

Not to be cited without prior reference to the authors

Demographically disconnected subpopulations in lesser sandeel (*Ammodytes marinus*) as basis of a high resolution spatial management system

Tore Johannessen (1) and Espen Johnsen (2)

(1) Institute of Marine Research, Flødevigen; 4817 His, Norway; (2) Institute of Marine Research; P.Box. 1870 Nordnes, Bergen, Norway; Presenter contact details:

torejo@imr.no, Phone +47 47 45 49 73

Abstract

Background: Knowledge about potential subpopulations is essential for sustainable management of fish stocks. However, obtaining such knowledge is increasingly difficult when subpopulations are genetically indistinguishable but demographically disconnected, i.e. the exchange of individuals between subpopulations is sufficient to homogenize genetics but too low to affect population dynamics. Demographic connectivity is often studied by modelling fish larval advection assuming passive drift. However, there is growing evidence to suggest that pelagic larvae of many marine species have developed advanced capabilities to cope with moving water masses and settle in preferred habitats.

Principal findings: Lesser sandeel (*Ammodytes marinus*) fishing grounds are distributed like a patchwork in the North Sea due to the burial behaviour of the fish in sandy bottom substrate. Here, we analyse landing statistics, satellite vessel tracking data and survey data from the Norwegian sector of the North Sea (NEEZ) and show that there have been repeated incidents of overfishing causing depletions of sandeel grounds, which have often been followed by long-term recruitment failure. Hence, local spawning stocks seem to be important for regular and high local recruitment, despite sandeel larvae being pelagic for 3-4 months. Our findings suggest that that active homing in pre-settled larvae and juveniles is the mechanism underlying return of sandeel to natal habitats.

Conclusion/significance: Subpopulations of sandeel appear to be demographically disconnected over relatively short distances. This forms the rationale for a novel management system for sandeel that was implemented in NEEZ in 2010: All major sandeel grounds are

split in two; sandeel grounds with sufficiently abundant spawning stocks will be open for fishing, but only one half each year (rotational).

Keywords: Sandeel, the North Sea, fishery management, connectivity, larval drift, homing

Introduction

Lesser sandeel (*Ammodytes marinus* Raitt, hereafter sandeel) is a small, highly abundant fish in the North Sea. Sandeel feed on plankton and thus form an important mid-trophic link between plankton production and a variety of top predators such as larger fish, sea mammals and sea birds [1,2,3]. Most of the time sandeel remain buried in the seabed where the proportion of fine silt and clay particles is low [4,5], and sandeel grounds are thus spread like a patchwork in the North Sea [6]. During winter sandeel hibernate in the sand. In spring sandeel, which are then very lean, start feeding on zooplankton again. They emerge from the seabed at dawn and form dense pelagic schools which are targeted by predators and trawlers. At dusk, sandeel return to their sandy habitat where they are protected from both predation and fishing. Around mid-summer ≥ 1 -year old sandeel has normally built up sufficient energy reserves to hibernate again [7], as reflected in the main fishing season lasting from April – June/July [8]. The majority of $\geq II$ -group sandeel [9] emerge for a short period from the sand to spawn around December-January [10]. The eggs are laid on the seabed where they remain until hatching around February-March [11]. Larvae are pelagic until around June [12]. In contrast to older sandeel, young-of-the-year (YOY) continue to feed until October-November in order to obtain sufficient energy to hibernate through the winter [13]. In some years there have been a substantial fishery of YOY sandeel in the second half of the year, in particular in the northern (>56.5 °N) part of the North Sea [14].

Tagging experiments have indicated that when released at distance from sandeel grounds, sandeel can travel at least 64 km [15]. Nevertheless, sandeel are considered to have high site fidelity after settlement [6]. It should be noted though that the empirical evidence for high site fidelity is limited and basically circumstantial [6].

The fishery for sandeel developed gradually from the early 1950s, and reached a plateau in the late 1970s of $\sim 800\,000$ t, with maximum annual landings of 1.2 million t. In 2003 landings dropped abruptly and have since then fluctuated between 177 000 t and 438 000 t [16].

Despite strong evidences of several distinct sub-stocks of sandeel in the North Sea [17], the International Council for the Exploration of the Sea (ICES) continued to present one advice of total allowable catch (TAC) until 2010 [18]. Furthermore, the TAC advice remained high also after the abrupt drop in landings in 2003, and 2007 was the only year in which the TAC advice by ICES limited landings [19]. Hence, the fishery was practically unrestricted until 2011, when ICES commenced treating sandeel in the North Sea as seven stock units [17].

An important question for managing spatially discrete populations is to determine to what extent subpopulations are demographically connected [20-22]. Leis [23] defined demographic connectivity as “the movement of individuals between populations in numbers large enough to be demographically significant”. He also pointed out that “significance” will depend upon the context, e.g. conservation objectives, yield etc. Here, we deal with “harvest connectivity” [24], i.e. connectivity that affects fishery yield and may have ecological consequences in terms of prey availability for predators of the various subpopulations. It is important to distinguish between genetic connectivity and demographic connectivity, where the former is defined as “the degree to which gene flow affects evolutionary processes within subpopulations” [24]. Relatively few immigrants may cause subpopulations to be genetically connected, but demographically disconnected because population dynamics are not affected [23].

No significant genetic structure in sandeel populations in the North Sea was found using the less sensitive method of starch gel electrophoresis of enzymes [25]. This may very well be true, at least between closely situated banks where the exchange of larvae is likely to occur [26,27]. With no genetic differentiation, only circumstantial evidence can be provided in order to disclose whether closely situated banks are demographically connected or not.

Based on historical landings in combination with satellite vessel tracking and acoustic survey data we show that the majority of sandeel grounds in NEEZ were depleted due to overfishing, which was then followed by relatively long periods of local recruitment failure. Hence, sandeel subpopulations appear to be demographically disconnected. This is the basis of a novel spatial management system that was implemented in NEEZ in 2010: All major sandeel grounds in NEEZ are split in two, and fishing grounds with sufficiently abundant sandeel stocks will be opened for fishing, but only one half each year (rotating). Here, we present the rationale for this novel management system, without going into details about the system. To our knowledge rotational spatial management has not been applied in large-scale finfish fisheries before. However, on the east coast of USA rotational harvesting of sedentary

scallops has been successfully applied [28], and kelp harvesting along the west coast of Norway is based on a 5-year rotational system [29].

Material and methods

Mapping of fishing grounds and sandeel areas

Satellite tracking data (VMS) providing vessel speed and position every 15 minute are available for the Norwegian sandeel fleet since 2001. As the sandeel fishing occur only during daytime, fishing activity maps were derived by excluding night-time observations and vessel speed ≥ 4 nm h⁻¹. In combination with trawl trajectory positions made available by the fishing vessel F/F Trål for the period 1996-2007, these maps were used to define the sandeel fishing grounds in Norwegian waters (Fig. 1).

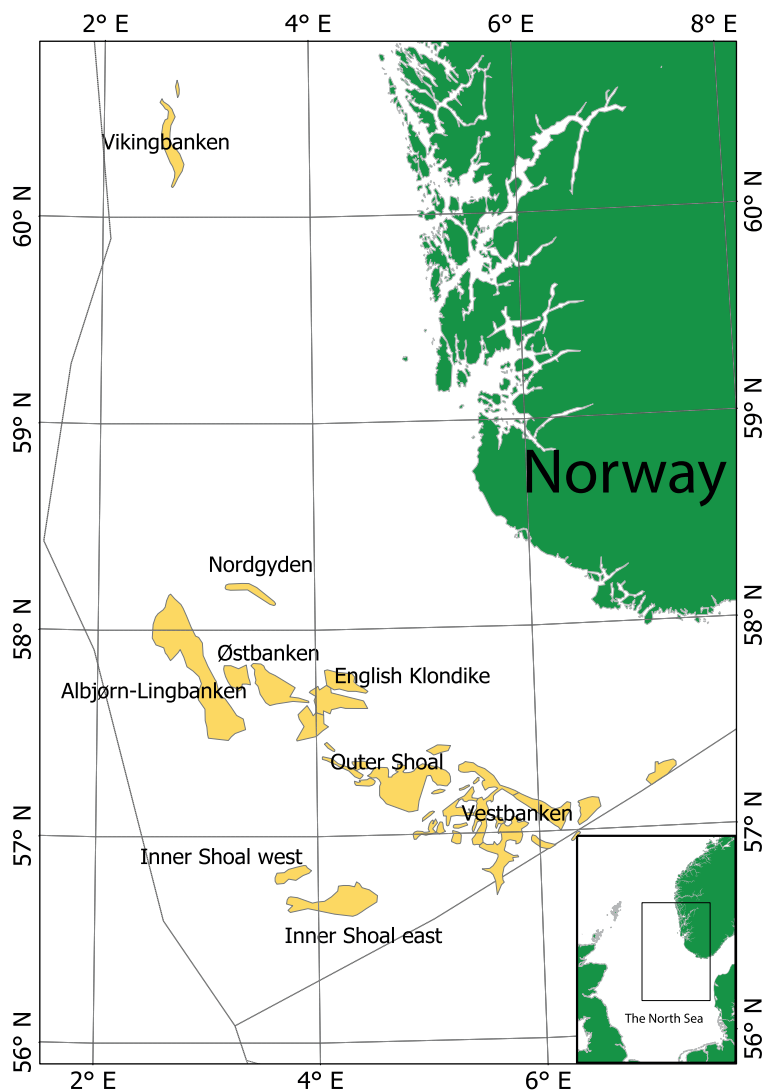


Fig. 1. Sandeel fishing grounds in NEEZ

Vestbanken consists of a conglomerate of fishing grounds, which are surrounded by relatively rough bottom that prevents fishing using sandeel trawls. Acoustic sandeel surveys

[30] have confirmed the occurrence of small spots with high densities of sandeel in these non-trawlable areas. There is no knowledge of similar natural refuges in the vicinity of the other sandeel grounds in NEEZ.

In order to illustrate fishing intensity during one fishing season, VMS data were used to reconstruct trawl trajectories (Fig. 2) at the fishing ground English Klondike in 2008 (Fig. 1).

Fishery data

A regular Norwegian sandeel fishery commenced developing from the early 1970s. However, the resolution and quality of the landing statistic have not been constant over the years. Between 1977 and 1993 Norwegian landings (Fig. 3) can be separated in a northern region ($>60^{\circ}\text{N}$, Vikingbanken; Fig. 1), a central-region (57.5° - 60°N ; Nordgyden, Albjørn-Lingbanken, Østbanken, English Klondike) and southern region ($<57.5^{\circ}\text{N}$; Outer Shoal, Vestbanken, Inner Shoal west and east).

From 1994 international landings (Fig. 4) are available per quarter of the year and statistical square (0.5° latitude by 1° longitude – $\sim 30 \times 30$ nautical miles; landings reported to ICES). Based on these data landings were allocated to fishing grounds in NEEZ for the period 1994-2008 (2008 is the last year in our study because there was a moratorium in NEEZ in 2009 and national spatial management was implemented in 2010).

Until 2005 there were practically no restrictions in the sandeel fishery in the North Sea and NEEZ. In more recent years Norwegian authorities have implemented restrictions in NEEZ independent of ICES advices. From 2005 the fishery has been closed in the second half of the year to protect YOY sandeel. In 2006 there was only a limited experimental fishery. From 2007 some fishing grounds have been closed, or open for experimental fishing only (see details in Fig. 4).

For stock assessment purposes, biological sampling of commercial landings has been carried out (more details in [31]). The sampling procedure has varied slightly over the years and before 1997 Norwegian sampling did not include ageing of sandeel. To identify year-classes before 1997 we converted length data into age 0-, I- and \geq II-group as there is normally limited overlap between these year-classes. It should be noted that a high level of precision of this conversion is not essential for this study.

Commercial depletion of sandeel grounds

Larger sandeel schools are readily identified using echo sounders [30]. Commercially

depleted sandeel grounds are thus defined as areas where the trawlers are unable to find fishable concentrations of sandeel using echo sounders. However, no landings from a sandeel ground do not necessarily imply that it is commercially depleted as the fleet may choose more attractive fishing grounds (high abundance, shorter distance, favourable bottom conditions). Therefore, we use three more conservative criteria in to identify commercially depleted sandeel grounds: 1) After years without landings, more than 90% of the landings consist of I-group sandeel (or YOY sandeel if evidence suggests re-depletion at that stage), 2) VMS data show that the fleet has visited a fishing ground several times without reporting landings (data available from 2001), and 3) no observation of fishable sandeel schools during the annual acoustic surveys (data available from 2005, see below). One of these criteria is considered sufficient for classify a fishing ground as commercially depleted.

Acoustic survey

Since 2005 annual acoustic surveys have been carried out between mid-April and mid-May in NEEZ to measure the abundance of \geq I-group sandeel [30]. In 2006 an additional survey was conducted between 27 July and 4 August, mainly to measure the abundance of 0-group sandeel. Here, these acoustic recordings were used to identify commercially depleted sandeel grounds, i.e. no sandeel schools were detected using conventional echo sounders. In addition, survey data were used to describe recruitment and age-structure at the various fishing grounds. During daytime sandeel in the water column were sampled using a demersal trawl, and during night-time buried individuals were sampled using a van Veen grab and a modified scallop dredge [32].

Statistical analyses of patterns in landings

The various fishing grounds have shown periods with several consecutive years with landings followed by several consecutive years without landings (Fig. 3 and Fig. 4). In order to test whether such patterns can be obtained by chance ($p \geq 0.05$), the significance probability was estimated as:

$$p(x \geq j) = \sum_{x=j}^m p(x) = \sum_{x=j}^m \frac{m * (m-1) * \dots * (m-x+1)}{n * (n-1) * \dots * (n-x+1)} \quad (1)$$

where j is the observed number of consecutive years “with” or ”without” landings , m is the total number of years “with” or “without” landings, and n ($=15$) is the total number of years in

the time series. The probability was estimated for each fishing ground and separately for consecutive years “with” and “without” landings. To avoid the influence of potential misreporting, all landings <2% of maximum landing reported from a fishing ground or below 1 kt were treated as zeros in these analyses.

As Vestbanken had no years “without” landings, Eq. 1 could not be used to estimate the probability for this bank. The number of years “with” and “without” landings combined for all years and fishing grounds were 68 and 67, respectively; i.e., the overall probability for both events was ~0.5. This was used to estimate the probability of obtaining 15 years with successive landings at Vestbanken ($p=1/2^{15}$).

Results

Depletion of a sandeel ground

In 2008 the fishery on English Klondike took place between 26 April and 13 May, only interrupted by a three-day moratorium (May 4-6). Historically, the main fishing activity has taken place on two parallel ridges (Fig. 1), but in 2008 fishing occurred only on the southern ridge (attempts to fish on the northern ridge is indicated in Fig. 2). The summarised trawl trajectories indicate high trawling activity during the 15 days of active fishing.

After 13 May 35 sandeel trawlers visited English Klondike (VMS data), but no landings were reported. In agreement with this, during the acoustic survey which covered English Klondike twice after 13 May, no fishable concentrations of sandeel were observed in the water column during daytime, nor did dredge stations conducted at night-time [see 32] reveal areas with high densities of sandeel in the bottom substrate. Furthermore, there was no evidence to suggest that the intensive fishing activity had “chased” sandeel away from English Klondike as no landings were reported from nearby fishing grounds (Outer Shoal, Østbanken and Albjørn-Lingbanken; Fig. 4), nor were fishable concentrations observed at these sandeel grounds during the 2008 acoustic survey. Hence, there is evidence to suggest that the sandeel stock on English Klondike was commercially depleted in 2008 after 15 days of intensive fishing.

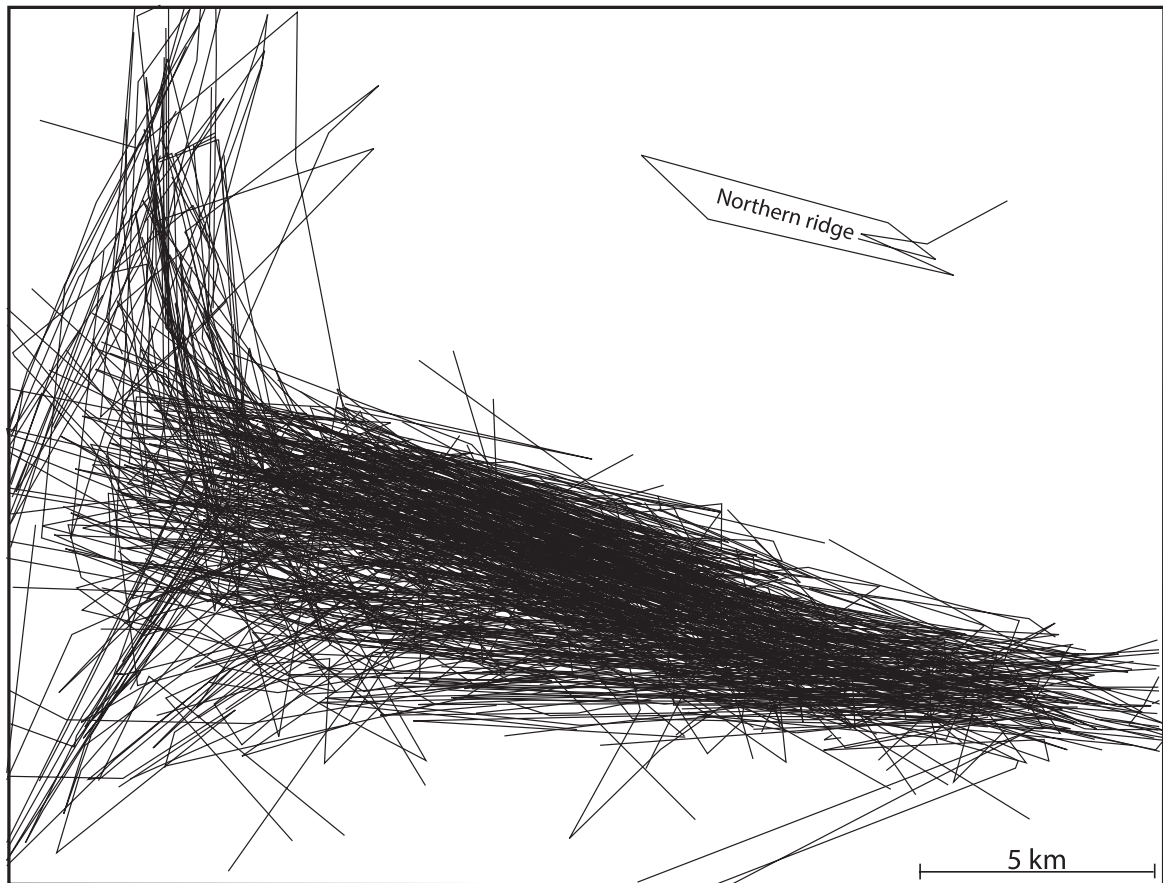


Fig 2. Trawl trajectories at English Klondike during 15 days of fishing in 2008. The line width corresponds to 75 m (the width of modern sandeel trawls).

Historical Norwegian landings

Most of the Norwegian landings were taken in the northern and central part of NEEZ around 1980 (Fig. 3). However, during the period 1982 and 1994 only sporadic landings were reported from the northern area (i.e., Vikingbanken). In 1995, the highest landings on records were taken in the northern area (Figs. 3 and 4), of which 98% were I-group thus suggesting the northern area was commercially depleted between 1982 and 1994. After three years of fishing (1995-1997) only small sporadic landings have been taken in the northern area.

The central area has shown consecutive years with relatively high landings and periods with low or no landings. Between 1980 and 1985 landings were low (Fig. 3). When increasing again in 1986 I-group dominated (97%), which suggests that the area was commercially depleted during the preceding period. Since, 1999 the landings have been very low in the central area, except for the intensive fishery on English Klondike in 2008 (Figs. 2 and 4).

Over the years the southern area has become increasingly important, and since 1999 almost all landings in NEEZ have been taken in this area (Fig. 3).

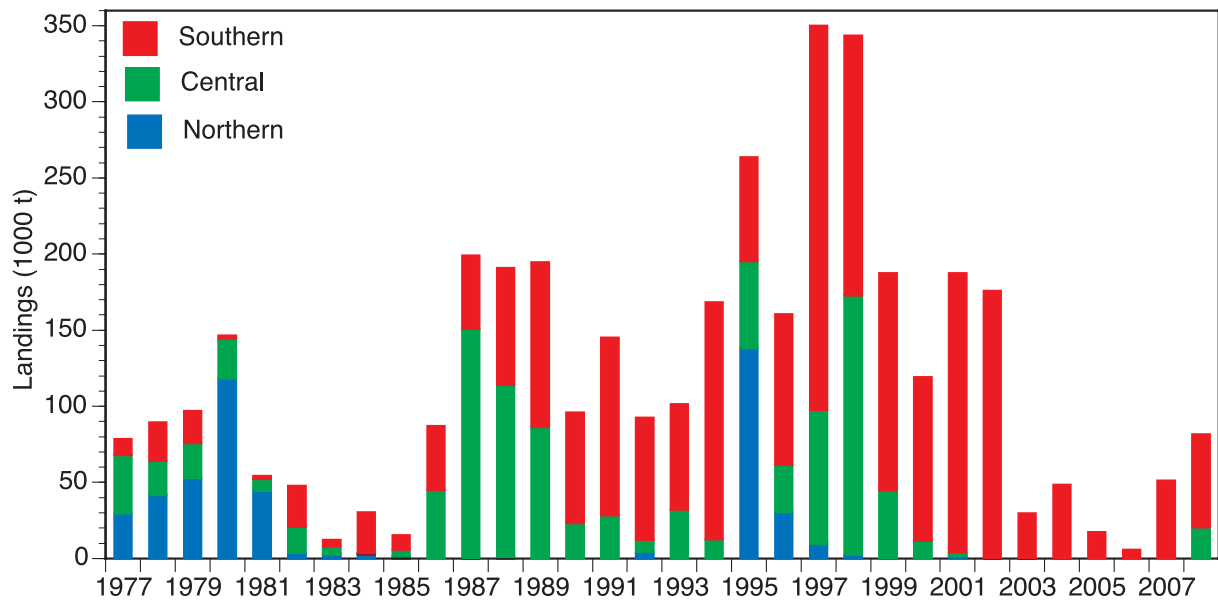


Fig. 3. Norwegian landings from the northern (>60°N), central (57.5°-60° N) and southern (<57.5° N) regions of NEEZ for the period 1977-2008.

International landing by fishing ground

With the higher geographical resolution of landings available from 1994 it is evident that landing patterns have varied between fishing ground (Fig. 4). All fishing grounds except Vestbanken have shown both consecutive years with and without landings, all of which were significantly non-random events (Table 1). In all instances fishing grounds with continues years without landings have been confirmed commercially depleted by at least two of the three criteria (Fig. 4). From 2002 onwards all sandeel ground in NEEZ except Vestbanken were commercially depleted for several years. There has been a pattern of commercial depletion been more pronounced in the northern fishing grounds ($\rho=-0.80$, $p=0.024$; Spearman rank correlation between number of years with landings and the ranked distance from south to north; e.g. Inner Shoal east is ranked as 1 and Vikingbanken as 9).

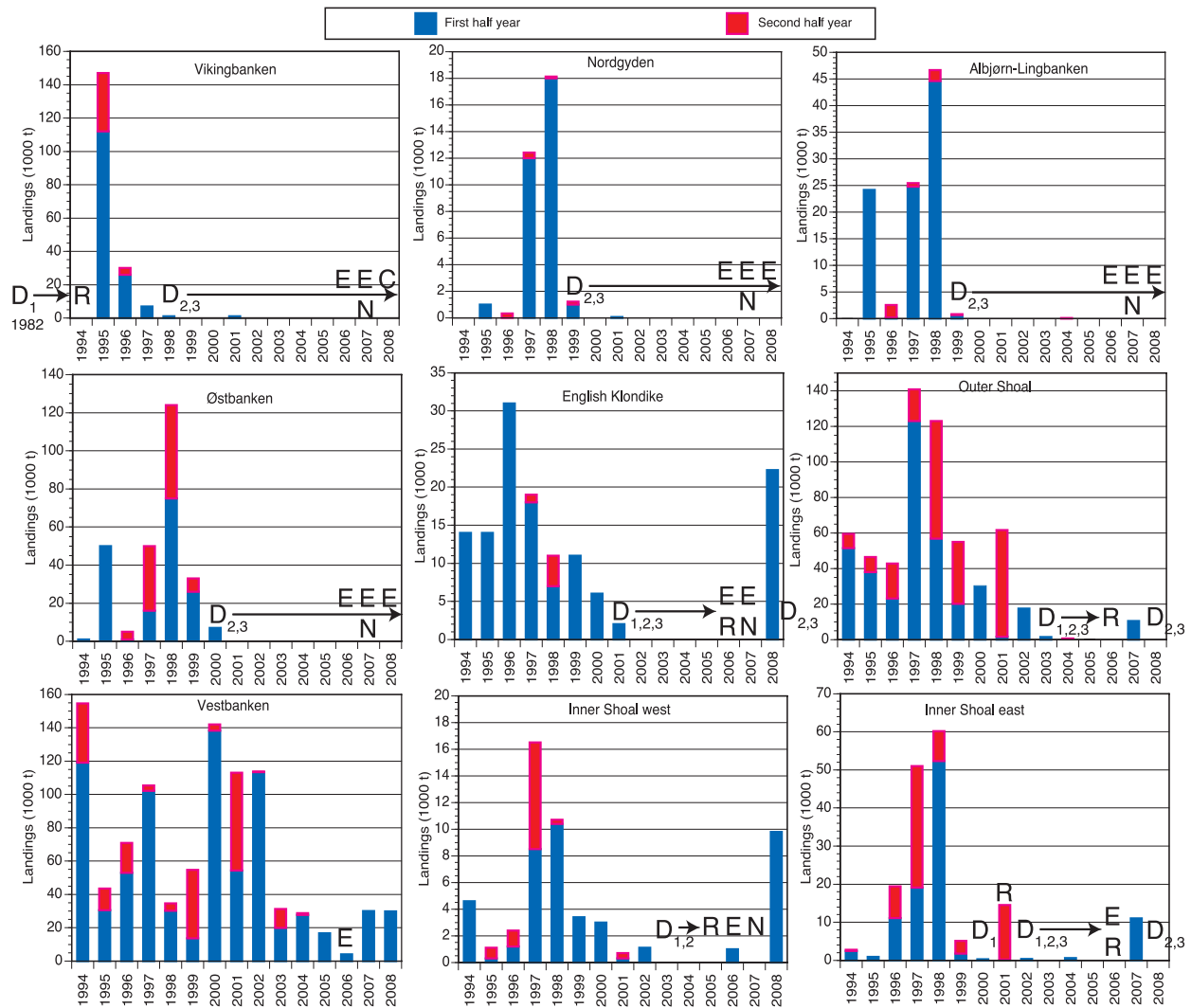


Fig. 4. International landings by fishing ground in NEEZ in the 1st (blue) and 2nd (red) half-year during the period 1994-2008. From 2005 onwards a moratorium was implemented in the second half of the year in NEEZ. E – experimental fishery only (i.e. low quotas), N – no visits by the fleet; C – closed fishery; R – new recruitment of 0-group sandeel, D – commercially depleted, confirmed by criteria indicated by subscripts: 1- >90% of landings consists of I-group (or 0-group), 2 – repeated visits by the fleet without landings, 3 - no observation of fishable sandeel schools during the acoustic sandeel surveys.

Table 1. Total number of years with landings (WL) and without landings (WOL), number of consecutive years without landings (CWL) and consecutive year without landings (CWOL), and the associated probabilities (pCWL and pCWOL). The sandeel grounds are organised from north the south in the table.

Fishing ground	WL	WOL	CWL	CWOL	pCWL	pCWOL
Vikingbanken	3	12	3	10	0.002	0.011
Nordgyden	4	11	3	9	0.01	0.015
Albjørn-Lingbanken	4	11	4	10	<0.001	0.004
Østbanken	6	9	6	8	<0.001	0.002
English Klondyke	9	6	8	6	0.002	<0.001
Outer Shoal	10	5	9	4	0.002	0.026
Vestbanken	15	0	15	0	<<0.001*	-
Inner Shoal west	10	5	7	3	0.028	0.026
Inner Shoal east	7	8	4	5	0.034	0.026

* $pCWL=1/(2^{**15})$, see methods

There are several incidents where commercially depleted sandeel grounds were re-colonized and then depleted again before the sandeel reached sexual maturity at the age of two. In the first half of 2001 landings were negligible at all fishing grounds except Vestbanken (Fig. 4). In the autumn an extensive fishery of 0-group (>99% of 144 kt) took place, but only on sandeel grounds in the southern area. Inner Shoal east was commercially depleted in 1999, but was recolonized in 2001. However, the 2001 year-class was depleted again at the 0-group stage at this bank. On Outer Shoal too the 2001-year class was mainly fished at the 0-group stage, before being finally depleted at the I-group stage in 2002 (91% I-group). In 2006 several of the commercially depleted southern sandeel grounds were recolonized by new recruitment (including English Klondike). However, at Outer Shoal and Inner Shoal east the 2006 year-class was depleted within one fishing season in 2007, and at English Klondike in 2008.

Vestbanken, which has natural refuges, is the only sandeel ground in NEEZ that has never been commercially depleted. At the outskirts of one of the fishing grounds on Vestbanken (close to a non-fishable area for sandeel trawls), on-target sampling of a sandeel school during the acoustic survey using trawl with rock-hopper gear (allows trawling on

rougher bottom) revealed up to 7-year old sandeels (Fig. 5). In contrast, I-group dominated the samples on the central part of the bank. This school must have avoided being captured during the intensive fishing pressure on Vestbanken for several years. Such old sandeels are hardly ever observed in commercial landings, but may be present at unexploited sandeel grounds [31]. Between 2003 and 2006, when all other sandeel grounds were commercially depleted in NEEZ, there was continuous recruitment at Vestbanken as reflected in the proportion of I-group in the landings varying from 39-88% (avg. 63%)

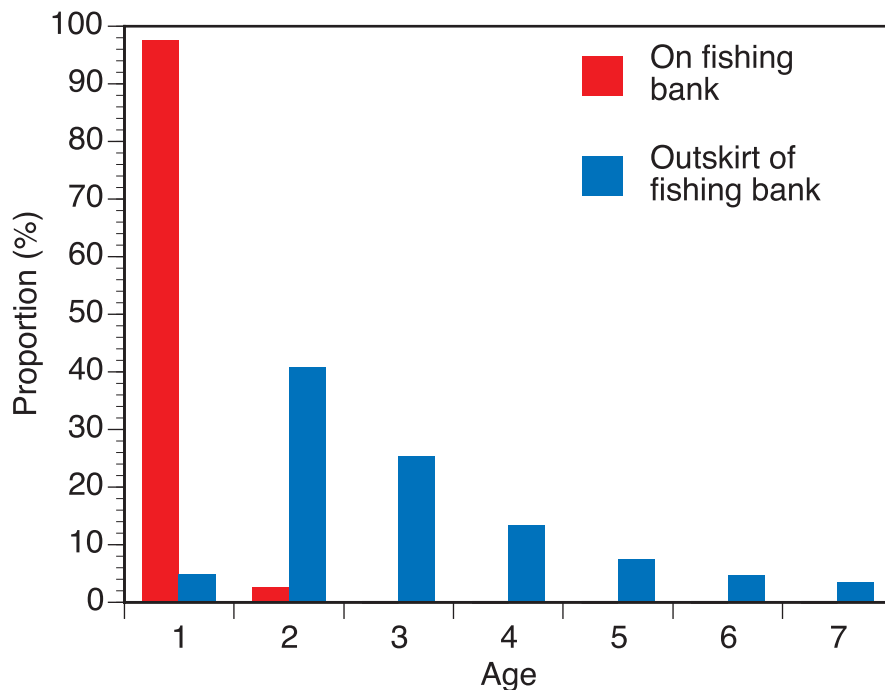


Fig. 5. Age composition of sandeel caught at Vestbanken in 2007, on the central part of a sandeel ground (red) and at the outskirts for the trawlable area (blue).

Discussion

Depletion of sandeel grounds

The sandeel fishery has developed substantially over the years with increasingly larger vessels, more powerful engines and larger trawls [33]. Further, more advanced echo sounders and sonars have made detection of sandeel schools easier. The navigational systems have also become better over the years, thus allow trawling on smaller sandeel grounds and closer to non-trawlable bottom substrate. Over the years new sandeel grounds have been discovered. Although the number of vessels has decreased, the fleet has become gradually more efficient and the fishing areas have expanded. After detecting a sandeel school, a vessel will often target the school repeatedly by hauling up the otter boards, turning around, deploying the trawl again and steer precisely towards the school using sonar and advanced navigational

systems. The potential for overfishing of sandeel has thus increased. In agreement with this, our study of the fishery in NEEZ have shown that in recent years the fleet has depleted sandeel grounds within one fishing season (Fig. 4), even at the 0-group and I-group stages before the sandeels have reached sexual maturity. However, evidence from Vikingbanken and the central area of NEEZ (Fig. 3) shows that the fleet had the capacity to deplete fishing grounds already in the early 1980s, possibly because there are few obstacles that hamper trawling in these areas. It has been long recognised that schooling fishes are particular vulnerable to overfishing because the fleet is able to maintain high efficiency as long as there are schools left [34,35].

In all known cases where commercially depleted sandeel grounds were recolonized in NEEZ, this occurred by new recruitment as reflected in landings being totally dominated by 0- or I-group. Hence, migration of older sandeel between sandeel grounds appears to be low or non-existing. High site fidelity in settled sandeel is in agreement with a study by Jensen *et al.* [6] and the general perception of sandeel behaviour (e.g. [26]).

Local stocks and recruitment

In a modelling study Berntsen *et al.* [36] found that sandeel larvae have the potential for long-distance advection, which is in line with a study by Proctor *et al.* [26] that predicted that the sandeel larvae in the Orkeney-Shetland area are advected away from for their natal banks. In another drift study Christensen *et al.* [27] predicted that sandeel larvae will be retained within 5 areas of the central and southern North Sea (Shetland and Vikingbanken were not included in their study), but pointed out that rare hydrographical events could advect larvae between areas with generally little connection. These three modelling studies, which all assumed that pre-settled pelagic sandeels are passive drifters, give theoretical support to long distance advection and thus could have explained re-colonization of the isolated Vikingbanken in the mid-1990s. However, they are in conflict with our findings, which show that all commercially depleted sandeel grounds in NEEZ suffered recruitment failure for several subsequent years (Fig. 4 and Table 1), whereas areas with local stocks of sandeel had markedly higher and regular recruitment. The importance of a local spawning stock for successful recruitment appears particularly evident for Vestbanken, which has never been commercially depleted as sandeel schools probably find protection in the untrawlable areas. The recruitment at Vestbanken was relatively strong also during periods when all nearby commercially depletes banks suffered from recruitment failure. Hence, advection of sandeel larvae even between the

closely situated banks in the southern area of NEEZ appears to be low, e.g. from Vestbanken to Outer Shoal or from Inner Shoal west to Inner Shoal east (Fig. 1).

Demographic connectivity and larval drift

There is obviously a great competitive advantage for larvae that can cope with moving water masses and therefore theoretically a selection pressure towards such abilities. Indeed, there is mounting evidence to suggest that many fish larvae do cope with moving water masses (reviewed by Leis [23]), either in terms of a return-based or retention strategy, or a strategy in which dispersal is important [37,38]. Behavioural studies have revealed that many fish larvae are capable of swimming at speeds faster than mean ambient currents [39], and endure over long periods thus travelling tenths of kilometres [40]. Further, vertical distribution is under strong behavioural control and can have substantial influence on dispersal trajectories or even result in larval retention [41].

In order to take advantage of their swimming capacities, fish larvae also need sensory abilities to navigate. Studies have shown that larvae of many fishes and invertebrates do have the necessary sensory organs and can detect gradients in water chemistry from biotic (e.g., amino acids) and abiotic sources (e.g., salinity), sound (e.g., breaking waves), visual stimuli (e.g., sunlight) and water pressure [23,42]. There is evidence to suggest that older fish can use the earth's magnetic field to navigate [43,44], and, although there are presently no studies to confirm such abilities in fish larvae [23], this raises the possibility that fish larvae also use magnetism as a navigational tool.

There are numerous studies that have revealed directional movement in larvae in both fish and invertebrates [23], including homing to natal habitats [45,46] and identification and swimming towards suitable habitats for settlement [47]. By vertical movement, larvae of estuarine crabs have been shown to undergo ebb-tide transport for migration out of estuaries for development offshore, whereas older post-larvae use flood-tide transport for movement up estuaries to nursery areas [38].

Just after hatching, most fish larvae are poorly developed and swim slowly in an energy costly, viscous environment (at such small scales water is like molasses), and can thus be regarded as plankton [23], i.e., close to passive drifters. The main hatching in sandeel in the North Sea occurs in February-March when the water is at the coldest with sea surface temperatures often below 5° C [48]. As the viscosity of water increases with decreasing temperatures [49], sandeel larvae are probably passive drifters for some time after hatching, and, as suggested by the three cited modelling studies, mainly advected away from their natal

banks. In agreement with this, a study of sandeel larvae in the North Sea indicated that the physical environment does have substantial influence on larval distribution in March [50]. However, sandeel larvae ≥ 20 mm TL show strong sampling gear avoidance [51] and are thus capable burst swimmers. The swimming ability probably improves substantially towards settlement (generally >55 mm TL [11]). As the smallest larvae are probably advected away from the spawning grounds, homing in post-larvae and juveniles appears as the mostly likely mechanism for their return to natal banks. There is evidence from the fishery to support this hypothesis. Occasionally, the trawlers catch high numbers of pre-settled juveniles, typically 5-7 cm TL, as observed in the landing samples (own unpublished data). This is not a gradually occurring phenomenon, but appears abruptly, thus indicating immigration of schooling juveniles onto the banks.

Although there is strong evidence to suggest that advection of sandeel larvae between sandeel grounds is limited, it cannot be excluded that re-colonisation of commercially depleted sandeel grounds could be a result of unusual hydrographical events advecting sandeel larvae from other sandeel grounds, as suggested by Christensen *et al.* [27]. On the other hand, none of the commercially depleted fishing grounds were biologically depleted. Using scientific echo sounders and advanced post-processing software as operated during the annual acoustic sandeel survey [30], small sandeel schools appearing as dots near the bottom were observed on all commercially depleted sandeel grounds. Hence, these small local stocks may under favourable conditions have given rise to re-colonisation. Strong year-classes from extremely small spawning stocks have been observed in other marine fishes, e.g. the Norwegian spring spawning herring (*Clupea harengus* L.) in 1983 [52]. The apparently strong homing tendency in sandeel supports the latter hypothesis.

In summary, as there seems to be little or no migration of settled sandeel between sandeel grounds and immigration during pelagic stage appears to be very low, sandeel in NEEZ are basically demographically disconnected and should be managed accordingly. Treating all sandeel ground in the central and southern part of NEEZ (and some part of the EU zone) as one stock, as ICES does [18], is not sufficiently detailed to prevent local depletions.

Spatial management of sandeel in NEEZ

Based on these arguments, a Norwegian sandeel management plan was developed with the main objective to rebuild the local spawning stocks on all historically important sandeel grounds, thus to improve the recruitment and yield potential, and provide predators with

adequate prey. Based on the major sandeel grounds six management areas have been defined in NEEZ (reduced to five areas in 2014). Each area is divided into two sub-areas (designed so that all major sandeel grounds are split in two). The sub-areas will be opened and closed alternately (year to year). If the spawning-stock in a particular area falls below a predefined limit (measured acoustically), both sub-areas will be closed. As most sandeel spawn at the age two, biannual rotation will, in addition to prevent local depletion, result in continuous presence of local spawning stocks.

Conclusion

In a comprehensive review of whether fish larvae are plankton or nekton, Leis [23] states: “We have a growing body of knowledge of the behavioural capabilities of larval fishes and of the potential influence these might have on dispersal. Much slower, however, is the growth of knowledge about the actual (as opposed to potential) influence these have.... Growth of the latter must accelerate if our understanding of dispersal is to avoid another potentially misleading path [like the classical perception that fish larvae are passive drifters]”. In this paper we have provided evidence to suggest that sandeels are not passive drifters during the entire pelagic stage, and that active homing prior to settlement (swimming or using currents) is the most likely mechanism for return to natal habitats. Hence, sandeel grounds seem to be demographically disconnected over relatively short distances. This forms the rationale for the novel rotational management system of sandeel in NEEZ. Rotational, spatial management is a system that may be generally applicable for fish stocks with low demographic connectivity between subpopulations, and which are vulnerable to local recruitment overfishing.

Acknowledgement

We are grateful for all the trawl track data provided by F/F Traal and all the important information provided from the fishery organization Sør-Norges Trålerlag. The Research Council of Norway is thanked for their financial contribution under contract 185065/S40,

References

1. Harwood J, Croxall JP. The assessment of competition between seals and commercial fisheries in the North Sea and the Antarctic. *Mar Mamm Sci.* 1988; 4: 13–33.
2. Greenstreet S, McMillan JA, Armstrong E. Seasonal variation in the importance of pelagic fish in the diet of piscivorous fish in the Moray Firth, NE Scotland: a response to variation in prey abundance? *ICES J Mar Sci.* 1998; 55: 121–133.
3. Wanless S, Harris MP, Redman P, Speakman JR. Low energy values of fish as a probable cause of a major seabird breeding failure in the North Sea. *Mar Ecol Prog Ser.* 2005; 294: 1–8.
4. Macer CT. Sand eels (*Ammodytidae*) in the southwestern North Sea; their biology and fishery. MAFF Fishery Invest Ser II. 1966; 24(6): 1–55
5. Wright P, Jensen H, Tuck I. The influence of sediment type on the distribution of the lesser sandeel, *Ammodytes marinus*. *J Sea Res.* 200; 44: 243–256.
6. Jensen H, Rindorf A, Wright PJ, Mosegaard H. Inferring the location and scale of mixing between habitat areas of lesser sandeel through information from the fishery. *ICES J Mar Sci.* 2011; 68: 43–51.
7. Winslade P. Behaviour studies on the lesser sandeel *Ammodytes marinus*. III. The effect of temperature on activity and the environmental control of the annual cycle of activity. *J Fish Biol.* 1974; 6: 587–599.
8. ICES. Report of the ICES Advisory Committee 2009. ICES Advice, 2009. Book 6.
9. Boulcott P, Wright PJ, Gibb FM, Jensen H, Gibb IM. Regional variation in maturation of sandeels in the North Sea. *ICES J Mar Sci.* 2007; 64: 369–376.
10. Bergstad OA, Høines ÅS, Krüger-Johnsen, EM. Spawning time, age and size at maturity, and fecundity of sandeel, *Ammodytes marinus*, in the north-eastern North Sea and in unfished coastal waters off Norway. *Aquat Living Resour.* 2001; 14: 293–301.
11. Wright PJ, Bailey MC. Timing of hatching in *Ammodytes marinus* from Shetland waters and its significance to early growth and survivorship. *Mar Biol.* 1996; 126: 143–152.
12. Lynam CP, Halliday NC, Hoffle H, Wright PJ, van Damme CJG, Edwards M, Pitois SG. Spatial patterns and trends in abundance of larval sandeels in the North Sea: 1950-2005. *ICES J Mar Sci.* 2013; 70: 540–553.
13. van Deurs M, Hartvig M, Steffensen JF. Critical threshold size for overwintering sandeels (*Ammodytes marinus*). *Mar Biol.* 2011; 58: 2755–2764.
14. ICES. Report of the ad hoc group on Sandeel – II. ICES CM 2009\ACOM: 51: 1-53.
15. Gauld JA. Movements of lesser sandeels (*Ammodytes marinus* Raitt) tagged in the northwestern North Sea. *J Cons Int Explor Mer.* 1990; 46: 229–231.

16. ICES. Report of the ICES Advisory Committee 2014. ICES Advice, 2014. Book 6.
17. Pedersen SA, Lewy P, Wright PJ. Assessments of the lesser sandeel (*Ammodytes marinus*) in the North Sea based on revised stock divisions. Fish Res. 1999; 41: 221–241.
18. ICES. Report of the ICES Advisory Committee 2011. ICES Advice, 2011. Book 6.
19. ICES. Report of the ICES Advisory Committee 2010. ICES Advice, 2010. Book 6.
20. Cowen RK, Lwiza KM, Sponaugle S, Paris CB, Olson DB. Connectivity of marine populations: open or closed? Science. 2000; 287: 857–859.
21. Sterner T. Unobserved diversity, depletion and . The importance of subpopulations for management of cod stocks. Ecol Econ. 2007; 61: 566–574.
22. Reiss H, Hoarau G, Dickey-Collas M, Wolff WJ. Genetic population structure of marine fish: mismatch between biological and fisheries management units. Fish Fish. 2009; 10: 361–395.
23. Leis JM. Are larvae of demersal fishes plankton or nekton? Adv Mar Biol. 2006; 51: 57–141.
24. Lowe WH, Allendorf FW. What can genetics tell us about population connectivity? Mol Ecol. 2010; 19: 3038–3051.
25. Nævdal G, Thorkildsen S. Genetic studies on species composition and population structure of sand eels (Genera : *Ammodytes*, *Hyperoplus* and *Gymnammodytes*) in Norwegian waters. J Appl Ichthyol. 2002; 18: 124–126.
26. Proctor R, Wright PJ, Everitt A. (1998) Modelling the transport of larval sandeels on the north-west European shelf. Fish Oceanogr. 1998; 7:347–354.
27. Christensen A, Jensen H, Mosegaard H, St John M, Schrum C. (2008) Sandeel (*Ammodytes marinus*) larval transport patterns in the North Sea from an individual-based hydrodynamic egg and larval model. Can J Fish Aquat Sci. 2008; 65: 1498–1511.
28. Hart DR, Rago PJ. Long-term dynamics of US *Atlantic* sea scallop *Placopecten magellanicus* populations. N Am J Fish Manage. 2006; 26: 490–501.
29. Veà J, Ask E. Creating a sustainable commercial harvest of *Laminaria hyperborea*, in Norway. J Appl Phycol. 2011; 23: 489–494.
30. Johnsen E, Pedersen R, Ona E. Size-dependent frequency response of sandeel schools. ICES J Mar Sci. 2009; 66: 1100–1105.
31. Bergstad OA, Høines ÅS, Jørgensen T. Growth of sandeel, *Ammodytes marinus*, in the northern North Sea and Norwegian coastal waters. Fish Res. 2002; 56: 9–23.

32. Johnsen E, Harbitz A. Small-scale spatial structuring of burrowed sandeels and the catching properties of the dredge. *ICES J Mar Sci.* 2013; 70: 379–386.
33. ICES Report of the benchmark workshop on sandeel (WKSAN). ICES CM 2010/ACOM:57: 1-194.
34. Pope JG. Some consequences for fisheries management of aspects of the behaviour of pelagic fish. *Rapp PV Reun Cons Int Explor Mer.* 1980; 177: 466-476.
35. Ulltang Ø. Factors affecting the reaction of pelagic fish stocks to exploitation and requiring a new approach. *Rapp PV Reun Cons Int Explor Mer.* 1980; 177: 489-504.
36. Berntsen J, Skagen DW, Svendsen E. Modelling the transport of particles in the North Sea with reference to sandeel larvae. *Fish Oceanogr.* 1994; 3: 81–91.
37. Armsworth PR, James MK, Bode L. When to press on or turn back: Dispersal strategies for reef fish larvae. *Am Nat.* 2001; 157: 434–450.
38. Forward RB, Tankersley RA. Selective tidal-stream transport of marine animals. *Oceanogr Mar Biol.* 2001; 39: 305–353.
39. Fisher R, Leis JM, Clark DL, Wilson SK. Critical swimming speeds of late-stage coral reef fish larvae: variation within species, among species and between locations. *Mar Biol.* 2005; 147: 1201–1212.
40. Stobutzki IC, Bellwood D.R. Sustained swimming abilities of the late pelagic stages of coral reef fishes. *Mar Ecol Prog Ser.* 1997; 149: 35–41.
41. Sponaugle S, Cowen RK, Shanks A, Morgan SG, Leis JM, Pineda JS et al. Predicting self-recruitment in marine populations: Biophysical correlates and mechanisms. *Bull Mar Sci.* 2002; 70: 341–375.
42. Kingsford MJ, Leis JM, Shanks A, Lindeman KC, Morgan SG, Pineda J. Sensory environments, larval abilities and local self-recruitment. *Bull Mar Sci.* 2002; 70: 309–340.
43. Quinn TP, Brannon EL. The use of celestial and magnetic cues by orienting sockeye salmon smolts. *J Comp Physiol A.* 1982; 147: 547–552.
44. Durif C.F, Browman HI, Phillips JB, Skiftesvik AB, Vøllestad LA, Stockhausen HH. Magnetic compass orientation in the European eel. *PLoS ONE.* 2013 15 Mar; 8(3).
45. Jones GP, Planes S, Thorrold SR. Coral reef fish larvae settle close to home. *Curr Biol.* 2005; 15: 1314–1318.
46. Gerlach G, Atema J, Kingsford MJ, Black KP, Miller-Sims V. Smelling home can prevent dispersal of reef fish larvae. *Proc Natl Acad Sci USA.* 2007; 104: 858–863.
47. Montgomery JC, Jeffs A, Simpson SD, Meekan M, Tindle C. Sound as an orientation cue for the pelagic larvae of reef fishes and decapod crustaceans. *Adv Mar Biol.* 2006; 51: 143–196.

48. Johannessen T. From an Antagonistic to a Synergistic Predator Prey Perspective: Bifurcations in Marine Ecosystems. London: Elsevier; 2014.
49. Hunt von Herbing I. Effects of temperature on larval fish swimming performance: the importance of physics to physiology. *J Fish Biol.* 2002; 61: 865–876.
50. Munk P, Wright PJ, Pihl NJ. Distribution of the early larval stages of cod, plaice and lesser sandeel across haline fronts in the North Sea. *Estuar Coast Shelf Sci*, 2002; 55: 139–149.
51. Jensen H, Wright PJ, Munk P. Vertical distribution of pre-settled sandeel (*Ammodytes marinus*) in the North Sea in relation to size and environmental variables. *ICES J Mar Sci.* 2003; 60: 1342–1351.
52. Toresen R, Østvedt O.J. Variation in abundance of Norwegian spring-spawning herring (*Clupea harengus*, Clupeidae) throughout the 20th century and the influence of climatic fluctuations. *Fish Fish.* 2000; 1: 231–256.