classes of the same species
13 (Nunn et al. 2012). Geange and Stier (2009) analyze the timing of settlement on coral reef
14 systems and find that species survive best in the absence of competitors and that survival
15 declines when species enter the community later than their competitors. These interspecific
16 effects related to settlement time provide additional evidence of the importance of
17 competition in nursery areas.

18 In spite of some intra-scale discrepancies, different approaches that measure common
19 parameters such as growth, condition, density or distribution allow us to draw different
20 conclusions about food limitation. Laboratory and field experiments, *in situ* studies at
21 population scales and interspecific competition show a significant influence of food limitation
22 on juvenile fish growth and survival. *In situ* studies that focus on individuals lead mainly to
23 opposite conclusions; growth of juvenile fishes, especially small juvenile fishes, on the
24 nursery grounds does not appear to be food limited. These opposing conclusions are obvious
25 for populations of juvenile flatfishes on C&E areas (Table 2). However, they are verified

1 elsewhere for other fish species in different types of nursery habitats, from tropical to
2 subarctic ecoregions.

3

4 **Bridging the gap between the different approaches and scales** 5 **and their opposing conclusions**

6 Size-selective mortality in juvenile stages of teleost fish is critical (Sogard 1997). If direct
7 evidence of density-dependent competition for food is weak (Cowan et al. 2000), especially
8 on an individual scale, the influence of food limitation on juvenile fish growth and survival
9 becomes obvious when changes in the size distribution associated with mortality are
10 distinguished from changes due to individual growth.

11 *Size-dependent mortality during juvenile life stages*

12 A range of daily mortality as high as 5-40%, with a mean of 18% (Selleslagh 2008), is
13 observed for the Eastern Channel plaice during the highly sensitive post-settlement period
14 (Geffen et al. 2007, Nash and Geffen, 2012). The same level of mortality is estimated for
15 tropical reef fishes (9-20%; Juanes 2007). Such high mortality rates for newly-settled larvae
16 are far from specific to flatfishes and reef fishes, i.e., Atlantic cod shows even higher
17 mortality rates at the juvenile stage (Houde 2002; Table 1).

18 These high mortality rates during the juvenile stages appear to select the faster
19 growing individuals (Hovenkamp 1992, Houde 1997, Marchand et al. 2003, Craig et al. 2007,
20 Juanes 2007, Selleslagh 2008). Natural mortality rates decline dramatically with increasing
21 body size (Houde 1987, Miller et al. 1988, Conover 2007), leading to size-selective processes:
22 as individuals grow rapidly, they spend less time in the smallest size classes that are most
23 vulnerable to predation (Sogard 1997). For example, growth of anchovies in the Bay of

1 Biscay was investigated using the otolith growth data collected during repeated larval and
2 juvenile surveys on spawning and nursery grounds (Allain et al. 2003). The surviving
3 juveniles show much faster growth rates during their larval period than the pool of larvae
4 from which they originate, indicating dramatic growth-selective survival. Similarly, Atlantic
5 cod have a high potential for growth- and starvation-induced mortality (Daewell et al. 2011).
6 Lekve et al. (2002) demonstrate that the size distribution of juvenile Atlantic cod is skewed to
7 the larger size classes on nursery grounds, indicating size-selective mortality. This skewness
8 increases with increased density in relation to density-dependent processes. More generally,
9 size distribution of juvenile fish within a cohort is strongly influenced by intraspecific
10 competition for resources, often leading to skewed frequency distributions (Ohlberger et al.
11 2012). The aforementioned studies and numerous others mentioned in Sogard (1997) provide
12 evidence that body size during the juvenile stages is a major determinant of survival. Thus,
13 the disproportionate removal of small fish causes an overestimation of growth rates if it is
14 based only on survivors (Sogard 1997).

15 Two explanations have been proposed to explain this size-selective mortality.

16 - Firstly, survival of larger fish is enhanced because larger members of a cohort can
17 better tolerate physical extremes and endure longer periods without food (Sogard 1997). A
18 lack of food affects energetic reserves of individuals and makes them more sensitive to other
19 sources of mortality (Nash et al. 2007). Faster growing juveniles gain survival advantages via
20 resistance to starvation and also through the ability of larger individuals to ingest a wider
21 variety of prey (Salgado et al. 2004; Nunn et al. 2012). Rapid growth provides a size
22 advantage in which larger fish have stronger competitive effects (Geange and Stier 2009).

23 - Secondly, predation is a significant size-selective process, especially for early stages,
24 as predation mortality is directly determined by fish size, with decreasing mortality rates with
25 the increasing size (van der Veer et al. 1994). Slow-growing and small fish remain vulnerable

1 to predation for a longer period (i.e., the stage duration hypothesis; Sheperd and Cushing
2 1980, Houde 1987; Anderson 1988). For example, individuals of newly metamorphosed
3 demersal fish, e.g., plaice (Gibson et al. 1995, Gibson and Robb 1996), are subject to strong
4 size-selective predation by crangonid shrimp (*Crangon crangon*, *Crangonidae*) (Burrows et
5 al. 2001), which primarily consume fish < 30 mm (van der Veer et al. 1997). Accordingly,
6 Ellis and Gibson (1995) estimate that flatfish reaching 45 mm are at much lower risk from
7 predators. More generally, after the dramatic decline in natural mortality with increasing size
8 in early life stages, a lower but steadier density level is maintained for large juveniles of
9 marine fish species (Conover 2007, Dingsor et al. 2007). Thus, growth limitation influences
10 body size and affects resistance to unfavorable environment factors and to food limitation. It
11 also affects foraging ability and vulnerability to predation, which in turn influence individual
12 fitness (Ohlberger et al. 2012) and recruitment.

13 ***The link between size-dependent mortality and growth explains the***
14 ***hidden effect of food limitation at individual scales***

15 Average growth rates of fish larvae and juveniles are lower under food-limited conditions
16 (Houde 2008). As demonstrated for larvae in the stage duration hypothesis (Sheperd and
17 Cushing 1980, Houde 1987), mortality rates of juvenile fish are inversely related to size and
18 linked to growth. According to the “bigger is better hypothesis”, mortality and predation
19 during young fish stages are related to nutritional deficiencies (Miller et al. 1988, Sogard
20 1997, Suthers 1998).

21 This link could explain why food limitation effects are not obvious for very young
22 fishes. If there is high mortality of starving juveniles, a disproportionate removal of small fish
23 causes an overestimation of the population mean growth rate from the size of survivors,
24 which could be misleading (Houde 2008). As the population is skewed toward faster growing

1 juveniles, the growth of survivors could be close to experimental values under optimal
 2 conditions (Table 2), even when food limitation is important. The relationship between food
 3 availability and size-dependent mortality hinders variability in growth by selecting faster-
 4 growing individuals and dampening recruitment variability. This also helps explain why the
 5 relationship between the mean length of a cohort and the year class strength appears to be
 6 relatively weak (van der Veer et al. 1994), even if food limitation alters growth performance
 7 (dynamic self-thinning, Nash et al. 2007). Similarly, this could explain why estimates of the
 8 total food consumption by juvenile fish over the summer period suggest that food is abundant
 9 enough to sustain juvenile growth (Table 2). The juvenile population size, in abundance, is
 10 adapted to the available food after the high mortality period during the first post-settlement
 11 stages. Growth limitation is more obvious for larger fish with lower mortality rates, e.g., 1
 12 year old juvenile common sole (Le Pape et al. 2003a) or sharks (Duncan and Holland 2006).

13

14 ***Testing the food limitation hypothesis using simulations***

15 Using a simulation framework, we test if, in conditions of limited food, the growth curve that
 16 is observed at the population scale during the first months of juvenile growth differs from the
 17 theoretical optimal growth curve. For illustrative purposes, we choose the life history traits of
 18 common sole and simulate a population of one million larvae.

19 *Model*

20 Individuals of the population grow according to a von Bertalanffy equation:

$$21 \quad L_{i,a} = L_{inf} \cdot \varepsilon_1(a) - (L_{inf} \cdot \varepsilon_1(a) - L_0) e^{(-k \cdot t \cdot \varepsilon_2(a))}$$

22 where t is the time (in months), $L_{i,a}$ is the length (in cm) of the individual i at age a (in months
 23 since metamorphosis), L_{inf} is the maximal length (i.e., 54 cm; Fishbase.org), L_0 is the length at
 24 metamorphosis (0.5 cm; Fonds 1979), k is the growth rate (0.26; Fishbase.org). $\varepsilon_1(a)$ and $\varepsilon_2(a)$

1 are random noise that have a normal distribution with a mean equal to 1 and a standard
 2 deviation equal to 0.1 (i.e., 10% noise). This random noise is added to k and L_{inf} to account
 3 for inter-individual variability. The growth of one million fish over their first year (from
 4 metamorphosis in the spring to the end of the year) is described in the size-at-age matrix ($L_{i,a}$).
 5 Two scenarios are developed: (S1) there is no food limitation and the growth is simulated as
 6 in Eq. 1. Ten thousand individuals are then randomly sampled in the population to simulate a
 7 survey. (S2) Food limitation is simulated. As food limitation is shown to decrease the
 8 maximal length (e.g., Kooijman 2010), a negative offset is subtracted from the infinite length.
 9 This offset corresponds to 20% of the maximal length ($L_{inf} = 43.2$). Individuals die following
 10 a size-related natural mortality as defined by Gislason et al. (2010). This mortality is defined
 11 for each individual for each age in a mortality-at-age matrix ($M_{i,a}$):

$$12 \quad M_{i,a} = 0.55 - 1.61 \cdot \log(L_{i,a}) + 1.44 \cdot \log(L_{inf}) + \log(k)$$

13 where $M_{i,a}$ is the instantaneous mortality rate per year of the individual i at age a (in months)
 14 and for its size, $L_{i,a}$.

15 The probability of survival of each individual per month is directly calculated from the
 16 mortality-at-age matrix with the equation $S_{i,a} = e^{-M_{i,a}}$. Over the first six months of the
 17 juvenile stage, the estimate of survival is about 10%, which is in accordance with estimates
 18 for the common sole (Rochette et al. 2013). The survival probability, $S_{i,a}$, is then used to
 19 define the probability that an observer would sample the larva i at age a in the wild. Ten
 20 thousand fish were sampled within the whole population using the survival probability as a
 21 weighting.

22 *Results*

23 For the two scenarios, the sampled population has an estimated mean length within the
 24 same range as the theoretical growth curve (Fig. 2). If sampling occurs over the whole
 25 population without accounting for the individual mortality (S1), the length of individuals is

1 randomly distributed over the theoretical growth curve. As only survivors are observed or
2 sampled in S2 (food limitation scenario; Fig. 2b), individuals having a slower growth rate due
3 to food limiting conditions are not sampled or are sampled less often. The mean length of
4 sampled individuals in S2 is very similar to the theoretical growth curve but the distribution is
5 less variable and skewed, with lower a longer tail towards higher lengths, corresponding to
6 the observation made for Atlantic cod by Lekve et al. (2002). This simulation demonstrates
7 the bias of *in situ* sampling; as only survivors are observed, i.e., juveniles with the fastest
8 growth; thus, the sampling is biased towards fast-growing individuals (Fig. 2b). This shows
9 that even in food-limited conditions, one observes individuals close to the theoretical growth
10 curve.

11
12 Thus, the synthesis of different approaches and scales demonstrates both the trophic
13 limitation in C&E nursery areas and the lack of an obvious signal when food limitation is
14 observed on survivors at the individual scale. Though the present approach is at first focused
15 on temperate and subarctic flatfish, further extension to other marine fishes (pelagic, demersal
16 and reef associated round fish, from tropical to subarctic ecoregions) allows us to broaden
17 these conclusions. As hypothesized by Gibson (1994), food appeared to be the main factor
18 affecting juvenile fish concentration in nursery grounds. Juvenile fish growth is related to
19 food availability, and its limitation interacts with other factors, such as size- (growth)
20 dependent predation (Wennhage 2000) and mortality (Sogard 1997) to determine survival
21 rates. Moreover, the negative relationship between growth and the duration of life stages
22 increases the period when mortality and predation are higher for food limited juveniles. Thus,
23 food limitation affects both the duration of the juvenile stage and the survival during this
24 stage (Sheperd and Cushing 1980, Houde 1987, van der Veer et al. 1994).

25

1 **The influence on fish populations of trophic limitation and habitat**
2 **capacity in C&E nursery grounds**

3 *An obvious but variable dependency of juvenile fish on the*
4 *productivity of C&E essential habitats*

5 Juvenile fish of many species aggregate in productive C&E nursery areas in order to enhance
6 their fitness (Blaber and Blaber 1980, Miller et al. 1984, Gibson 1994, Beck et al. 2001).
7 Habitat suitability, which is linked to production and food quality and availability, is highly
8 influential on the spatio-temporal patterns of juvenile fish (Holbrook et al. 2000, Nicolas et al.
9 2007). Though trophic limitation is a primary factor in determining the suitability of nursery
10 habitat, juvenile fish-habitat interactions are complex (Fulford et al. 2011). Habitat suitability
11 is a trade-off between habitat selection, foraging quality and predator avoidance (Sogard
12 1992, Wennhage and Gibson 1998, Laegdsgaard and Johnson 2001, Able 2005, Sheaves
13 2009). The level of juvenile dependence on trophic limitation varies with time, among cohorts
14 (i.e., density-dependent variations related to interannual variations in settled larvae; Fig. 3)
15 and even among subcohorts during the settlement period (Fonseca et al. 2006, Geange and
16 Stier 2009, Nash and Geffen 2012, Geffen et al. 2011). This dependence varies at small
17 spatial scales and between different nursery habitats of the same population (Nash et al. 2007,
18 de Raedemaecker et al. 2011), with relations to juvenile density and food availability. It also
19 varies between different populations of the same species, e.g., the influence of food limitation
20 appears significantly higher for plaice in the Irish Sea (Nash and Geffen 2000) relative to
21 those in the North Sea (van der Veer et al. 1986) or in the Wadden Sea (van der Veer et al.
22 2000a). Finally, it varies from one species to another, even in the same area, e.g., in the North
23 Sea, trophic dependence is important for common sole (van der Veer et al. 2001) but limited
24 for plaice (van der Veer et al. 1986).

1

2

An influence on marine fish population renewal

3 For a fish population to persist, habitat must be available to sustain all periods of development
4 (Nunn et al. 2012). As such, the capacity of nursery habitats is a key contributor to the overall
5 population fitness (Fodrie et al. 2009), stability and extinction risk (Ohlberger et al. 2012).

6 Nash et al. (2007) provide evidence of self-thinning for plaice at the local population scale:
7 when juvenile population density is high, food limitation depends on the number of
8 individuals that settle relative to the productivity of the nursery ground. Populations that
9 strictly depend on limited nursery habitats approach the carrying capacity of the habitat, at

10 least when settlement is high. Post-settlement survival depends on nursery habitat size and
11 productivity, in relation to the amount of larval settlement (Rooper et al. 2004, Johnson 2007,
12 Nash et al. 2007). Thus, fish populations are limited by the quantity and quality of habitat and
13 food available for juvenile fishes (Nunn et al. 2012). Food dependent size-selective mortality
14 dampens the variability in size distribution and reduces among-year variability in recruitment
15 strength (van der Veer et al. 1994, Le Pape et al. 2003b, Minto et al. 2008). Accordingly,

16 habitat bottlenecks have been identified for juvenile fish stages of species or populations for
17 which the variation in habitat quality has a disproportionate effect on renewal (Fulford et al.
18 2011). This dependence appears especially important for C&E nursery dependent flatfish

19 species (Iles, 1994), but is also of important concern for many other fishes. Iles and Beverton
20 (2000) demonstrate that nursery-dependent species at high spawning stock biomass have
21 asymptotic stock recruitment relationships, with a maximum recruitment level hiding a linear
22 relationship to spawning biomass (i.e., the concentration hypothesis). These species depend
23 on the capacity of nursery habitats for their recruitment (Fig. 3): density-dependent processes
24 are at least partly linked to prey resources that regulate recruitment strength and dampen

1 recruitment variability (Cowan et al. 2000, van der Veer et al. 2000a, Le Pape et al. 2003c,
2 Houde 2008, Minto et al. 2008).

3 Thus, if variability-generating processes operating at the egg and larval stages are of
4 major importance, processes occurring during the juvenile stage are also important in
5 determining recruitment strength (van der Veer et al. 2000a) and variability (Iles and
6 Beverton 2000, Minto et al. 2008). Among these juvenile processes, density-dependent effects
7 related to food limitation appear to be a main governing factor (Cowan et al. 2000).
8 Nevertheless, food limitation influence differs for different species, populations, cohorts,
9 nursery habitats, and years in relation to the balance between juvenile density and food
10 availability (van der Veer et al. 2000a, Nash and Geffen 2000, Nash et al. 2007).

11

12 *The critical first juvenile stages*

13 The present synthesis provides evidence of trophic limitation on juvenile marine fishes in
14 their C&E nursery grounds but the question remains for which juvenile stage(s) this limitation
15 constrains the recruitment strength.

16 The transition phase, after the last larval metamorphosis (Geffen et al. 2007), is
17 demonstrated to be a critical stage (Juanes 2007), and thus demands thorough attention (Nash
18 and Geffen 2012). Indeed, for the juvenile stages, density-dependent processes in young fish
19 survival decline as they grow (Dingsor et al. 2007), with an especially dramatic decline of
20 mortality with increasing body size (Houde 1987, Miller et al. 1988). Size-selective mortality
21 appears to be mainly restricted to the first year of life (van der Veer et al 1994) and is
22 especially high during the first juvenile stages. Indeed, during ontogeny at young stages, both
23 improvements in vision and swimming performances and increases in gape size lead to shifts
24 in diet composition and a larger choice of prey (Nunn et al. 2012). The density-dependent

1 regulation of a cohort derived from a reduction in prey resources is hypothesized to occur at a
2 critical size and/or weight following the larval settlement (van der Veer 1986, Houde 1997,
3 Cowan et al. 2000; Nash and Geffen 2012). Fish are most vulnerable in the period following
4 the larval settlement, as the lack suitable prey due to their limited predation abilities,
5 potentially leading to either reduced growth or starvation, reduce survival (Nunn et al. 2012).
6 This limitation occurs when densities of fish populations and consumption of resources
7 remain high relative to the prey density and the replenishment rate (Cowan et al. 2000, Nash
8 et al. 2007), and before the shift in resource use (Nunn et al, 2012) and the drop in
9 vulnerability. At young stages, the decline in prey density by juvenile consumption is large
10 enough to result in density-dependent effects, as is demonstrated in several cases studies
11 (Cowan et al. 2000).

12 In summary, after an exponential decrease in mortality with body size/weight
13 (Conover 2007), fish reach a body size related both to lower predation and to an increase in
14 prey size, energy content and availability (i.e., a larger choice of species item and size spectra,
15 Nunn et al. 2012), and mortality is dramatically reduced (Ellis and Gibson 1995, Gibson et al.
16 1995). Thus, a dramatic regulation of the size of a population occurs for the lowest juvenile
17 size (Dingsor et al. 2007) during the critical period (Houde, 2008) when mortality is high
18 enough to sharply modulate the population via limited food resources (Fig. 3). Indeed,
19 density-dependent processes influence year-class strength mainly during the first weeks after
20 settlement in the nurseries (van der Veer 1986, Rijnsdorp et al. 1992).

21

22

23 **Implication of food limitation for management of essential**

24 **nursery habitats**

1 *The need to preserve the functionality of C&E nursery habitats for*
2 *marine fish population renewal*

3 The present synthesis focuses on the important influence of the biotic habitat capacity, i.e.,
4 food availability, on the early life stages of fish (Rijndorp et al. 1992, Schmitt and Holbrook
5 2000, Johnson 2007, Nash et al. 2007, Hayes et al. 2009). Recruitment strength and
6 population dynamics are strongly determined by the productivity and food resources in C&E
7 nursery habitats. Maintaining large and high quality nursery habitats should be a primary
8 focus to preserve fish species whose population range depends on the trophic capacity of their
9 habitat at the juvenile stage (Hodgson et al. 2011, van de Wolfshaar et al. 2011). There is a
10 need for protection of the quality and productivity of nursery habitats to maintain fish stock
11 renewal. The nutrient supply from C&E areas stimulates primary production, which supplies
12 food sources for larvae and juveniles, consequently, sustains the related fisheries (Beck et al.
13 2001, Lamberth et al. 2009, Sheaves et al. 2009). Quantitative and qualitative factors related
14 to anthropogenic disturbances influence the capacity of C&E nurseries and, thus, the
15 recruitment and the renewal of populations (Cowan et al. 2000, Meng et al. 2000, Peterson et
16 al. 2000, Peterson 2003, Phelan et al. 2000, Scharf 2000, Rochette et al. 2010). It is important
17 to maintain a high ecological quality of essential nursery habitat in C&E areas in order to
18 sustain marine populations and fisheries. Measures aiming at improving or preserving the
19 capacity of juvenile habitat are the most effective for improving adult biomass of populations
20 regulated by density dependence during the juvenile phases (van de Wolfshaar et al. 2011).
21 Preservation and rehabilitation measures should be designed to provide nursery habitats for
22 fishes and enhance their food base (Nunn et al. 2012). Nursery function must be accounted for
23 in monitoring systems of C&E waters to maintain high ecological status (Beck et al. 2001)
24 and especially for the establishment of MPAs to provide and export juveniles, to enhance
25 fishing yields (Pelletier and Magal 1996, Gell and Roberts 2003, Kaplan 2009) and benefit the

1 fisheries (Mesnildrey et al. 2013).

2

3 ***Estimating habitat suitability from large juvenile fish growth and***
4 ***density: an appropriate tool***

5 The density, growth and condition of juvenile fishes are relevant indicators to estimate the
6 ecological quality of nursery habitats (e.g., Guindon and Miller 1995, Suthers 1998, Able et
7 al. 1999, Duffy-Anderson and Able 1999, Phelan et al. 2000; Selleslagh and Amara, 2013).
8 However, as starving and newly-settled juveniles are removed from the population by high
9 mortality rates, growth rates are overestimated for very young stages and cannot be used as
10 indicators of the nursery function. With regards to high mortality rates of post-settlement
11 juvenile fishes in relation to the nutritional deficiencies of their nursery grounds (i.e., the food
12 limitation hypothesis, Fig. 3), it could be misleading to determine essential nursery habitats
13 and estimate their quality from the density and growth of newly post-settled fish.

14 In contrast, large juveniles experience dramatically lower mortality and it is more
15 reliable to collect data on larger juvenile fish to identify nursery habitat and estimate its
16 ecological status. Indeed, density is less variable, food limitation is more obvious (Duncan
17 and Holland 2006), and growth is less biased due to size-dependent selection (Meng et al.
18 2000, Le Pape et al. 2003a, Gilliers et al. 2006, Amara et al. 2007, Amara et al., 2009;
19 Selleslagh and Amara, 2013). Nevertheless, biased and incorrect decisions regarding habitat
20 quality can still be made when using a growth-based assessment without identifying factors,
21 such as temperature and density, that may underlie differences in growth rates (Searcy et al.
22 2007).

23 A given habitat is considered a nursery if it contributes disproportionately to the size
24 and number of adults relative to other juvenile habitats (Beck et al. 2001). The most

1 environmentally-sensitive fish populations are those whose nursery areas are restricted to a
2 few coastal sites (Parrish et al. 1997). The identification of these sites is an important
3 consideration for coastal management (Cogan et al. 2009, Vasconcelos et al. 2011,
4 Vasconcelos et al. in press). During the settlement period, the high spatiotemporal variability
5 in juvenile abundance linked to both the pulses of larval supply and high mortality rates (Nash
6 et al. 2007) leads to spurious estimates of juvenile abundance and habitat capacity. On the
7 contrary, the abundance of juvenile fish is dramatically less variable after larval settlement
8 and the huge decline in mortality caused by the dampening effects of density-dependent
9 processes (Iles and Beverton 2000, Rooper et al. 2004, Johnson 2007). At this older juvenile
10 stage, the habitat contribution to the population, i.e., the total biomass of individuals added to
11 adult populations (Beck et al. 2001) from a given habitat, can be estimated from juvenile
12 abundance. It is possible to quantify essential and effective juvenile habitats (i.e., the overall
13 contribution from specific habitats to the adult population; Dahlgren et al. 2006), from habitat
14 suitability models (Norcross et al. 1997, 1999, Guisan and Zimmermann 2000, Beck et al.
15 2001, Le Pape et al. 2007, Stoner et al. 2007, Dahlgren et al. 2006) and related mapping
16 approaches (Le Pape et al. 2003b, Fodrie and Mendoza 2006, Rotenberry et al. 2006,
17 Trimoreau et al. in press). Such procedures can be based on populations but can also be
18 estimated from a multimetric index for a more general definition of the essential fish habitats
19 of C&E ecosystems (Courrat et al. 2009, Delpech et al. 2010). Policy objectives, such as the
20 sustainability of fish resources, ecosystem health or the design of MPAs, should be based on
21 quantitative maps of essential fish habitats (Cogan et al. 2009; Johnson et al; 2012).
22 Furthermore, quantitative indices of habitat suitability can be useful tools to assess the
23 vulnerability of fishes to various anthropogenic disturbances (Steizenmuller et al. 2010), such
24 as habitat loss and degradation linked to xenobiotics (Rochette et al. 2010) or invasive species
25 (Kostecki et al. 2011).

1

2

Conclusion and suggestions for future research

3 The aim of the present synthesis is to shed light on the controversy of food limitation for
4 juvenile fishes in their C&E nursery grounds and to analyze the related consequences for
5 survival and future recruitment. We demonstrate that the relative lack of observed growth
6 limitation for young fishes at the individual scale in their nursery grounds is at least partly
7 related to size-selective mortality affecting food-limited and newly-settled fishes (Sogard
8 1992). This synthesis confirms the conclusions of studies that use different approaches (i.e.,
9 experiments on individual juvenile fishes and *in situ* observations at the population scale) and
10 enhances the understanding of the strategy of food partitioning developed between age groups
11 and between species to limit competition for food resources. Though the present approach
12 focuses on temperate and subarctic flatfish for illustration purposes, a large amount of
13 references to other marine fishes allows us to extend these conclusions to other fish species,
14 and especially to the large proportion of C&E nursery dependent fishes (Beck et al. 2001).

15 The food limitation hypothesis is such: juveniles aggregate in C&E productive areas
16 where their fitness is enhanced through better feeding conditions and optimal growth (Beck et
17 al. 2001). Food limitation is of major importance in determining the nursery habitat capacity
18 (Nash et al. 2007). Nevertheless, this influence can vary between species, populations, cohorts
19 (and even subcohorts), locations and years (van der Veer et al. 2000a). Habitat structure,
20 refuge opportunities and connectivity between habitats modulate this ecological function
21 (Able 2005, Sheaves 2009).

22 This synthesis provides enough information to demonstrate the influence of the
23 productivity of C&E nursery habitats on the recruitment of fish populations (Rijnsdorp et al.
24 1992, Gibson 1994, Iles and Beverton 2000). After the nursery stage, juvenile fish move out

1 of C&E ecosystems to join and sustain fish populations on the continental shelf (Beck et al.
2 2001, Sheaves 2009). Breaking closure of life history cycle causes severe problems and C&E
3 habitat degradation is one of the most serious threats to the recovery of fish stocks. There is a
4 need to maintain and restore the ecological function of C&E nursery grounds to sustain
5 marine fish populations and related fisheries (Hall 1998, Elliott et al. 2007). Spatial and
6 temporal relationships between fisheries species and habitats must be included in fisheries
7 management plans (Peterson 2003). In this context, an important challenge is to account for
8 nursery function in MPA designs to protect juvenile fish from various anthropogenic
9 pressures. To that aim, observations of *in situ* density and growth of relatively large and old
10 juvenile fish could provide useful tools when density estimates become reliable and size-
11 selective mortality is not hindered by food limitation. Data on these large juveniles could be
12 used to develop habitat suitability models to identify and map essential nursery habitats and to
13 estimate indicators of ecological status for these essential fish habitats.

14 Nevertheless, the underlying ecological processes are still unknown and further studies
15 are needed for young juvenile stages when food limitation is mostly influential (Cowan et al.
16 2000, Juanes 2007, Vasconcelos et al. in press; Fig. 3). It is critical to investigate the
17 dependence level of recruitment on food availability and the variability of this dependence
18 (e.g., interannual or interspecific). In forthcoming research, there is a need to focus on the
19 young post-settlement stage to understand the trophic dependence of juvenile fish on their
20 nursery grounds (Able 2005), as this is one life stage that has not received enough study
21 (Nash and Geffen 2012, Vasconcelos et al. in press). However, the study of food availability
22 for these very young fish remains a challenge and requires a fine analysis of biological and
23 ecological processes to determine the critical stage and to understand the trophic limitation.
24 The uncertainty of the precise life stage on which to focus, the high spatiotemporal variability
25 in both larval supply and mortality (and, thus, density) and the high turnover rate of fish and

1 small invertebrate prey during the first juvenile stages requires data with small time steps
2 (Fonseca et al. 2006, Geange and Stier 2009, Nash and Geffen 2012) and fine spatial scales
3 (de Raedemaeker et al. 2011; Johnson et al. 2012). Moreover, as the main governing process
4 varies among species and even among populations (Van der Veer et al. 2000a), solving the
5 problem with a general explanation may be an unrealistic goal. Numerous specific case
6 studies are necessary before drawing generic conclusions on the trophic limitations of fish
7 populations.

8

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20

21 References

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23 Able, K.W. (2005) A re-examination of fish estuarine dependence: Evidence for connectivity
24 between estuarine and ocean habitats. *Estuarine, Coastal and Shelf Science* **64**, 5–18.

- 1 Able, K.W., Manderson, J.P. and Studholme, A.L. (1999) Habitat quality for shallow water
2 fishes in an urban estuary: the effects of man-made structures on growth. *Marine Ecology*
3 *Progress Series* **187**, 227–235.
- 4 Allain, G. (2004) Modélisation biophysique pour la prévision du recrutement. PhD thesis,
5 Agrocampus Ouest, Rennes, France.
- 6 Allain, G., Petigas, P., Grellier, P. and Lazure, P. (2003) The selection process from larval to
7 juvenile stages of anchovy (*Engraulis encrasicolus*) in the Bay of Biscay investigated by
8 Lagrangian simulations and comparative otolith growth. *Fisheries Oceanography* **12**, 407–
9 418.
- 10 Amara, R. (2004) 0-group flatfish growth conditions on a nursery ground (Bay of Canche,
11 Eastern English Channel). *Hydrobiologia* **518**, 23–32.
- 12 Amara, R. and Galois, R. (2004) Nutritional condition of metamorphosing sole: spatial and
13 temporal analyses. *Journal of Fish Biology* **64**, 72–88.
- 14 Amara, R., Laffargue, P., Dewarumez, J.M., Maryniak, C., Lagardère, F. and Luczac, C.
15 (2001) Feeding ecology and growth of 0-group flatfish (sole, dab and plaice) on a nursery
16 ground (southern Bight of the North sea). *Journal of Fish Biology* **58**, 788–803.
- 17 Amara, R., Lagardère, F., Désaunay, Y. and Marchand, J. (2000) Metamorphosis and
18 estuarine colonisation in the common sole, *Solea solea* (L.): implications for recruitment
19 regulation. *Oceanologica Acta* **23**, 469–483.
- 20 Amara, R., Meziane, T., Gilliers, C., Hermel, G. and Laffargue, P. (2007) Growth and
21 condition indices in juvenile sole *Solea solea* measured to assess the quality of essential fish
22 habitat. *Marine Ecology Progress Series* **351**, 201–208.
- 23 Amara, R., Selleslagh, J., Billon, G. and Minier, C. (2009) Growth and condition of 0-group
24 European flounder, *Platichthys flesus* as indicator of estuarine habitat quality. *Hydrobiologia*
25 **627**, 87-98.

- 1 Anderson, J.T. (1988) A review of size dependent survival during pre-recruit stages of fishes
2 in relation to recruitment. *Journal of Northwest Atlantic Fishery Science* **8**, 55–66.
- 3 Bacheler, N., Buckel, J., Paramore, L. (2012) Density-dependent habitat use and growth of an
4 estuarine fish. *Canadian Journal of Fisheries and Aquatic Science* **69**, 1734-1747.
- 5 Baker, R. and Sheaves, M. (2005) Redefining the piscivores assemblage of shallow estuarine
6 nursery habitats. *Marine Ecology Progress Series* **291**, 197–213.
- 7 Bakun, A. (1996) Patterns in the ocean: Ocean processes and marine population dynamics.
8 San Diego, University of California Sea Grant.
- 9 Beck, M.W., Heck, K.L., Able, K.W., Childers, D.L., Eggleston, D.B., Gillanders, B.M.,
10 Halpern, B., Hays, C.G., Hostino, K., Minello, T.J., Orth, R.J., Sheridan, P. and Weinstein,
11 M.P. (2001) The role of nearshore ecosystems as fish and shellfish nurseries. *Bioscience* **51**,
12 633–641.
- 13 Bell, J., Bartley, D., Lorenzen, K. and Loneragan, N. (2006) Restocking and stock
14 enhancement of coastal fisheries: Potential, problems and progress. *Fisheries Research* **80**, 1–
15 8.
- 16 Blaber, S.J.M. and Blaber, T.G. (1980) Factors affecting the distribution of juvenile estuarine
17 and inshore fish. *Journal of Fish Biology* **17**, 143–162.
- 18 Bonhommeau, S., Le Pape, O., Tréguier, A.M., Blanke, B., Grima, N., Gascuel, D., Vermard,
19 Y. and Rivot, E. (2009) Estimates of the mortality and the duration of the trans-Atlantic
20 migration of European eel leptocephali using a particle tracking model. *Journal of Fish*
21 *Biology* **74**, 1891–1914.
- 22 Burrows, M.T., Gontarek, S.T.J., Nash, R.D.M., Gibson, R.N. (2001) Shrimp predation on 0-
23 group plaice: contrasts between field data and predictions of an individual based model.
24 *Journal of Sea Research* **45**, 243-254.

- 1 Cabral, H.N. (2000) Comparative feeding ecology of sympatric *Solea solea* and *S.*
2 *senegalensis*, with in the nursery areas of the Tagus estuary, Portugal. *Journal of Fish Biology*
3 **57**, 1550–1562.
- 4 Cabral, H.N. and Costa, M. (1999) Differential Use of Nursery Areas Within the Tagus
5 Estuary by Sympatric Soles, *Solea solea* and *Solea senegalensis*. *Environmental Biology of*
6 *Fishes* **56**, 389–397.
- 7 Cabral, H.N., Vasconcelos, R., Vinagre, C., França, S., Fonseca, V., Maia, A., Santos, P.R.,
8 Lopes, M., Ruano, M., Campos, J., Freitas, V., Santos, P.T. and Costa, M.J. (2007) Relative
9 importance of estuarine flatfish nurseries along the Portuguese coast. *Journal of Sea Research*
10 **57**, 209–217.
- 11 Chittaro, P., Finley, R. and Levin, P. (2009) Spatial and temporal patters in the contribution of
12 fish from their nursery habitats. *Oecologia* **160**, 49–61.
- 13 Ciotti, B.J., Targett, T.E., Nash, R.D.M., Batty, R.S., Burrows, M.T., Geffen, A.J. (2010)
14 Development, validation and field application of an RNA-based growth index in juvenile
15 plaice *Pleuronectes platessa*. *Journal of Fish Biology* **77**, 2181–2209.
- 16 Ciotti, B.J., Targett, T.E.R., Burrows, M.T., (2013). Spatial variation in growth rate of early
17 juvenile European plaice *Pleuronectes platessa*. *Marine Ecology Progress Series* **475**, 213-
18 232.
- 19 Ciotti, B., Targett, T., and Burrows, M. (2013) Decline in growth rate of juvenile European
20 plaice (*Pleuronectes platessa*) during summer at nursery beaches along the west coast of
21 Scotland. *Canadian Journal of Fisheries and Aquatic Sciences* **70**, 720-34.
- 22 Cogan, C., Todd, B., Lawton, P. and Noji, T. (2009) The role of marine habitat mapping in
23 ecosystem based management. *ICES Journal of Marine Science* **66**, 2033–2042.
- 24 Conover, D.O. (2007) Nets versus nature. *Nature* **450**, 179–180.

- 1 Costa, M.J. and Bruxelles, A. (1989) The structure of fish communities in the Tagus Estuary,
2 Portugal and its role as nursery for commercial fish species. *Scientia Marina Topics in*
3 *Marine biology* (eds J.D. Ros) **53**, 561–566.
- 4 Courrat, A., Lobry, J., Nicolas, D., Laffargue, P., Amara, R., Lepage, M., Girardin, M. and Le
5 Pape, O. (2009) Anthropogenic disturbance on nursery function of estuarine areas for marine
6 species. *Estuarine, Coastal and Shelf Science* **81**, 179–190.
- 7 Cowan, J.H., Rose, K.A. and de Vries, D.R. (2000) Is density dependent growth in young of
8 the year fishes a question of critical weight? *Reviews of Fish Biology and Fisheries* **10**, 61–
9 89.
- 10 Craig, J.K., Rice, J.A., Crowder, L.B. and Nadeau, D.A. (2007) Density dependent growth
11 and mortality in an estuary-dependent fish: an experimental approach with juvenile spot
12 *Leiostomus xanthurus*. *Marine Ecology Progress Series* **343**, 251–262.
- 13 Curran, M.C. and Able, K.W. (2002) Annual stability in the use of coves near inlets as
14 settlement areas for Winter Flounder (*Pseudopleuronectes americanus*). *Estuaries* **25**, 227–
15 234.
- 16 Cushing, D. (1995) Population production and regulation in the Sea: a fishery perspective.
17 Cambridge university press, Cambridge.
- 18 Daewel, U., Peck, M. and Shrum, C. (2011) Life history strategy and impacts of
19 environmental variability on early life stages of two marine fishes in the North Sea: an
20 individual based modelling approach. *Canadian Journal Fisheries and Aquatic Sciences* **68**,
21 426–443.
- 22 Dahlgren, C.P., Kellison, G.T., Adams, A.J., Gillanders, B.M., Kendall, M.S., Layman, C.A.,
23 Ley, J.A., Nagelkerken, I. and Serafy, J.E. (2006) Marine nurseries and effective juvenile
24 habitats: concepts and applications. *Marine Ecology Progress Series* **312**, 291–295.

- 1 Darnaude, A. (2005) Fish ecology and terrestrial carbon use in coastal areas: implications for
2 marine fish production. *Journal of Animal Ecology* **74**, 864–876.
- 3 Darnaude, A.M., Harmelin-Vivien, M.L. and Salen-Picard, C. (2001) Food partitioning
4 among flatfish (Pisces: Pleuronectiforms) juveniles in a mediterranean coastal shallow sandy
5 area. *Journal of the Marine Biological Association of the United Kingdom* **81**, 119–127.
- 6 Darnaude, A.M., Salen-Picard, C., Polunin, N. and Harmelin-Vivien, M.L. (2004)
7 Trophodynamic linkage between river runoff and coastal fishery yield elucidated by stable
8 isotope data in the Gulf of Lions (NW Mediterranean). *Oecologia* **138**, 325–332.
- 9 De Raedemaeker, F., Keating, J., Brophy, D., O'Connor, I. and Mc Grath, D. (2011) Spatial
10 variability in diet, condition and growth of juvenile plaice (*Pleuronectes platessa*) at sandy
11 beach nursery grounds on the south-west coast of Ireland. *Journal of the Marine Biological*
12 *Association of the UK* **91**, 1215-1223.
- 13 Delpech, C., Courrat, A., Pasquaud, S., Lobry, J., Le Pape, O., Nicolas, D., Girardin, M.,
14 Boët, P. and Lepage, M. (2010) Development of a fish-based index to assess the ecological
15 quality of transitional waters: The case of French estuaries. *Marine Pollution Bulletin* **60**,
16 908–918.
- 17 description, calibration, and sensitivity analysis. *Ecological Modelling* **202**, 144–164.
- 18 Diaz, M.P.M., Olivar, M., Martos, P. and Macchi, G. (2011) Nutritional condition of
19 Argentine anchovy *Engraulis anchoita* larvae in connection with nursery grounds properties.
20 *Fisheries Research* **109**, 330–341.
- 21 Dingsor, G.E., Cianelli, L., Chan, K.S., Ottersen, G. and Stenset, N.C. (2007) Density
22 dependence and density independence during the early life stages of four marine fish stocks.
23 *Ecology* **88**(3), 625–634.

- 1 Duffy-Anderson, J.T. and Able, G. (1999) Effects of municipal piers on the growth of
2 juvenile fishes in the Hudson river estuary: a study across pier edge. *Marine Biology* **133**,
3 409–418.
- 4 Duncan, K. and Holland, K. (2006) Habitat use, growth rates and dispersal patterns of
5 juvenile scalloped hammerhead sharks *Sphyrna lewini* in a nursery habitat. *Marine Ecology*
6 *Progress Series* **312**, 211–221.
- 7 Elliott, M. and Dewailly, F. (1995) The structure and components of European estuarine fish
8 assemblages. *Netherlands Journal of Aquatic Ecology* **29**, 397–417.
- 9 Elliott, M. and Taylor, C.J.L. (1989) The production ecology of the subtidal benthos of the
10 Forth Estuary, Scotland. *Scientia Marina* **53**, 531–541.
- 11 Elliott, M., Whitfield, A.K., Potter, I.C., Blaber, S.J.M., Cyrus, D.P., Nordlie, F.G. and
12 Harrison, T.D. (2007) The guild approach to categorizing estuarine fish assemblages: a global
13 review. *Fish and Fisheries* **8**, 241–268.
- 14 Ellis, T. and Gibson, R.N. (1995) Size-selective predation of O-group flatfishes on a Scottish
15 nursery ground. *Marine Ecology Progress Series* **127**, 27–37.
- 16 Fodrie, F.J. and Mendoza, G. (2006) Availability, usage and expected contribution of
17 potential nursery habitats for the California halibut. *Estuarine Coastal and Shelf Science* **68**,
18 149–164.
- 19 Fodrie, F.J., Levin, L. and Lucas, A. (2009) Use of population fitness to evaluate the nursery
20 function of juvenile habitats. *Marine Ecology Progress Series* **385**, 39–49.
- 21 Fonds, M. (1975). The influence of temperature and salinity on growth of young sole *Solea*
22 *solea* L. 10th *European Symposium on Marine Biology* **1**, 109-125.
- 23 Fonds, M. (1979) Laboratory observations on the influence of temperature and salinity on
24 development of the eggs and growth of the larvae of *Solea solea*. *Marine Ecology Progress*
25 *Series* **1**, 91-99.

- 1 Fonds, M. and Saksena, V.P. (1977) The daily food intake of young soles (*Solea solea*, L.) on
2 relation to their size and the water temperature. Actes de Colloques du Centre National pour
3 l'Exploitation des Océans. Nantes, France **4**, 51–58.
- 4 Fonds, M., Cronie, R., Vethaak, A.D. and Van der Puyl, P. (1992) Metabolism, food
5 consumption and growth of plaice (*Pleuronectes platessa*) and flounder (*Platichthys flesus*) in
6 relation to fish size and temperature. *Netherlands Journal of Sea Research* **29**, 127–143.
- 7 Fonds, M., Drinkwaard, B., Resink, J.W., Eysink, G.G.J. and Toet, W. (1989) Measurements
8 of metabolism, food intake and growth of *Solea solea* (L.) fed with mussel meat or with dry
9 food. In: *Aquaculture – A biotechnology in progress* (eds N. De Pauw, E. Jaspers, H.
10 Ackefors, and N. Wilkins). European Aquaculture Society, Bredene, Belgium, pp. 851–874.
- 11 Fonseca, V., Neill, W., Miller, J. and Cabral, H. (2010) Ecophys.Fish perspectives on growth
12 of juvenile soles, *Solea solea* and *Solea senegalensis*, in the Tagus estuary, Portugal. *Journal*
13 *of Sea Research* **64**, 118–124.
- 14 Fonseca, V., Vinagre, C. and Cabral, H. (2006) Growth variability of juvenile soles *Solea*
15 *solea* and *Solea senegalenses*, and comparison with RNA: DNA ratios in the Tagus estuary;
16 Portugal. *Journal of Fish Biology* **68**, 1551–1562.
- 17 Franco, A., Elliott, M., Franzoi, P. and Torricelli, P. (2008) Life strategies of fishes in
18 European estuaries: the functional guild approach. *Marine Ecology Progress Series* **354**, 219–
19 228.
- 20 Freitas, V., Kooijman, S., van der Veer, H. (20012) Latitudinal trends in habitat quality of
21 shallow water flatfish nurseries. *Marine Ecology Progress Series* **471**, 203-214.
- 22 Friedland, K.D., Ahrenholz, D.W. and Guthrie, J.F. (1996) Formation and seasonal evolution
23 of atlantic menhaden juvenile nurseries in coastal Estuaries. *Estuaries and Coasts* **19**(1), 105–
24 114.

- 1 Fujii, T. and Noguchi, M. (1995) Interactions between released and wild Japanese flounder
2 (*Paralichthys olivaceus*) on a nursery ground. Proceedings of the twenty second US-Japan
3 aquaculture panel symposium. (eds M.R. Collie and J.P. McVey)., *United States Japan*
4 *Cooperation Technical Report* **22**, 57–65.
- 5 Fulford, R.S., Peterson, M.S and Grammer, P.O. (2011) An ecological model of the habitat
6 mosaic in estuarine nursery areas: Part I-Interaction of dispersal theory and habitat variability
7 in describing juvenile fish distributions. *Ecological Modelling* **222**, 3203-3215.
- 8 Gallego, A., North, E. and Houde, E.D. (2012) Understanding and quantifying mortality in
9 pelagic, early life stages of marine organisms - Old challenges and new perspectives. *Journal*
10 *of Marine Systems* **93**, 1-3.
- 11 Geange, S. and Stier, A.C. (2009) Order of arrival affects competition in two reef fishes.
12 *Ecology* **90**, 2868–2878.
- 13 Geffen, A., Van der Veer, H. and Nash, R. (2007) The cost of metamorphosis in flatfishes.
14 *Journal of Sea Research* **58**, 35–45.
- 15 Geffen, A.J., Nash, R.D.M., Dau, K., Harwood, A.J.P. (2011) Sub-cohort dynamics of 0-
16 group plaice, *Pleuronectes platessa* L., in the Northern Irish Sea: Settlement, growth and
17 mortality. *Journal of Experimental Marine Biology and Ecology*, **400**, 108-119.
- 18 Gell, F.R. and Roberts, C.M. (2003) Benefits beyond boundaries: the fishery effects of marine
19 reserves. *Trends in Ecology and Evolution* **18**, 448-455.
- 20 Gibson, R.N. (1994) Impact of habitat quality and quantity on the recruitment of juvenile
21 flatfishes. *Netherlands Journal of Sea Research* **32**, 191–206.
- 22 Gibson, R.N. and Robb, L. (1996) Piscine predation on juvenile fishes on a Scottish sandy
23 beach. *Journal of Fish Biology* **49**, 120–138.

- 1 Gibson, R.N., Yin, M.C. and Robb, L. (1995) The behavioural basis of predator-prey size
2 relationships between shrimp (*Crangon crangon*) and juvenile plaice (*Pleuronectes platessa*).
3 *Journal of the Marine Biological Association UK* **57**, 337–349
- 4 Gilliers, C., Amara, R., Bergeron, J. and Le Pape, O. (2004) Comparison of growth and
5 condition indices of juvenile flatfish in different coastal nursery grounds. *Environmental*
6 *Biology of Fishes* **71**, 189–198.
- 7 Gilliers, C., Le Pape, O., Désaunay, Y., Bergeron, J.P., Schreiber, N., Guérault, D. and
8 Amara, R. (2006) Growth and condition of juvenile sole (*Solea solea* L.) as indicators of
9 habitat quality in coastal and estuarine nurseries in the Bay of Biscay with a focus on sites
10 exposed to the Erika oil spill. *Scientia Marina* **70**S1, 183-192.
- 11 Gislason, H., Daan, N., Rice, J.C. and Pope, J.G. (2010) Size, growth, temperature and the
12 natural mortality of marine fish. *Fish and Fisheries* **11**, 149–158.
- 13 Goto, D. and Wallace, W. (2010) Bioenergetic responses of a forage fish (*Fundulus*
14 *heteroclitus*) to habitat degradation and altered prey community in polluted salt marshes.
15 *Canadian Journal Fisheries and Aquatic Sciences* **67**, 1566–1584.
- 16 Goto, T. (2006) Stock size fluctuations and recruitment characteristics of Japanese flounder
17 *Paralichthys olivaceus* in the coastal waters off Iwate Prefecture Pacific coast of northern
18 Honshu, Japan. *Nippon Suisan Gakkaishi* **72**(5), 839–849.
- 19 Grover, J.J., Buckley, T.W. and Woodbury, D. (2002) Effects of the 1997-1998 El Niño on
20 early-juvenile Pacific hake *Merluccius productus*: age, growth, abundance, and diet in coastal
21 nursery habitats. *Marine Ecology Progress Series* **240**, 235–247.
- 22 Guindon, K.Y. and Miller, J.M. (1995) Growth potential of juvenile southern flounder,
23 *Paralichthys lethostigma*, in low salinity nursery areas of Pamlico Sound, North Carolina,
24 USA. *Netherlands Journal of Sea Research* **34**(1-3), 89–100.

- 1 Guisan, A. and Zimmermann, N.E. (2000) Predictive habitat distribution models in ecology.
2 *Ecological Modelling* **135**, 147–186.
- 3 Hall, S.J. (1998) The effects of fishing on marine ecosystems and communities. Blackwell
4 Science, Oxford.
- 5 Halpin, P.M. (2000) Habitat use by an intertidal salt-marsh fish: trade offs between predation
6 and growth. *Marine Ecology Progress Series* **198**, 203–214.
- 7 Hamerlynck, O., Janssen, C.R. and Landschoote, E. (1989) Fasting and feeding in late larval
8 and early post-larval plaice (*Pleuronectes platessa* L.). *Report of the International Council for*
9 *the Exploration of the Sea* 191: 465.
- 10 Hampel, H., Cattijisse, A. and Elliott, M. (2005) Feeding habits of young predatory fishes in
11 marsh creeks situated along the salinity gradients of the Shelde estuary, Belgium, The
12 Netherlands. *Helgoland Marine Research* **59**, 151–162.
- 13 Harding, D. and Talbot J.W. (1973) Recent studies on the eggs and larvae of the plaice
14 (*Pleuronectes platessa* L.) in the Southern Bight. *Rapport de Procès Verbal du Conseil*
15 *International pour l'Exploration de la mer* **164**, 261-269.
- 16 Hayes, D., Jones, M., Lester, N., Chu, C., Doka, S., Netto, J., Stockwell, J., Thompson, B.,
17 Minns, C., Shuter, B. and Collins, N. (2009) Linking fish population dynamics to habitat
18 conditions: insights from the application of a process-orienter approach to several Great lakes
19 species. *Reviews of Fish Biology and Fisheries* **19**, 295–312.
- 20 Hayes, D.B., Ferreri, C.P. and Taylor, W.W. (1996) Linking fish habitat to their recruitment
21 dynamics. *Canadian Journal of Fisheries and Aquaculture Science* **53**, 383–390.
- 22 Hixon, M. and Jones, G. (2005) Competition, predation and density-dependent mortality in
23 demersal marine fishes. *Ecology* **86**, 2847–2859.
- 24 Hjort, J. (1914) Fluctuations in the year classes of important food fishes. *ICES Journal of*
25 *Marine Science* **1**, 5–38.

- 1 Hodgson, J., Moilanen, A., Wintle, B. and Thomas, C. (2011) Habitat area, quality and
2 connectivity: striking the balance for efficient conservation. *Journal of Applied Ecology* **48**,
3 148–152.
- 4 Holbrook, S.J., Forrester, G.E. and Schmitt, R.J. (2000) Spatial patterns in abundance of a
5 damselfish reflect availability of suitable habitat. *Oecologia* **122**, 109–120.
- 6 Houde, E. (2008) Emerging from Hjort's shadow. *Journal of Northwest Atlantic Fishery*
7 *Science* **41**, 53–70.
- 8 Houde, E.D. (1987) Fish early life dynamics and recruitment variability. *American Fisheries*
9 *Society Symposium* **2**, 17–29.
- 10 Houde, E.D. (1997) Patterns and consequences of selective processes in teleost early life
11 histories. *Early life history and recruitment in fish populations* (eds R.C. Chambers and E.A.
12 Trippel). Chapman and Hall, New York.
- 13 Houde, E.D. (2002) Mortality. **In:** *The unique contributions of early life stages. Fishery*
14 *science* (eds L.A. Fuiman and R.G. Werner), Blackwell Publishing, Oxford, pp. 64–87.
- 15 Hovenkamp, F. (1992) Growth dependent mortality of larval plaice *Pleuronectes platessa* in
16 the North Sea. *Marine Ecology Progress Series* **82**, 95–101.
- 17 Howell, P.T., Molnar, D.R. and Harris, R.B. (1999) Juvenile winter flounder distribution by
18 habitat type. *Estuaries* **22**, 1090–1095.
- 19 Hutchings, J.A. and Jones, M.E.B. (1998) Life history variation and growth rate thresholds for
20 maturity in Atlantic salmon, *Salmo salar*. *Canadian Journal of Fisheries and Aquatic*
21 *Sciences* **55**(Suppl. 1), 22–47.
- 22 Iles, T. (1994) A review of stock-recruitment relationships with reference to flatfish
23 populations. *Netherlands Journal of Sea Research* **32**(3-4), 399-420.
- 24 Iles, T.C. and Beverton, J.H. (2000) The concentration hypothesis: the statistical evidence.
25 *ICES Journal of Marine Science* **57**, 216–227.

- 1 Islam, M.S. and Tanaka, M. (2005) Nutritional condition, starvation status and growth of early
2 juvenile Japanese sea bass (*Lateolabrax japonicus*) related to prey distribution and feeding in
3 the nursery ground. *Journal of Experimental Marine Biology and Ecology* **323**(2), 172–183.
- 4 Iwata, S., Fujioka, K., Fukuda, H., and Takeuchi, Y. (2012) Reconsideration of natural
5 mortality of age 0 Pacific bluefin tuna and its variability relative to fish size. Working paper
6 of the ISC Pacific Bluefin Tuna Working Group Meeting, 31 January-7 February 2012, La
7 Jolla, California, USA. ISC/12/PBFWG1/13.
- 8 Johnson, DW. (2007) Habitat complexity modifies post-settlement mortality and recruitment
9 dynamics of marine fish. *Ecology* **88**, 1716–1725.
- 10 Johnson, A., Jenkins, S., Hiddink, J. and Hinz, H. (2013) Linking temperate demersal fish
11 species to habitat: scales, patterns and future directions. *Fish and Fisheries* **14**(3), 256-80.
- 12 Jones, R.F., Baltz, D.M. and Allen, R.L. (2002) Patterns of resource use by fishes and
13 macroinvertebrates in Barataria Bay, Louisiana. *Marine Ecology Progress Series* **237**, 271–
14 289.
- 15 Juanes, F. (2007) Role of habitat in mediating mortality during the post-settlement transition
16 phase of temperate marine fishes. *Journal of Fish Biology* **70**, 661–677.
- 17 Kaplan, D.M. (2009) Fish life histories and marine protected areas: an odd couple? *Marine*
18 *Ecology Progress Series* **377**, 213-225.
- 19 Karakiri, M., Berghahn, R. and Von Westernhagen, H. (1989) Growth differences in 0-group
20 plaice *Pleuronectes platessa* as revealed by otolith microstructure analysis. *Marine Ecology*
21 *Progress Series* **55**, 15–22.
- 22 Klanjscek, T., Caswell, H., Neubert, M.G. and Nisbet, R.M. (2006) Integrating dynamic
23 energy budgets into matrix population models. *Ecological Modelling* **196**, 407–420.
- 24 Kooijman, S.A.L.M. (2000) Dynamic Energy and Mass Budgets in Biological Systems.
25 Cambridge University Press, Great Britain. Second Edition.

- 1 Kostecki, C., Le Loc'h, F., Roussel, J.M., Desroy, N., Huteau, D., Le Bris, H. and Le Pape, O.
2 (2010) Dynamics of an estuarine nursery ground: the spatio-temporal relationship between the
3 river flow and the food web of the juvenile common sole (*Solea solea*) as revealed by stable
4 isotopes analysis. *Journal of Sea Research* **64**, 54–60.
- 5 Kostecki, C., Rochette, S., Girardin, R., Blanchard, M., Desroy, N. and Le Pape, O. (2011)
6 Reduction of flatfishes habitat as a consequence of the proliferation of an invasive mollusc.
7 *Estuarine, Coastal and Shelf Science* **92**, 154–160.
- 8 Kostecki, C., Roussel, J.M., Desroy, N., Roussel, G., Lanshere, J., Le Bris, H. and Le Pape,
9 O. (2012). The main influence of microphytobenthos on juvenile flatfish food web in a
10 macrotidal nursery Bay. *Marine Ecology Progress Series* **449**: 221-232.
- 11 Koutsikopoulos, C., Desaunay, Y., Dorel, D. and Marchand, J. (1989) The role of coastal
12 areas in the life history of sole (*Solea solea* L.) in the Bay of Biscay. *Scientia marina* **53**, 567–
13 575.
- 14 Koutsikopoulos, C., Fortier, L. and Gagne, J.A. (1991) Cross-well dispersion of dover sole
15 (*Solea solea* (L.)) eggs and larvae in Biscay Bay and recruitment to inshore nurseries.
16 *Journal of plankton research* **13**, 923–945.
- 17 Laegdsgaard, P. and Johnson, C. (2001) Why do juvenile fish utilise mangrove habitats.
18 *Journal of Experimental Marine Biology and Ecology* **257**, 229–253.
- 19 Lafaille, P., Feunteun, E. and Lefeuvre, J.C. (2000) Composition of fish communities in a
20 European macrotidal salt marsh (the Mont Saint Michel Bay, rance). *Estuarine, Coastal and*
21 *Shelf Science* **51**, 429–438.
- 22 Laffargue, P., Lagardère, F. Rijnsdorp, A.D., Fillon, A. and Amara, R. (2007) Growth
23 performances of juvenile sole *Solea solea* under environmental constraints of embayed
24 nursery areas. *Aquatic Living Resources* **20**, 213–221.

- 1 Lamberth, S., Drapeau, L. and Branch, G.M. (2009) The effects of altered freshwater inflows
2 on catch rates of non estuarine dependent fish in multispecies nearshore fisheries. *Estuarine,*
3 *Coastal and Shelf Science* **84**, 527–538.
- 4 Le Pape, O., Holley, J., Guérault, D. and Désaunay, Y. (2003a) Quality of coastal and
5 estuarine essential fish habitat: estimations based on the size of juvenile common sole (*Solea*
6 *solea* L.). *Estuarine, Coastal and Shelf Science* **58**, 793–803.
- 7 Le Pape, O., Chauvet, F., Mahévas, S., Lazure, L., Guérault, G. and Désaunay, Y. (2003b)
8 Quantitative description of habitat suitability for the juvenile common sole (*Solea solea*, L.)
9 and contribution of different habitats to the adult population in the Bay of Biscay (France).
10 *Journal of Sea Research* **50**(2-3), 139–149.
- 11 Le Pape, O., Chauvet, F., Désaunay, Y. and Guérault, G. (2003c) Relationship between
12 interannual variations of the river plume and the extent of nursery grounds for the common
13 sole (*Solea solea*, L.) in Vilaine Bay. Effects on recruitment variability. *Journal of Sea*
14 *Research* **50**(2-3), 177–185.
- 15 Le Pape, O., Désaunay, Y. and Guérault, D. (2003d) Relationship between fluvial discharge
16 and sole (*Solea solea*, L.) recruitment in the Bay of Biscay (France). Study of an estuarine
17 nursery ground and application on a stock scale. *ICES Marine Science Symposia* **219**, 241–
18 248.
- 19 Le Pape, O., Baulier, L., Cloarec, A., Martin, J., Le Loc'h, F. and Désaunay, Y. (2007) Habitat
20 suitability for juvenile common sole (*Solea solea*, L.) in the Bay of Biscay (France): A
21 quantitative description using indicators based on epibenthic fauna. *Journal of Sea Research*
22 **57**, 126–136.
- 23 Le Pape, O., Modéran, J., Beaunée, G., Riera, P., Nicolas, D., Savoye, N., Harmelin-Vivien,
24 M., Darnaude, A., Brind'Amour, A., Le Bris, H., Cabral, H., Vinagre, C., França, S. and
25 Kostecki, C. (2013) Organic matter sources for flatfish juveniles in coastal and estuarine

- 1 nursery grounds: a meta-analysis for the common sole (*Solea solea*) in contrasted systems of
2 Western Europe. *Journal of Sea research* **75**, 85-95.
- 3 Leakey, C.D.B., Atrill, M.A., Jennings, S. and Fitzsimons, M.F. (2008) Stable isotopes in
4 juvenile marine fishes and their invertebrate prey from the Thames estuary, UK, and adjacent
5 coastal regions. *Estuarine, Coastal and Shelf Science* **77**, 513–522.
- 6 Leakey, C.D.B., Atrill, M.A., Jennings, S. and Fitzsimons, M.F. (2008) Stable isotopes in
7 juvenile marine fishes and their invertebrate prey from the Thames estuary, UK, and adjacent
8 coastal regions. *Estuarine, Coastal and Shelf Science* **77**, 513–522.
- 9 Lekve, K., Ottersen, G., Stenseth, N.C. and Gjosaetter, J. (2002) Length dynamics in juvenile
10 coastal skagerrak cod: effects of biotic and abiotic processes. *Ecology* **86**, 1676–1688.
- 11 Levin, P., Petrik, R. and Malone, J. (1997) Interactive effects of habitat selection, food supply
12 and predation on recruitment of an estuarine fish. *Oecologia* **112**, 55–63.
- 13 Levin, P.S. and Stunz, G.W. (2005) Habitat triage for exploited fishes: can we identify
14 essential fish habitat? *Estuarine, Coastal and Shelf Science* **64**, 70–78.
- 15 Lewis, D.B. (2001) Trade-offs between growth and survival responses of freshwater snails to
16 predacious crayfish. *Ecology* **82**, 758–765.
- 17 López-Rasgado, F.J., Herzka, S.Z. (2009) Assessment of habitat quality for juvenile
18 California halibut (*Paralichthys californicus*) in a seasonally arid estuary. *Fishery Bulletin*
19 **107**, 343-358.
- 20 Malloy, K.D., Yamashita, Y., Yamada, H., Targett, T.E. (1996) Spatial and temporal patterns
21 of juvenile stone flounder *Kareius bicoloratus* growth rates during and after settlement.
22 *Marine Ecology Progress Series* **131**, 49-59.
- 23 Manderson, J.P., Phelan, B.A., Stoner, A.W. and Hilbert, J. (2000) Predator prey relations
24 between age-1+ summer flounder (*Paralichthys dentatus*, L.) and age 0 winter flounder

- 1 (*Pseudopleuronectes americanus*, Walbaum): predator diets, prey selection, and effects of
2 sediments and macrophytes. *Journal of Experimental Marine Biology Ecology* **251**, 17–39.
- 3 Marchand, J. (1993) The influence of seasonal salinity and turbidity maximum variations on
4 the nursery function of the Loire estuary (France). *Netherlands Journal of Aquatic Ecology*
5 **27**, 427–436.
- 6 Marchand, J. and Masson, G. (1989) Process of estuarine colonization by 0-group sole (*Solea*
7 *solea*): hydrological conditions, behaviour and feeding activity in the Vilaine estuary.
8 *Rapport de Procès Verbal de la Réunion du Conseil International pour l'Exploration de la*
9 *Mer* **191**, 287–295.
- 10 Marchand, J., Tanguy, A., Laroche, J., Quiniou, L. and Morales, D. (2003) Responses of
11 European flounder *Platichthys flesus* populations to contaminant in different estuaries along
12 Atlantic coast of France. *Marine Ecology Progress Series* **260**, 273–284.
- 13 McConnaughey, R.A. and Smith, K.R. (2000) Associations between flatfish abundance and
14 surficial sediments in the eastern Bering Sea. *Canadian Journal of Fishery and Aquatic*
15 *Sciences* **57**, 2410–2419.
- 16 McCormick, M.I. and Molony, B. (1993) Quality of the tropical reef fish, *Upeneus tragula*
17 (family: Mullidae), at settlement: Is size a good indicator of condition? *Marine Ecology*
18 *Progress Series* **98**, 45–54.
- 19 McErlean, A.J., O'Connor, S.G., Mihursky, J.A. and Gibson, C.I. (1973) Abundance, diversity
20 and seasonal patterns of estuarine fish populations. *Estuarine and Coastal Marine Science* **1**,
21 19–36.
- 22 McLusky, D.S. and Elliott, M. (2004) *The Estuarine Ecosystem; ecology, threats and*
23 *management*, 3rd Edn. Oxford University Press, Oxford.

- 1 Megrey, B.A., Rose, K.A., Klumb, R.A., Hay, D.E., Werner, F.E., Eslinger, D.L. and Smith,
2 S.L. (2007) A bioenergetics-based population dynamics model of Pacific herring (*Clupea*
3 *harengus pallasii*) coupled to a lower trophic level nutrient-phytoplankton-zooplankton model:
- 4 Meng, L. and Cicchetti, G. (2005) Relationships between juvenile winter flounder and
5 multiple scale habitat variation in Narraganset Bay, Rhode Island. *Transactions of the*
6 *American Fisheries* **134**, 1509–1519.
- 7 Meng, L., Gray, C., Talpin, B. and Kupcha, E. (2000) Using winter flounder growth rates to
8 assess habitat quality in Rhode Islands coastal lagoons. *Marine Ecology Progress Series* **201**,
9 287–299.
- 10 Meng, L., Orphanides, C.D. and Powell, J.C. (2002) Use of fish index to assess habitat quality
11 in Narragansett Bay, Rhode Island. *Transactions of the American Fisheries Society* **131**, 731–
12 742.
- 13 Mesnildrey L., Gascuel D. and Le Pape O. (2013) Marine Protected Areas and fisheries
14 management: some criteria for ecological efficiency. *Aquatic living resources* **26**, 159-170.
- 15 Meyer, S., Caldarone, E.M., Chicharo, M.A., Clemmesen, C., Faria, A.M., Faulk, C.,
16 Folkvord, A., Holt, G.J., Hoie, H., Kanstinger, P., Malzahn, A., Moran, D., Petereit, C.,
17 Stottrup, J.G. and Peck, M.A. (2012) On the edge of death: Rates of decline and lower
18 thresholds of biogeochemical condition in food-deprived fish larvae and juveniles. *Journal*
19 *of Marine Systems* **93**, 11-24.
- 20 Miller, J.M., Reed, J.P. and Pietrafesa, L.J. (1984) Patterns, mechanisms and approaches to
21 the study of migrations of estuarine dependent fish larvae and juveniles. In: *Mechanisms of*
22 *migration in fishes* (eds J.D. McCleave, G.P. Arnold, J.J. Dodson and W.H. Neill). Plenum
23 Press, New York. pp 209-225.

- 1 Miller, T.J., Crowder, L.B., Rices, J.A. and Marshall, E.A. (1988) Larval size and recruitment
2 mechanisms in fishes: Toward a conceptual framework. *Canadian Journal of Fisheries and*
3 *aquaculture Sciences* **45**, 1657–1667.
- 4 Minto, C., Myers, R.A. and Blanchard, W. (2008) Survival variability and population density
5 in fish populations. *Nature* **452**, 344–348.
- 6 Moore, D.M. (1978) Seasonal changes in distribution of intertidal macrofauna in the lower
7 Mersey Estuary, U.K. *Estuarine and Coastal Marine Science* **7**, 117–125.
- 8 Nash, R.D.M. and Geffen, A.J. (2000) The influence of nursery grounds processes in the
9 determination of year-class strength in juvenile plaice *Pleuronectes platessa* L. in Port Erin
10 Bay, Irish Sea. *Journal of Sea Research* **44**, 101–110.
- 11 Nash, R.D.M. and Geffen, A.J. (2012) Mortality through the early life-history of fish: What
12 can we learn from European Plaice (*Pleuronectes platessa* L.)? *Journal of Marine Systems* **93**,
13 58-68.
- 14 Nash, R.D.M., Geffen, A.J, Burrows, M.T. and Gibson, R.N. (2007) Dynamics of shallow-
15 water juvenile flatfish nursery grounds: application of the shelf-thinning rule. *Marine Ecology*
16 *Progress Series* **344**, 231–244.
- 17 Nicolas D., Lobry, J., Le Pape, O. and Boët, P. (2010) Functional diversity in European
18 estuaries: Relating the composition of fish assemblages to the abiotic environment. *Estuarine,*
19 *Coastal and Shelf Science* **88**, 9–338.
- 20 Nicolas, D., Le Loc'h, F., Desaunay, Y., Hamon, D., Blanchet, A. and Le Pape, O. (2007)
21 Relationship between benthic macrofauna and habitat suitability for juvenile common sole
22 (*Solea solea*, L.) in the Vilaine estuary (Bay of Biscay, France) nursery ground. *Estuarine*
23 *Coastal and Shelf Science* **73**, 639–650.
- 24 Norcross, B.L., Blanchard, A. and Holladay, B.A. (1999) Comparison of models for defining
25 nearshore flatfish nursery areas in Alaskan waters. *Fisheries Oceanography* **8**, 50–67.

- 1 Norcross, B.L., Muter, F.J. and Holladay, B. (1997) Habitat models for juvenile pleuronectids
2 around Kodiak Island, Alaska. *Fishery Bulletin* **95**, 504–520.
- 3 Nunn, A., Tewson, L., Cow X. (2012) The foraging ecology of larval and juvenile fishes.
4 Review in *Fish Biology and Fisheries* **22**, 377-408.
- 5 Ohlberger, J., Otero, J., Edeline, E., Winfield, I.J., Stenseth, N.C. and Vollestad, L.A. (2012)
6 Biotic and abiotic effects on cohort size distributions in fish. *Oikos* **122**(6):835-44.
- 7 Pappal, A.L., MacDonald, D.G. and Rountree, R.A. (2009) Evidence of cobble habitat
8 preference in age-0 winter flounder, *Pseudopleuronectes americanus*. *Marine and Freshwater*
9 *Behaviour and Physiology*, **42**, 43–53.
- 10 Parrish, F.A., DeMartini, E.E. and Ellis, D. (1997) Nursery habitat in relation to production of
11 juvenile snapper *Pristipomoides filamentosus* in the Hawaiian Archipelago. *Fisheries Bulletin*
12 **95**, 137–149.
- 13 Pasquaud, S., David, V., Lobry, J., Girardin, M., Sautour, B. and Elie, P. (2010) Exploitation
14 of trophic resources by fish under stressful estuarine conditions. *Marine Ecology Progress*
15 *Series* **400**, 207–219.
- 16 Pasquaud, S., Elie, P., Jeantet, C., Billy, I., Martinez, P. and Girardin, M. (2008) A
17 preliminary investigation of the fish food web in the Gironde estuary, France, using dietary
18 and stable isotope analyses. *Estuarine Coastal and Shelf Science* **78**, 267–279.
- 19 Pasquaud, S., Pillet, M., David, V., Sautour, B. and Elie, P. (2010) Determination of fish
20 trophic levels in an estuarine system. *Estuarine, Coastal and Shelf Science* **86**, 237–246.
- 21 Percy, W.G. (1962a) Ecology of an estuarine population of winter flounder,
22 *Pseudopleuronectes americanus* (Walbaum). II. Distribution and dynamics of larvae. *Bulletin*
23 *of the Bingham Oceanographic Collection* **18**, 16-37.
- 24 Percy, WG (1962b) Ecology of an estuarine population of winter flounder,
25 *Pseudopleuronectes americanus* (Walbaum). III. Distribution, abundance, growth, and

- 1 production of juveniles, survival of larvae and juveniles. *Bulletin of the Bingham*
2 *Oceanographic Collection* **18**, 39-64.
- 3 Pelletier, D. and Magal, P. (1996) Dynamics of a migratory population under different fishing
4 effort allocation schemes in time and space. *Canadian Journal of Fisheries and Aquatic*
5 *Sciences* **53**, 1186–1199.
- 6 Peterman, R., Bradford, M., Lo, N.C.H. and Methot, R.D. (1988) Contribution of early life
7 stages to interannual variability in recruitment of Northern Anchovy. *Canadian Journal of*
8 *Fisheries and Aquatic Sciences* **45**, 8–16.
- 9 Peterson, C.H., Summerson, H.C., Thomson, E., Lenihan, H.S., Grabowski, J., Manning, L.,
10 Micheli, F. and Johnson, G. (2000) Synthesis of linkages between benthic and fish
11 communities as key to protecting essential fish habitat. *Bulletin of Marine Science* **66**, 759–
12 774.
- 13 Peterson, M. (2003) A conceptual view of environment-habitat-production linkages in tidal
14 river estuaries. *Reviews in Fisheries science* **11**, 291–313.
- 15 Phelan, B.A., Goldberg, R., Bejda, A.J., Pereira, J., Hagan, S., Clark, P., Studholme, A.L.,
16 Calabrese, A. and Able K.W. (2000) estuarine and habitat related differences in growth rates
17 of young of the year winter flounder (*Pseudopleuronectes americanus*) and tautog (*Tautoga*
18 *onitis*) in three northeastern US estuaries. *Journal of Experimental Marine Biology and*
19 *Ecology* **247**, 1–28.
- 20 Phelan, B.A., Manderson, J.P., Stoner, A.W. and Bejda, A.J. (2001) Size-related shifts in the
21 habitat associations of young-of-the-year winter flounder (*Pseudopleuronectes americanus*):
22 field observations and laboratory experiments with sediments and prey. *Journal of*
23 *Experimental Marine Biology and Ecology* **257**, 297–315.

- 1 Pihl, L., Modin, J. and Wennhage, H. (2000) Spatial distribution patterns of newly settled
2 plaice (*Pleuronectes platessa* L.) along the Swedish Skagerrak archipelago. *Journal of Sea*
3 *Research* **44**, 65–80.
- 4 Polacheck, T., Hearn, W.S., Miller, C., Whitelaw, W., and Stanley, C. (1997) Updated
5 estimates of mortality rates for juvenile SBT from multi-year tagging of cohorts.
6 CCSBTSC/9707/26.
- 7 Rauck, G. and Zijlstra, J.J. (1978) On the nursery-aspects of the Wadden sea for some
8 commercial fish species and possible long term changes. *Rapport de Procès Verbal de la*
9 *Réunion Annuelle du Conseil International pour l'Exploration de la Mer* **172**, 266–275.
- 10 Rijnsdorp, A.D., Van, B.F.A, Flatman, S, Millner, R.M., Riley, J.D, Giret, M. and De Clerck,
11 R. (1992) Recruitment of sole stocks, *Solea solea* (L.), in the northeast Atlantic. *Netherlands*
12 *Journal of Sea Research* **29**, 173–192.
- 13 Riley, J.D., Symonds, D.J. and Woolner, L. (1981) On the factors influencing the distribution
14 of 0-group demersal fish in coastal waters. *Rapport de Procès Verbal de la Réunion Annuelle*
15 *du Conseil International pour l'Exploration de la Mer* **178**, 223–228.
- 16 Riou, P., Le Pape, O. and Rogers, S.I. (2001) Relative contributions of different sole and
17 plaice nurseries to the adult population in the Eastern Channel: application of a combined
18 method using generalized linear models and a geographic information system. *Aquatic Living*
19 *Resources* **14**, 125–135.
- 20 Rochette, S., Huret, M., Rivot, E and Le Pape, O. (2012) Coupling hydrodynamic and
21 individual-based transport models to simulate long-term larval supply on coastal nursery area.
22 *Fisheries and oceanography* **21**, 229-242.
- 23 Rochette, S., Le Pape, O., Vigneau, J. and Rivot, E. (2013) A bayesian state-space model
24 approach to integrate the whole life cycle in marine fish population model. *Ecological*
25 *applications* **23**, 1659-1676.

- 1 Rochette, S., Rivot, E., Morin, J., Mackinson, S., Riou, P. and Le Pape, O. (2010) Effect of
2 nursery habitat degradation on flatfish population: Application to *Solea solea* in the Eastern
3 Channel (Western Europe). *Journal of Sea Research* **64**, 34–44.
- 4 Rogers, S.I. (1992) Environmental factors affecting the distribution of sole (*Solea solea* (L.))
5 within a nursery area. *Netherlands Journal of Sea Research* **29**, 153–161.
- 6 Rogers, S.I. (1994) Populations density and growth rate juvenile sole *Solea solea* (L.).
7 *Netherlands Journal of Sea Research* **32**, 353–360.
- 8 Rooper, C., Gunderson, D. and Armstrong, D. (2004) Application of the concentration
9 hypothesis to English sole in nursery estuaries and potential contribution to coastal fisheries.
10 *Estuaries* **27**, 102–111.
- 11 Rose, K.A., Tyler, J.A., Chambers, R.C., Klein-MacPhee, G. and Danila, D.J. (1996)
12 Simulating winter flounder population dynamics using coupled individual-based young-of-
13 the-year and age-structured adult models. *Canadian Journal of Fisheries and Aquatic*
14 *Sciences*, 53, 1071-1091.
- 15 Ross, S. (2003) The relative value of different estuarine nursery areas in North Carolina for
16 transient juvenile marine fishes. *Fishery bulletin* **101**, 384–404.
- 17 Rotenberry, J., Preston, K. and Knick, S. (2006) GIS-based niche modeling for mapping
18 species habitat. *Ecology* **87**, 1458–1464.
- 19 Ruiz, J., Gonzalez-Quiros, R., Prieto, L. and Navarro, G. (2009) A Bayesian model for
20 anchovy (*Engraulis encrasicolus*): the combined forcing of man and environment. *Fisheries*
21 *oceanography* **18**, 62–76.
- 22 Salen-Picard, C., Darnaude, A.M., Arlhac, D. and Harmelin-Vivien, M.L. (2002) Fluctuations
23 of macrobenthic populations: a link between climate-driven run-off and sole fishery yields in
24 the Gulf of Lions. *Oecologia* **133**, 380–388.

- 1 Salgado, J.P., Cabral, H.N. and Costa, M.J. (2004) Feeding ecology of the gobies
2 *Pomatoschistus minutes* (Pallas, 1770) and *Pomatoschistus microps* (Kroyer, 1838) in the
3 upper Tagus estuary, Portugal. *Scientia Marina* **68**, 425–434.
- 4 Scharf, F. (2000) Patterns in abundance, Growth, and Mortality of Juvenile red drum across
5 estuaries on the Texas coast with Implications for recruitment and stock enhancement.
6 *Transactions of the American Fisheries Society* **129**, 1207–1222.
- 7 Schmitt, R.J. and Holbrook, S.J. (2000) Habitat-limited recruitment of coral reef damselfish.
8 *Ecology* **81**, 3479–3494.
- 9 Searcy, S.P., Eggleston, D.B. and Hare, J.A. (2007) Is growth a reliable indicator of habitat
10 quality and essential fish habitat for a juvenile estuarine fish? *Canadian Journal of Fisheries*
11 *and Aquaculture Science* **64**, 681–691.
- 12 Selleslagh, J. (2008) Fonctionnement des nurseries intertidales et estuariennes: influence
13 de l'environnement sur la dynamique et les performances physiologiques de l'ichtyofaune.
14 PhD Thesis, Université du littoral Côte d'Opale, France.
- 15 Selleslagh, J. and Amara, R. (2008) Environmental factors structuring fish composition and
16 assemblages in a small macrotidal estuary (eastern English Channel). *Estuarine, Coastal and*
17 *Shelf Science* **79**, 507-517.
- 18 Selleslagh, J. and Amara, R. (2013) Effect of starvation on condition and growth of juvenile
19 plaice *Pleuronectes platessa*: nursery habitat quality assessment during the settlement period.
20 *Journal of the Marine Biological Association of the United Kingdom* **93**, 479-488.
- 21 Selleslagh, J., Lesourd, S. and Amara, R. (2012) Comparison of macrobenthic assemblages of
22 three fish estuarine nurseries and their importance as foraging grounds. *Journal of the Marine*
23 *Biological Association of the United Kingdom* **92**, 85-97.
- 24 Sheaves, M. (2009) Consequences of ecological connectivity: the coastal ecosystem mosaic.
25 *Marine Ecology Progress Series* **391**, 107–115.

- 1 Shepherd, J.G and Cushing, D.H.(1980) A mechanism for density-dependent survival of
2 larval fish as the basis of a stock–recruitment relationship. *ICES Journal of Marine Science*
3 **185**, 255–267.
- 4 Shi, Y., Gunderson, D.R. and Sullivan, P.J. (1997) Growth and survival of 0 super (+) English
5 sole, *Pleuronectes vetulus*, in estuaries and adjacent nearshore waters off Washington. *Fishery*
6 *Bulletin* **95**, 161–173.
- 7 Simon, M., Fromentin, J.M., Bonhommeau, S., Gaertner, D., Brodziak, J., Etienne, M.P.
8 (2012) Effects of Stochasticity in Early Life History on Steepness and Population Growth
9 Rate Estimates: An Illustration on Atlantic Bluefin Tuna. *PLoS ONE* **7**(10): e48583.
- 10 Sinclair, M. (1997) Recruitment in fish populations: the paradigm shift generated by ICES
11 Committee A. In: *Early life history and recruitment in fish populations* (eds R.C. Chambers
12 and E.A. Trippel). Chapman & Hall 21, London.
- 13 Sogard, S.M. (1992) Variability in growth rates of juvenile fishes in different estuarine
14 habitats. *Marine Ecology Progress Series* **85**, 35–53.
- 15 Sogard, S.M. (1997) Size-selective mortality in the juvenile stage of teleost fishes: a review.
16 *Bulletin of Marine Science* **60**, 1129–1157.
- 17 Steizenmuller, V., Ellis, J. and Rogers, S. (2010) Towards spatially explicit risk assessment
18 for marine management; assessing the vulnerability of fish to aggregate extraction. *Biological*
19 *Conservation* **143**, 230–238.
- 20 Stier, A., Geange, S., Hanson, K., and Bolker, B. (2013) Predator density and timing of arrival
21 affect reef community assembly. *Ecology* **94**, 1057-1068.
- 22 Stoner, A., Spencer, M.L. and Ryer, C.H. (2007) Flatfish-habitat associations in Alaska
23 nursery grounds: Use continuous video records for multiscale spatial analysis. *Journal of Sea*
24 *Research* **57**, 137–151.

- 1 Stottrup, J.G. and Sparrevojn, C.R. (2007) Can stock enhancement enhance stocks? *Journal*
2 *of Sea Research* **57**, 104–113.
- 3 Stunz, G.W., Minello, T.J. and Levin, P.S. (2002) Growth of newly settled red drum
4 *Sciaenops ocellatus* in different estuarine habitats types. *Marine Ecology Progress Series* **238**,
5 227–236.
- 6 Suthers, I.M. (1998) Bigger? Fatter? Or is faster growth better? Considerations on condition
7 in larval and juvenile coral-reef fish. *Australian Journal of Ecology* **23**, 265–273.
- 8 Suthers, I.M., Fraser, A. and Fran, K.T. (1992) Comparison of lipid, otolith and morphometric
9 condition indices of pelagic juvenile cod (*Gadus morhua*) from the Canadian Atlantic. *Marine*
10 *Ecology Progress Series* **84**, 31–40.
- 11 Swain, D.P. (1993) Age and density dependent bathymetric pattern of Atlantic cod (*Gadus*
12 *morhua*) in the Southern Gulf of St Lawrence. *Canadian Journal of Fisheries and Aquatic*
13 *Sciences* **50**, 1255–1264.
- 14 Swain, D.P. and Morin, R. (1996) Relationships between geographic distribution and
15 abundance of American plaice (*Hippoglossoides platessoides*) in the southern Gulf of St.
16 Lawrence. *Canadian Journal of Fishery and Aquaculture Sciences* **53**, 106–119.
- 17 Talbot, J. W. (1977) The dispersal of plaice eggs and larvae in the Southern Bight of the
18 North Sea. *ICES Journal of Marine Science* **37**, 221-48.
- 19 Teal, L.R., De Leeuw, J.L, Van der Veer, H.W. and Rijnsdorp, A.D. (2008) Effects of climate
20 change on growth of 0-group sole and plaice. *Marine Ecology Progress Series* **358**, 219–230.
- 21 Trimoreau, E., Arcambault, B., Brind'Amour, A., Guitton J. and Le Pape O. (in press).
22 Quantitative estimate of the function of soft sheltered productive coastal areas as essential
23 flatfish nursery habitat. *Estuarine, Coastal and Shelf Science*.
- 24 Tsuji, S. (1998) Stock status of Southern bluefin tuna. 7th Expert Consultation on Indian
25 Ocean Tunas, Victoria, Seychelles. IOTC Proceedings **1**, 219-226.

- 1 Van de Wolfshaar, K.E., HilleRisLambers, R. and A. Gårdmark, A. (2011) Effect of habitat
2 productivity and exploitation on populations with complex life cycles. *Marine Ecology*
3 *Progress Series* **438**, 175-184.
- 4 Van der Veer, H., Bergham, R., Miller, J. and Rijnsdorp, A. (2000a) Recruitment in flatfish,
5 with special emphasis on North Atlantic species: Progress made by the Flatfish Symposia.
6 *ICES Journal of Marine Science* **57**, 202–215.
- 7 Van der Veer, H., Freitas, V., Koot, J. and Witte, J.Z.A. (2010) Food limitation in epibenthic
8 species in temperate intertidal systems in summer: analysis of 0-group plaice *Pleuronectes*
9 *platessa*. *Marine Ecology Progress Series* **416**, 215–227.
- 10 Van der Veer, H.K., Dapper, R. and Witte, J.I.J. (2001) The nursery function of the intertidal
11 areas in the western Wadden Sea for 0-group sole *Solea solea* (L.). *Journal of Sea Research*
12 **45**, 271–279.
- 13 Van der Veer, H.W. (1986) Immigration, settlement and density-dependent mortality of a
14 larval and early post-larval 0-group plaice (*Pleuronectes platessa*) population in the western
15 Dutch Wadden Sea. *Marine Ecology Progress Series* **29**, 223–236.
- 16 Van der Veer, H.W. and Witte, J.I.J. (1993) The 'maximum growth/optimal food condition'
17 hypothesis: a test for 0-group plaice *Pleuronectes platessa* in the Dutch Wadden Sea. *Marine*
18 *Ecology Progress Series* **10**, 81–90.
- 19 Van der Veer, H.W., Berghahn, R. and Rijnsdorp, A.D. (1994) Impact of juvenile growth on
20 recruitment in flatfish. *Netherlands Journal of Sea Research* **32**, 153–173.
- 21 Van der Veer, H.W., Ellis, T., Miller, J.M., Pihl, L. and Rijnsdorp, A. (1997) Size-selective
22 predation on juvenile North Sea flatfish and possible implications for recruitment. In: *Early*
23 *life history and recruitment in fish populations* (eds R.C. Chambers and E.A. Trippel).
24 Chapman and Hall, New York.

- 1 Van der Veer, H.W., Geffen, A. and Witte, J.I.J. (2000b) Exceptionally strong year classes in
2 plaice *Pleuronectes platessa*: are they generated during the pelagic stage only, or also in the
3 juvenile stage? *Marine Ecology Progress Series* **199**, 255–262.
- 4 Van der Veer, H.W., Kooijman, S. and Van der Meer, J. (2003) Body size scaling
5 relationships in flatfish as predicted by Dynamic Energy Budgets (DEB theory): implications
6 for recruitment. *Journal of Sea Research* **50**, 255–270.
- 7 Vasconcelos, R.P., Reis-Santos, P., Costa, M. and Cabral, H.N. (2011) Connectivity between
8 estuaries and marine environment: integrating metrics to assess estuarine nursery function.
9 *Ecological indicators* **11**, 1123–1133.
- 10 Vasconcelos, R.P., Eggleston, D.E., Le Pape, O., Tulp, I. (in press) Patterns and processes of
11 habitat-specific demographic variability in exploited marine species. *ICES Journal of Marine*
12 *Science*.
- 13 Vinagre, C. and Cabral, H. (2008) Prey consumption by juvenile soles, *Solea solea* and *Solea*
14 *senegalensis*, in the Tagus estuary, Portugal. *Estuarine, Coastal and Shelf Science* **78**, 45–50.
- 15 Vinagre, C., Fonseca, V., Cabral, H. and Costa, M. (2006) Habitat suitability index models for
16 juvenile soles, *Solea solea* & *S. senegalensis*, in the Tagus estuary: defining variables for
17 species management. *Fisheries research* **82**, 140–149.
- 18 Vinagre, C., Franca, S., Costa, M.J. and Cabral, H.N. (2005) Niche overlap between
19 flatfishes, *Platichthys flesus* and *Solea solea*, in a southern European estuary and adjacent
20 coastal waters. *Journal of Applied Fish Biology* **21**, 114–120.
- 21 Vinagre, C., Salgado, J., Costa, M. and Cabral, H. (2008) Nursery fidelity, food web
22 interactions and primary sources of nutrition of the juveniles of *Solea solea* and *S.*
23 *senegalensis* in the Tagus estuary (Portugal): a stable isotop approach. *Estuarine, Coastal and*
24 *Shelf Science* **76**, 255–264.

- 1 Wahl, D.H. and Stein, R.A. (1989) Comparative vulnerability of three Esocids to largemouth
2 bass. *Canadian Journal of Fisheries and Aquatic Sciences* **46**, 2095–2103.
- 3 Walsh, S.J. (1996) Life history and ecology of long rough dab *Hippoglossoides platessoides*
4 (F) in the Barents Sea. *Journal of Sea Research* **36**, 285–310.
- 5 Wennhage, H. (2000) Vulnerability of settling plaice *Pleuronectes platessa* to predation:
6 effects of developmental stage and alternative prey. *Marine Ecology Progress Series* **203**,
7 289–299.
- 8 Wennhage, H. and Gibson, R.N. (1998) Influence of food supply and a potential predator
9 (*Crangon crangon*) on settling behaviour of plaice (*Pleuronectes platessa*). *Journal of Sea*
10 *Research* **39**, 103–112.
- 11 Wennhage, H. and Pihl, L. (2001) Settlement patterns of newly settled plaice (*Pleuronectes*
12 *platessa*) in a non tidal Swedish fjord in relation to larval supply and benthic predators.
13 *Marine Biology* **139**, 877–889.
- 14 Wetz, M., Hutchinson, E., Lunetta, R., Paerl, H. and Taylor, J. (2010). Severe droughts reduce
15 estuarine primary productivity with cascading effects on higher trophic levels. *Limnology*
16 *Oceanography* **56**, 627–638.
- 17 White, J.W. and Caselle, J.E. (2008) Scale-dependent changes in the importance of larval
18 supply and habitat to abundance of a reef fish. *Ecology* **89**(5), 1323–1333.
- 19 Whitlock, R.E., McAllister, M.K and Block, B.A. 2012 Estimating fishing and natural
20 mortality rates for Pacific bluefin tuna (*Thunnus orientalis*) using electronic tagging data.
21 *Fisheries Research* **119-120**: 115-127.
- 22 Wouters, N. and Cabral, H.N. (2009) Are flatfish nursery grounds richer in benthic preys.
23 Estuarine, *Coastal and shelf science* **83**, 613–620.
- 24 Yamashita, Y., Tanaka, M. and Miller, J.M. (2001) Ecophysiology of juvenile flatfish in
25 nursery grounds. *Journal of Sea Research* **45**, 205–218.

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Table 1: Mortality during the pre-adult life phases in some marine fish populations

Species	Populations	Overall pre-adult survival*	Eggs & larvae surv.*	Juvenile surv.*	Reference
Northern anchovy (<i>Engraulis mordax</i> , <i>Engraulidae</i>)	All or whole	10^{-5}	10^{-3}	10^{-2}	Peterman et al. 1988
European anchovy (<i>Engraulis encrasicolus</i> , <i>Engraulidae</i>)	Bay of Biscay	10^{-5}	10^{-3}	10^{-2}	Calculated from Allain et al. 2003 and Allain 2004
Atlantic cod (<i>Gadus morhua</i> , <i>Gadidae</i>)	North Sea	$10^{-7} - 10^{-8}$	$10^{-5} - 10^{-6}$	10^{-2}	Houde 2002
Common sole (<i>Solea solea</i> , <i>Soleidae</i>)	Bay of Biscay	10^{-5}	10^{-3}	10^{-2}	calculated from Koutsikopoulos et al. 1989 & 1991 Rochette et al. 2013.
	Eastern Channel	10^{-5}	10^{-3}	10^{-2}	
Plaice (<i>Pleuronectes platessa</i> , <i>Pleuronectidae</i>)	North Sea	$10^{-5} - 10^{-6}$	$10^{-3} - 10^{-4}$	10^{-2}	Geffen et al. 2007
	Irish Sea	10^{-5}	10^{-3}	10^{-2}	Calculated from Harding and Talbot 1973 and Talbot 1977
	English Channel	10^{-5}	10^{-3}	10^{-2}	
Winter flounder (<i>Pseudopleuronectes americanus</i> , <i>Pleuronectidae</i>)	All or whole	$10^{-5} - 10^{-6}$	$10^{-3} - 10^{-4}$	10^{-2}	Rose et al. 1996
Atlantic eel (<i>Anguilla Anguilla</i> , <i>Anguillidae</i>)	All or whole	10^{-4}	$3 \cdot 10^{-4}$	0.3	Bonhommeau et al. 2009
Atlantic bluefin tuna (<i>Thunnus thynnus</i> , <i>Scombridae</i>)	All or whole	10^{-4}	$4 \cdot 10^{-4}$	0.3	Simon et al. 2012
Pacific bluefin tuna (<i>Thunnus orientalis</i> , <i>Scombridae</i>)	All or whole	$6-8 \cdot 10^{-5}$	$4 \cdot 10^{-4}$	0.1-0.2	Iwata et al. 2012, Polacheck et al. 1997, Whitlock et al (2012)
Southern bluefin tuna (<i>Thunnus macoyii</i> , <i>Scombridae</i>)	All or whole	$2 \cdot 10^{-5}$	$4 \cdot 10^{-4}$	0.06	Tsuji (1998)

* Survival rates are estimated with important associated variability and estimation error.

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Table 2: Analysis of food limitation in temperate and subarctic juvenile flatfish: species, location, methods and conclusions

Species	Area	Approach	Conclusion	Reference
Common sole		Experimental	Food limitation	Fonds and Saksena 1977
Common sole		Experimental	Food limitation	Fonds et al. 1989
Plaice, European Flounder (<i>Platichthys flesus</i> , <i>pleuronectidae</i>)		Experimental	Food limitation	Fonds et al. 1992
Stone flounder (<i>Kareius bicoloratus</i> , <i>Pleuronectidae</i>)		Experimental	Food limitation	Malloy et al. 1996
California flounder (<i>Paralichthys californicus</i> , <i>Pleuronectidae</i>)		Experimental	Food limitation	López-Rasgado and Herzka 2009
Plaice		Experimental	Food limitation	Ciotti et al. 2010
Plaice		Experimental	Link to prey availability	Selleslagh and Amara 2013
Plaice		Experimental	Link to prey availability	Wennhage and Gibson 1998
Winter flounder		Experimental	Link to prey availability	Phelan et al. 2001
Senegalese sole (<i>Solea senegalensis</i> , <i>Soleidae</i>), Common sole	Iberian shelf	Field, individual	No food limitation	Fonseca et al. 2006
Winter flounder	New Jersey, USA	Field, individual	No food limitation	Curran and Able 2000
Common sole, Plaice, Dab (<i>Limanda limanda</i> , <i>Pleuronectidae</i>)	English Channel	Field, individual	No food limitation	Gilliers et al. 2004
Plaice	English Channel	Field, individual	No food limitation	Selleslagh and Amara 2013
Common sole	French coasts	Field, individual	No food limitation	Gilliers et al. 2006
Common sole, Plaice, Dab	English Channel	Field, population	No food limitation	Amara 2004
Senegalese sole, Common sole	Iberian shelf	Field, population	No food limitation	Vinagre and Cabral 2008
Common sole	Bay of Biscay	Field, population	No link to prey availability	Amara et al. 2000
American plaice (<i>Hippoglossoides platessoides</i> , <i>Pleuronectidae</i>)	Gulf of St Lawrence	Field, population	No link to prey availability	Swain and Morin 1996
Common sole	North Sea	Field, population	No link to prey availability	Rogers, 1994
Plaice	North Sea	Field, population	No link to prey availability	Van der Veer et al. 2000b
Senegalese sole, Common sole	Iberian shelf	Field, population	No link to prey availability	Fonseca et al. 2010
English sole (<i>Parophrys vetulus</i> , <i>Pleuronectidae</i>)	Washington, USA	Field, population	No link to prey availability	Shi et al. 1997
English sole	Washington, USA	Field, population	No link to prey availability	Chittaro et al. 2009
Common sole	Bay of Biscay	Field, individual	Partial food limitation	Amara and Galois 2004
Plaice	Wadden Sea	Field, individual	Food limitation	Karakiri et al. 1989
Plaice	North Sea	Field, individual	Food limitation	Van der Veer et al. 2001
Plaice	Irish Sea	Field, individual	Food limitation	Ciotti et al. 2013
Common sole	Bay of Biscay	Field, population	Food limitation	Laffargue et al 2007
Common sole, Plaice; European flounder	Western Europe	Field, population	Food limitation	Freitas et al. 2012
Plaice	North Sea	Field, population	Food limitation	Teal et al. 2008

Plaice	North Sea	Field, population	Food limitation	Van der Veer et al. 2010
Plaice	Baltic Sea	Field, population	Food limitation	Pihl et al. 2000
Plaice	North Sea	Field, population	Food limitation	Ciotti et al., 2013
Plaice	Irish Sea	Field, population	Food limitation	de Raedemacker et al., 2011
Plaice	Wadden Sea	Field, population	Food limitation	van der Veer and Witte 1993
Plaice	Irish Sea	Field, population	Food limitation	Nash and Geffen 2000
Plaice	Irish Sea	Field, population	Food limitation	Nash et al. 2007
Common sole	Bay of Biscay	Field, population	Link to prey availability	Le Pape et al. 2003c
Common sole	Bay of Biscay	Field, population	Link to prey availability	Marchand and Masson, 1989
Winter flounder	Connecticut, USA	Field, population	Link to prey availability	Howell et al. 1999
Pleuronectiforms	Eastern Bering Sea	Field, population	Link to prey availability	McConnaughey and Smith, 2000
American plaice	Bering Sea	Field, population	Link to prey availability	Walsh 1996
Common sole, Plaice	English Channel	Field, population	Link to prey availability	Riou et al. 2001
Common sole	Bay of Biscay	Field, population	Link to prey availability	Le Pape et al 2007
Common sole	Bay of Biscay	Field, population	Link to prey availability	Nicolas et al. 2007
Common sole, European flounder	Iberian shelf	Field, population	Link to prey availability	Costa and Bruxelas 1989
Common sole, European flounder	Iberian shelf	Field, population	Link to prey availability	Vinagre et al. 2005
Senegalese sole, Common sole	Iberian shelf	Field, population	Link to prey availability	Vinagre et al. 2006
Bastard halibut (<i>Paralichthys olivaceus</i> , , <i>Pleuronectidae</i>)	Northwestern Japan	Field, population	Link to prey availability	Fujii and Noguchi 1995
Common sole	North Sea	Field, population	Link recruitment / food	Leakey et al. 2008
Common sole	Bay of Biscay	Field, population	Link recruitment / food	Le Pape et al. 2003a
Common sole	Bay of Biscay	Field, population	Link recruitment / food	Le Pape et al. 2003b
Common sole	Bay of Biscay	Field, population	Link recruitment / food	Le Pape et al. 2003d
Common sole	Western Europe	Field, population	Link recruitment / food	Le Pape et al. 2013
Common sole	Bay of Biscay	Field, population	Link recruitment / food	Kostecki et al. 2010
Common sole	Gulf of Lions	Field, population	Link recruitment / food	Salen Picard et al. 2002
Common sole	Gulf of Lions	Field, population	Link recruitment / food	Darnaude et al. 2004
Pleuronectiforms	Gulf of Lions	Field, population	Link recruitment / food	Darnaude et al. 2005
Senegalese sole, Common sole	Iberian shelf	Field, population	Link recruitment / food	Vinagre et al. 2008
Pleuronectiforms	Iberian shelf	Field, interspecific	Link to prey availability	Wouters and Cabral 2009
Pleuronectiforms	Iberian shelf	Field, interspecific	Food partitioning	Cabral et al. 2007
Senegalese sole, Common sole	Iberian shelf	Field, interspecific	Food partitioning	Cabral and Costa 1999
Senegalese sole, Common sole	Iberian shelf	Field, interspecific	Food partitioning	Cabral 2000
Common sole, Plaice, Dab	English Channel	Field, interspecific	Food partitioning	Amara et al. 2001
Pleuronectiforms	Gulf of Lions	Field, interspecific	Food partitioning	Darnaude et al. 2001
Common sole, Plaice	English Channel	Field, interspecific	Food partitioning	Kostecki et al. 2012
Flounder, Common sole	Iberian shelf	Field, interspecific	Food partitioning	Vinagre et al. 2005,

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Figure legends

2 Fig. 1: Location of the regional seas in Western Europe where many of the studies in this
3 review have taken place.

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5 Fig. 2: Comparison of the theoretical growth curve of the common sole after settlement
6 during their first year (grey line) and simulations of sampling carried out each month for
7 10,000 (out of 1,000,000) juvenile common sole that experienced a) no food limitation and b)
8 food-limited conditions (i.e., maximal length reduced by 20% in the model).

9

10 Fig. 3: Processes involved in the food limitation hypothesis: consequences of the limited
11 trophic capacity of nursery habitats during the settlement and post-settlement period on the
12 recruitment variability of marine fishes (pluriannual variability in cohort abundance is
13 represented for two different life stages, larval / large juveniles, before and after the stage of
14 food limitation).

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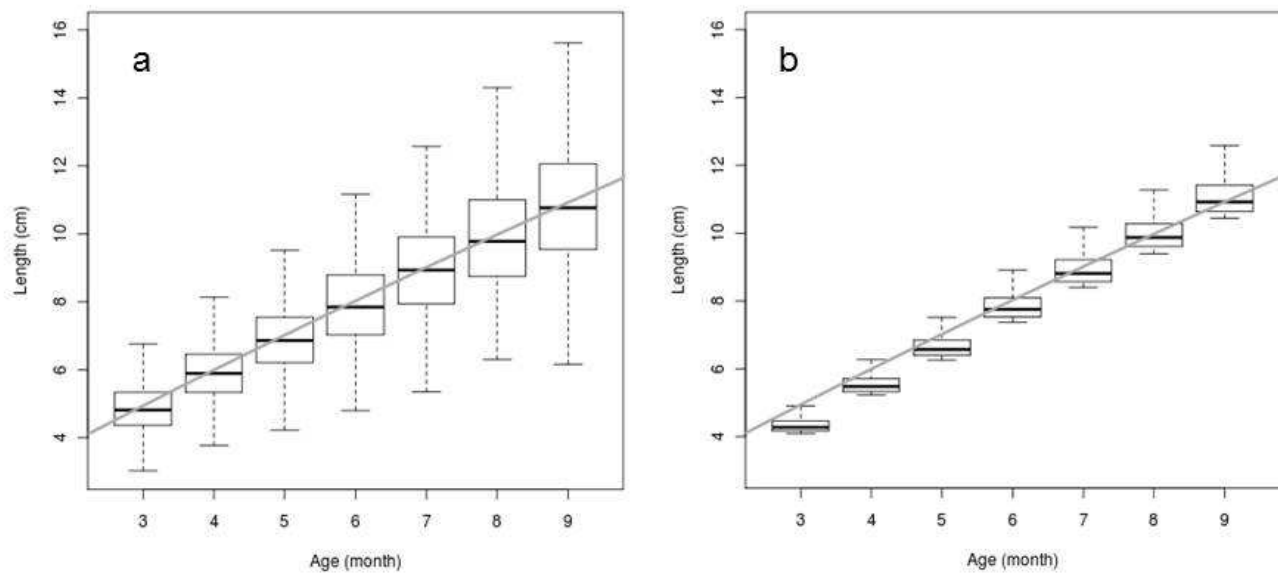
1 Figure 1



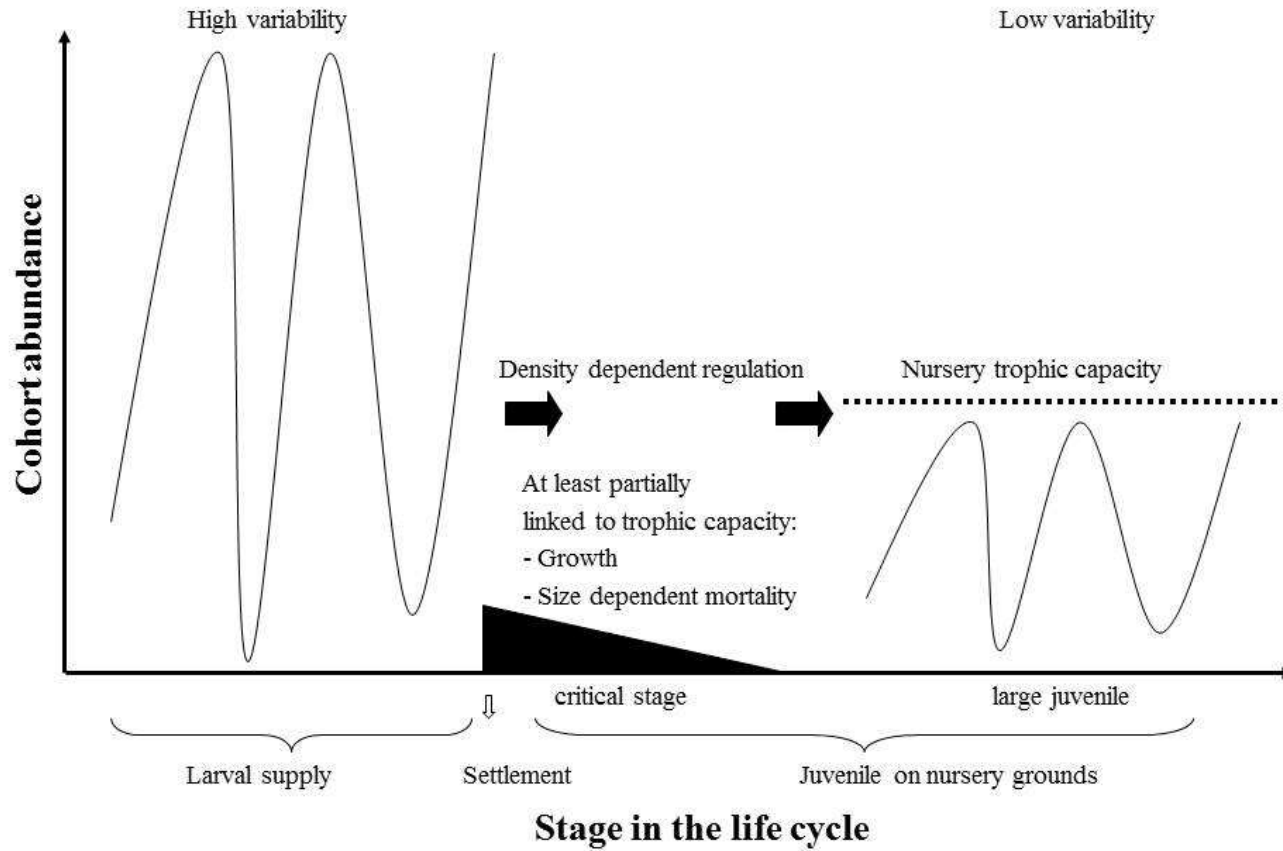
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1 Figure 2



1 Figure 3



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