



Patterns of extirpation. II. The role of connectivity in the decline and recovery of elasmobranch populations in the German Bight as inferred from survey data

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ABSTRACT: Abundance trends and distribution patterns from 1902 to 1932 for 7 elasmobranch species in the German Bight (eastern central North Sea) were analyzed and compared to survey trends for 1991 to 2009. Abundances of thornback ray *Raja clavata*, common skate *Dipturus batis*, smoothhound *Mustelus* spp., tope shark *Galeorhinus galeus*, and spiny dogfish *Squalus acanthias* declined and common skate was extirpated, while abundances of starry ray *Amblyraja radiata* and lesser spotted dogfish *Scyliorhinus canicula* increased. A meta-population approach was developed to analyze connectivity in terms of the surrogate parameter \hat{C} representing donor population N_j , separation distance $D_{i,j}$, and migration range parameter α . As populations declined, connectivity between sub-populations was lost before resident populations finally collapsed. The loss of connectivity was caused by both a loss of sub-populations and a subsequent increase in the distance separating the remaining sub-populations. For lesser spotted dogfish, an increase in the donor population fostered the establishment of a local sub-population after 2000. For starry rays, an apparent increase in N_j due to a concentration of the donor population near the study area increased connectivity with the local sub-population. The interpretation of local abundances in terms of meta-population dynamics demonstrates the importance of seasonally resolved survey information for conservation planning.

KEY WORDS: Meta-population models · North Sea · Fish diversity · Historic time series

INTRODUCTION

Parameters of longevity, body size, and fecundity/maturity receive the most attention when life-history traits in elasmobranchs are considered, and body size appears to be a suitable proxy to summarize life-history traits, which in turn reflect the vulnerability of elasmobranchs to fishing (Jennings et al. 1998, Dulvy et al. 2000, Rogers & Ellis 2000, Stevens et al. 2000, Frisk et al. 2001, García et al. 2008). As a further aspect of life-history traits, the role of dispersal capabilities of sub-populations and as a corollary, connectivity, between occupied habitats has only begun to be understood in practice (see Fagan et al.

2001, Metcalfe 2006). Connectivity is an important parameter to explain persistence of meta-populations within migratory networks (Taylor & Hall 2011) and thus changes in local abundance (Simpfendorfer et al. 2002). As a prerequisite to connectivity between patches, habitat quality within patches must be sufficient to maintain sub-populations (Hodgson et al. 2009). Decreasing habitat quality due to human impacts, an overall decrease of available habitat, and thus weakened connectivity between suitable patches of habitats are considered to interact when populations are driven towards extirpation (Hodgson et al. 2009). Accordingly, habitat characteristics and exchange processes are important parameters to sup-

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port conservation planning (Botsford et al. 2003, Palumbi 2003).

The simplest meta-population model, Levin's patch occupancy model describing colonization and extinction processes with presence/absence data (in Hanski & Gilpin 1991), is well applied to discrete habitats such as treeholes and their amphibian fauna (Etienne et al. 2004). Connectivity is established through a flow of specimens between all patches unconfined by spatial structure and habitat quality, and extinction and immigration are the main processes that maintain a meta-population. Apart from these 'classical' meta-populations, in fisheries biology a concept with a stronger emphasis on local population dynamics is required, which is not dependent only on immigration and extinction rates and which covers a wider range of spatial scales (Kritzer & Sale 2004). Hence, a hierarchical system of meso-populations nested into a meta-population may be envisaged (Kritzer & Sale 2004), with a complex scheme of possible source-sink relationships based, among other factors, on migration behavior and dispersal (Lipcius et al. 2008). Dispersal takes place at the larval stage in terms of population connectivity (Cowen et al. 2007, Bradbury et al. 2008, Cowen & Sponaugle 2009) or at the adult stage on a seasonal or multi-annual scale (known as migratory connectivity) (Webster et al. 2002). Migratory connectivity is strongly directional and links essential habitats during the life cycle. Long-range migratory connectivity is known for several shark species (spiny dogfish: Templeman 1984, McFarlane & King 2003; whale shark: Sequeira et al. 2013), whereas less vagile species such as skates undertake shorter migrations, resulting in accordingly higher inter-population differences in genetic structure (Chevolot et al. 2006, Veríssimo et al. 2010). As a more realistic tool, incidence function models incorporate quality, size/abundance, and spatial structure of habitats, i.e. distance between patches, and with these extensions, Levin's meta-population model is also applicable to migratory species (Taylor & Hall 2011).

Several elasmobranch species have become extirpated in the southeastern North Sea (Wolff 2000), and elasmobranch distribution in the North Sea has changed considerably. Comparisons between historical compilations (Rijnsdorp et al. 1996, Rogers & Ellis 2000, Fock et al. 2014) and present North Sea survey data (Walker & Heessen 1996, Ellis et al. 2004, Daan et al. 2005) reveal a now conspicuous east-west gradient with elasmobranch aggregations concentrated along the east coast of England and Scotland. Available fishery-independent data indicate a severe decline of elasmobranch populations in the southern

North Sea from the early 1900s to the present, while commercial catch indicators reveal declines already starting in the late 1880s (Lundbeck 1962, Fock et al. 2014), and bycatch and mortality analyses (Philippart 1998, Piet et al. 2009) show a consistently high pressure on elasmobranch populations in the North Sea up until the present day.

In marine ecosystems, connectivity modeling as a key parameter of meta-population dynamics was often hindered through a lack of empirical data (Cowen et al. 2007). We hypothesize that field data can be used to track changes in spatial connectivity and that this can be linked to declines and increases in local populations. We refer to the rationale developed by Dulvy & Reynolds (2002) that the loss history of species reflects population dynamics in the field, that seasonal dynamics may be understood as an annual cycle of immigration and emigration in meta-populations (Buckley 2010), and that external replenishment of a local population may be interpreted as part of meta-population processes (Kritzer & Sale 2004). On the meta-population level, effects on connectivity appear as losses of the distributional ranges of species (Worm & Tittensor 2011) and population diversity (Cardinale et al. 2011). Experimental evidence exists (Dai et al. 2013) that the loss of spatial connectivity serves as a prerequisite for the subsequent collapse of sub-populations. Thus, trend analyses are supported by analyses of distribution and of species diversity, and the analyses of seasonal differences are applied to infer meta-population processes related to extirpations and local recoveries.

MATERIALS AND METHODS

Sampling and study area

Fisheries survey data from 3 historical periods (1902–1908, 1919–1923, and 1930–32) were available with a total of 457 hauls for Quarters 2 and 3 of the year (Fock et al. 2014). Hauls for Quarters 1 and 4 were less abundant and were missing in 1903–1905, 1921, and 1930–1932 ($n = 111$). Historical samples encompass samples from the German Bight proper and the German Exclusive Economic Zone except for the first period, when samples from the Dogger Bank area farther west were also available (See Fig. S1 in Supplement 1 at www.int-res.com/articles/suppl/n025p209_supp.pdf). The methodology for calculating historical time series and standardizing historical and International Bottom Trawl Survey (IBTS) time series data is given in Fock et al. (2014). Data were not sep-

arated between day ($n = 407$) and night catches ($n = 50$) in Quarters 2 and 3 samples for diversity analysis. For abundance time series, only daytime catches were considered.

Historical data were compared to Quarter 1 data from 1966 to 2009 and Quarter 3 ICES IBTS data from 1991 to 2009, respectively (see Rijnsdorp et al. 1996) from rectangles representing the German Bight and the coastal zone (Fig. S1). Seasonal differences were analyzed for historical samples from Quarters 2 and 3 as compared to IBTS Quarter 3 data, whereas samples from Quarters 1 and 4 were compared to IBTS Quarter 1 series.

Spatial distribution

Historic spatial distributions were calculated using all samples from a selected period (Ellis et al. 2004, see Daan et al. 2005), applying universal kriging to account for non-stationarity in data. Distributions were calculated for the periods 1902–1908 and 1930–1932 to reveal changes from the earliest period with limited fishing effort and about 17% of untrawled ground to the period after which commercial fisheries had increased considerably (Fock 2014a). In the area under investigation, utilization of poorer-quality habitat under increased fishing pressure was evidenced for thornback ray (Fock 2014b this issue).

Diversity

A resampling method was applied to derive a diversity index based on presence/absence data unbiased from sample coverage (for coverage see Table S1 in Supplement 1 at www.int-res.com/articles/suppl/n025p209_supp.pdf). Years with fewer than 10 samples were excluded (1902, 1905, 1906); for all other years, 200 bootstrap subsamples (each consisting of 9 samples) were drawn, which is approximately half the number of samples in years of low sampling effort (e.g. 1903). The mean number of elasmobranch species per sample was calculated as well as the cumulative number of elasmobranch species in the 9-sample pool. The cumulative number of elasmobranch species is comparable to the diversity index of Daan et al. (2005), with the difference that the cumulative number is aggregated over space to account for a temporal trend, whereas Daan et al. (2005) aggregated samples over time to account for differences in space. Prior to the calculation of diversity, each species' presence was corrected for trawl duration to ad-

just for the likelihood of encounter using a rarefaction method (Fock et al. 2014) (see Supplement 4 at www.int-res.com/articles/suppl/n025p209_supp.pdf).

Incidence function model

We considered all elasmobranch populations to be meta-populations, the individuals encountered in the German Bight representing a sub-population of one of these meta-populations. An incidence function model was applied to analyze connectivity between sub-populations, relating successful colonization events to patch size or abundance (given that area A is proportional to abundance N), distance to donor patches, and immigration and extinction rates (Hanski et al. 1996, Hanski 1998).

In meta-population dynamics, 'straying' individuals in search of unoccupied patches are essential to broaden the range of a population, and immigration to unoccupied patches increases with overall meta-population abundance, referred to as the 'mass' effect to enhance sub-population persistence (Hanski 1998, Smedbol & Wroblewski 2002, Leibold et al. 2004). Density-dependent modification of migration and extinction rates, known as the 'rescue' effect to reduce or the 'Allee' effect to increase extinction probabilities, requires a specific parameterization which is not accounted for (e.g. Hanski & Gilpin 1991, see 'Discussion'). Immigration for a single specimen is determined by migration rate m_0 and distance D between sites (Hanski 1991):

$$m = m_0 e^{-\alpha D} \quad (1)$$

where parameter α equals the inverse of the migration range (Hanski 1998).

Consider sub-populations in patches i with $i = 1, 2, 3, \dots$, and the meta-population $N = N_i + \sum_{j \neq i} N_j$. Connectivity C_i to patch i is understood as the sum of migrations from patch j to patch i across distance D_{ij} weighted by the donor population N_j (after Hanski 1998):

$$C_i = m_0 \sum_{j \neq i} \sum_{D=D_{i,j} \text{ to } \infty} e^{-\alpha D} N_j \quad (2)$$

Connectivity (Eq. 2) is described analogous to extinction probability, where temporal differences in observations are considered instead of spatial distances (Solow 2005, his Eq. 16, McPherson & Myers 2009). The incidence J or probability π of patch i to be colonized in relation to C_i is (Hanski 1998):

$$\pi_i = 1 - \frac{E}{M} = \frac{1}{1 + \left(\frac{Y}{C_i}\right)^2} \quad (3)$$

where E and M are annual extinction and migration processes. The shape of the probability function p_i (Eq. 3) depends on regression parameter γ . This term can be rearranged as the product of $\gamma \times m_0^{-1}$ (i.e. proportional to the inverse of m_0), and p_i increases both with m_0 and \hat{C} (see Fig. S2 in Supplement 2 at www.int-res.com/articles/suppl/n025p209_supp.pdf).

To qualitatively assess connectivity for a single species, it is convenient to rearrange C_i so that changes in connectivity can be analyzed without knowledge of m_0 , which is constant at the species level:

$$C_i = m_0 \hat{C}_i \tag{4}$$

\hat{C} depends on migration range and neighbor patch abundance (Eq. 2). Assuming that migratory connectivity takes place as sequential events (see Taylor & Hall 2011), the nearest neighbor N_j can be described as a multiple of N_{ir} , i.e. as a ratio of seasonal differences in abundance at patch i , given that migration in either direction is proportional to patch abundance:

$$\hat{C} \propto N_j \propto \frac{N_{im} - N_{ir} + \Delta N_{ir}}{\Delta N_{ir}} N_{ir} \tag{5}$$

where N_{ir} is the resident, i.e. smaller remaining population in patch i and N_{im} is the larger population after seasonal migration has taken place, given that ΣN_j comprises several patches similar to N_i (Fig. 1). N_{ir} exchanges portion ΔN_{ir} with the meta-population and receives $\Delta N_{ir} + (N_{im} - N_{ir})$ from the surrounding patches N_j . The quantity ΔN_{ir} remains unknown and therefore \hat{C} can only be assessed as a proxy. Assuming that the entire resident population migrates, N_j is the ratio of seasonal abundances multiplied by the resident term. We applied the more conservative proxy $(N_{im} - N_{ir}) / N_{ir}$. Connectivity from patch j towards patch i is lost, i.e. becomes negative, when the seasonal value of the resident population is larger than the abundance after (potential) immigration has taken place. The maximum negative value is -1 .

A second case is considered when the resident population is 0 (= patch unoccupied at certain times of the year), and connectivity is solely dependent on the donor patch, so that \hat{C} proxy is defined as:

$$\hat{C}_i \stackrel{\text{def}}{=} 1 \text{ for } N_{ir} = 0, N_{im} > 0 \tag{6}$$

Considering the case for several species k , long-term average conditions for \hat{C} proxy should reflect differences in migration rate $m_{0,k}$ and migration range R_k . The rationale is that in a closed system where no new N_j can emerge, and due to averaging in a long enough time series over all realizations of N_i and N_j and all possible distances between N_i and N_j (Eq. 5), these terms appear as constants for all species k .

Hence the average for \hat{C} proxy increases with migration range R with $\alpha = 1/R$ and m_0 (see Eq. 2):

$$\bar{C}_k \propto m_{0,k} e^{\frac{1}{R}} \tag{7a}$$

Assuming a relationship between m_0 and R , replacing m_0 with R and $1/R$ with x , approximating the denominator $x e^x$ by Taylor expansion, considering the expansion term for $n = 0$:

$$\bar{C}_k \propto \frac{1}{\sum \frac{x^{n+1}}{n!}} \propto R_k \tag{7b}$$

Analysis of trends

Differences in seasonal trends, i.e. \hat{C} proxy, are analyzed by linear tools with regard to their intersection on the time axis, i.e. first or last occurrence, and slope parameters, whereas after substituting Eq. (3) into Eq. (4), \hat{C} is modeled as:

$$\hat{C}_i = \frac{1}{\sqrt{\frac{1}{\pi_i} - 1}} \gamma m_0^{-1} + \epsilon \tag{8}$$

where π_i is treated as a function of elapsed time assuming that probabilities are a function of time

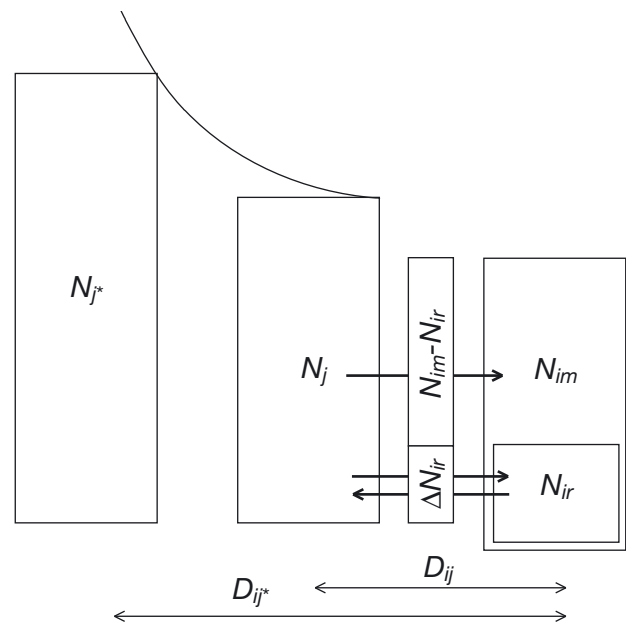


Fig. 1. Seasonal model of immigration and emigration for a local population N_i , its resident part N_{ir} , and the portion with increased abundance after seasonal migration has taken place (N_{im}), in relation to the donor population N_j . A much larger donor population N_{j^*} at a larger distance D_{ij^*} or a smaller donor population N_j separated by distance D_{ij} yield the same seasonal migration effect at N_i . The non-linear increase of N_j with distance is indicated by the connecting curve between N_j and N_{j^*} .

according to external pressures such as fisheries (e.g. thornback ray *Raja clavata*, see Fock 2014b). Additionally, the error term ε may contain a linear trend. Outlier sensitive regression and non-linear regression are applied (procedures ROBUSTREG and NLIN, SAS Institute 2010).

RESULTS

Abundance and distribution

Four shark species and 3 skate species were encountered in the German Bight in trawl surveys. Due to their rarity, smoothhound *Mustelus* spp. were not considered further (Table 1), since only 5 specimens determined as *M. mustelus* were indicated in 1907, and this species was often mistaken in historical data (Daan et al. 2005). Summer presence of lesser spotted dogfish *Scyliorhinus canicula* was only observed in the recent period 2001–2009, whereas all other species were frequently observed in 1902–1932 and 1991–2009 (Fig. 2).

Abundance has declined sharply for all species considered except for lesser spotted dogfish and starry ray *Amblyraja radiata* (Fig. 2). Before 1930, the largest summer abundances were found for spiny dogfish *Squalus acanthias* and tope shark *Galeorhinus galeus*. Abundances of both sharks declined sharply in the period 1930–1932, and both were present in the periods after 1991, with spiny dogfish abundance declining almost to 0 after 2001 and a similarly rigorous decline observed for tope sharks. Summer abundance of thornback rays increased slightly after 1919 to drop significantly towards 1932. During 1919–1932, thornback rays were the most common elasmobranch species in the area, whereas only 4 specimens were encountered after 1991. While common skates *Dipturus batis* disappeared, starry rays increased significantly in the period 1991–2009. A first increase was observed in 1930–1932, when the second and third highest historical values were recorded. In all 3 years with high summer abundance of starry rays, thornback ray abundance was low.

With regard to distribution patterns in the period 1902–1908 (Fig. 3), thornback rays (Fock 2014b), spiny dogfish, and tope sharks (see Fig. S3 in Supplement 3 at www.int-res.com/articles/suppl/n025p209_supp.pdf) were distributed in the entire German Bight, although a gradient towards the eastern and northeastern areas is evident. Peak abundance was modeled for coastal waters. For 1902–1908, abun-

dance over the Dogger Bank was only indicated in the northern section, in particular for thornback rays and spiny dogfish. Only local presence remained for spiny dogfish in 1930–1932. One area of abundance was located in deeper waters in the central German Bight, while the other patch was found to be in association with coastal waters in the eastern part of the German Bight. The same decline in range with only a remaining eastern patch was observed for thornback rays. In turn, a patchy distribution for common skates was found in both historical periods and appeared to be spatially stable, i.e. 1 central patch, 1 northern patch, and 1 patch around the island of Helgoland in conjunction with coastal waters. In 1902–1908, starry rays were distributed along the northern edge of the investigation area. In 1930–1932, only 1 tope shark specimen was recorded.

Historic diversity trends

The observed decline in abundance was paralleled by a decline in diversity (Fig. 4). Whereas the average number of species per haul showed a slight increase in 1919, the cumulative number of species in 9 hauls declined almost steadily from 1902 to 1932. By 1932, the average number had dropped to 0.5 per haul and the cumulative number to <2 per 9 hauls. For the IBTS Quarter 1 data series after 1977, cumulative diversity in the study area dropped further to about 0.5 species encountered per 20 hauls (Daan et al. 2005).

Connectivity

In the period 1902–1932, the seasonal pattern for spiny dogfish and tope sharks featured high summer abundances and almost 0 abundances in Quarters 1 and 4 (Table 2). For tope sharks, this pattern persisted in the period 1991–2009, although at lower summer abundance levels. In turn, all skates and lesser spotted dogfish and spiny dogfish showed higher winter time abundances, the latter 2 species for the period after 1991. Average \hat{C} proxy, which is assumed to be proportional to migration range (Eq. 7), ranged from low values of 0.3 (spiny dogfish, 1991–2000) to 0.6 (common skate, 1902–1932), indicating a moderate migration range, to 1.2 to 1.5 (starry ray, lesser spotted dogfish) and 5.2 to 6.3 (thornback ray). Highest values of >40 were found for tope sharks and spiny dogfish, for the latter in the early period only. Rates for average \hat{C} proxy for

Table 1. Life history parameters and habitat preferences of select elasmobranchs. If not otherwise mentioned, all entries are according to García et al. (2008). L_{max} is the maximum size reported in the literature or that observed in 1902–1932, L_{mat} and A_{mat} are length and age at maturity, respectively, $F_{extinct}$ is maximum sustainable fishing mortality. For reproductive mode, O: oviparity, V: viviparity, n: miles; nautical miles

| Family | Species | Biogeographic affiliation / distribution | Migration range, mobility (n miles) | Habitat | Reproductive mode | Vertical habitat classification | Litter size (n) | L_{max} (cm) ^a | L_{max} 1902–1932 (cm) | L_{mat} (cm) | A_{mat} (yr) | $F_{extinct}$ |
|----------------|--|--|---|-----------------------------------|-------------------|----------------------------------|---------------------------------|-----------------------------|--------------------------|---------------------------------------|----------------------|-------------------|
| Rajidae | Starry ray <i>Amblyraja radiata</i> | Boreal ^b | Limited range, 20–100 ^c | Shelf | O | Benthic ⁱ | 31 | 69 ^d | 41–52 | 36–38 ^l to 50 ^d | 5 ^m | 0.73 ^p |
| Rajidae | Common skate <i>Dipturus batis</i> | Temperate–boreal ^b | Limited range, 1–50 ^e | Shelf | O | Benthic ⁱ | 48 | 235 | 47–199 | 140 ^d | 11 | 0.38 ^p |
| Rajidae | Thornback ray <i>Raja clavata</i> | Widespread – Lusitanian ^{b,f} | Inshore–offshore migrations, 100–150 ^{e,g} | Shelf, shallow water ^f | O | Benthic ⁱ | 142 | 109 ^d | 77–113 | 70 ^h –74 ^l | 6.2 ^h –10 | 0.52 ^p |
| Scyliorhinidae | Lesser spotted dogfish <i>Scyliorhinus canicula</i> | Widespread – Lusitanian | Limited range, 20–50 ⁿ | Shelf | O | Benthic ⁱ | 45.5 | 71 | | 57 | 7.6 | 0.49 |
| Squalidae | Spiny dogfish <i>Squalus acanthias</i> | Widespread – temperate antitropical ^l | Extended migrations, 200–1000 ^o | Shelf | V | Near–bottom pelagic ⁱ | 8 (interbirth interval 2 yr) | 110 | 57–102 | 78.5 | 12.5 | 0.15 |
| Triakidae | Tope shark <i>Galeorhinus galeus</i> | Widespread – Lusitanian ^b | Extended migrations, 500–1500 ^k | Shelf | V | Near–bottom ⁱ | 24.9 (interbirth interval 3 yr) | 164.5 | 46–125 | 131 | 12.6 | 0.21 |

^aThe von Bertalanffy growth function parameter L_{∞} is dependent on sample size; L_{max} as an observed maximum size is preferable (Dulvy et al. 2000)
^bStehmann & Bürkel (1989)
^cWalker et al. (1997)
^dWalker & Heessen (1996)
^eScottish Sea Angling Conservation Network (2012), also cited in OSPAR background document for the conservation of the common skate, and Wearmouth & Sims (2009)
^fLundbeck (1937)
^gHunter et al. (2005), stock description in ICES (2002)
^hGallagher et al. (2005)
ⁱFollowing the classification scheme of Fock et al. (2002) augmented through data in ICES (2004) from a comparison of catchabilities between 8 m beam trawl and grande ouverture verticale (GOV) otter trawl net opening
^jVerissimo et al. (2010)
^kNot considering extreme migrations, data from Holden & Horrod (1979)
^lMcCully et al. (2012)
^mFrisk et al. (2005)
ⁿRodriguez-Cabello et al. (1998)
^oNot considering transoceanic migrations, data from Templeman (1984), McMillan & Morse (1999), McFarlane & King (2003), stock description in ICES (2002), but differing in ICES (2007)
^pWalker & Hislop (1998)

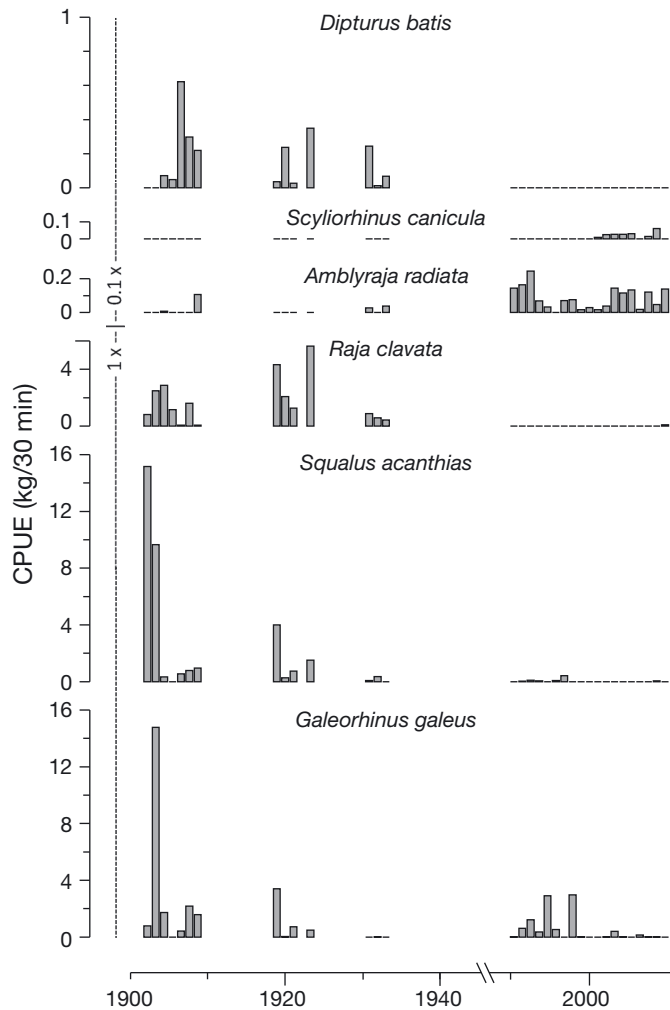


Fig. 2. Summer survey trends for elasmobranch species in the German Bight. Change in y-axis scaling indicated. CPUE: catch per unit effort. Periods sampled: 1902–1908, 1919–1921, 1923, 1930–1932 and 1991–2009

thornback and starry rays in both periods were very similar despite highly different abundances, and rates for small sharks at relatively low average abundances (<0.1 specimens per 30 min) were similar to those of skates. For spiny dogfish, the rate declined with abundance, and the seasonal pattern changed accordingly from high abundances in summer in the early period to relatively high abundances during winter after 1991. The similarity in ratios between skates and small sharks at low abundances probably indicates that the migration tendency for small sharks has a density-dependent component in relation to schooling behavior (see Viscido et al. 2004), since schooling and/or aggregation may hinder free and unconstrained selection of sites, a prerequisite for populating empty patches. Overall, the long-term

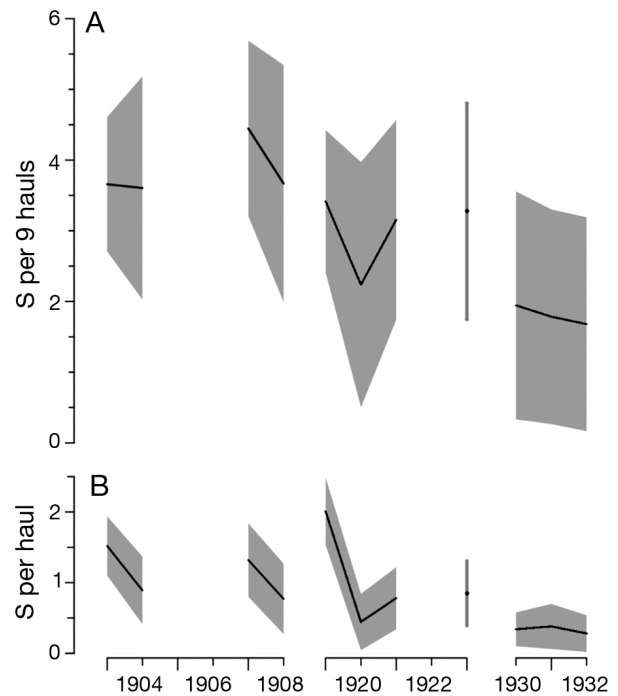


Fig. 3. Elasmobranch diversity trends in the German Bight 1902–1932. (A) Cumulative number of species (S) per 9 hauls, (B) average number of species per 30 min haul. Means (black lines) and 95% CI (gray areas) are indicated

averages for \hat{C} proxy are correlated with reported migration ranges in accordance with Eq. (7b) (correlation $p < 0.001$ considering mean ranges, see Fig. 5).

Considering connectivity and \hat{C} proxy in terms of seasonal dynamics as differences of abundance between resident populations and immigrating components (Eq. 5) shows a clear pattern of declining and increasing local populations (Table 3, Fig. 6). In particular, \hat{C} can be analyzed when connectivity is lost or reversed. Decreasing \hat{C} from patch j to patch i can be linked to either increasing distance between subpopulations and/or decreasing abundances in the donor patches. The lower limit for \hat{C} proxy is -1 , when no seasonal migration towards patch i is observed. It appears that for declining populations, \hat{C} proxy was declining and the modeled trend became negative (Fig. 6C2,D2), whereas for increasing populations, \hat{C} proxy appeared fairly constant (Fig. 6A2) or was increasing (Fig. 6B2), and modeled trends were positive. With regards to common skate (not shown), spiny dogfish and thornback ray, the decline in \hat{C} proxy was reflected by a more rapid decline in wintertime abundance (dashed linear trend line in Fig. 6C1,D1) as compared to summer abundance (bold trend line). Differences in slopes between summer and wintertime trends were signif-

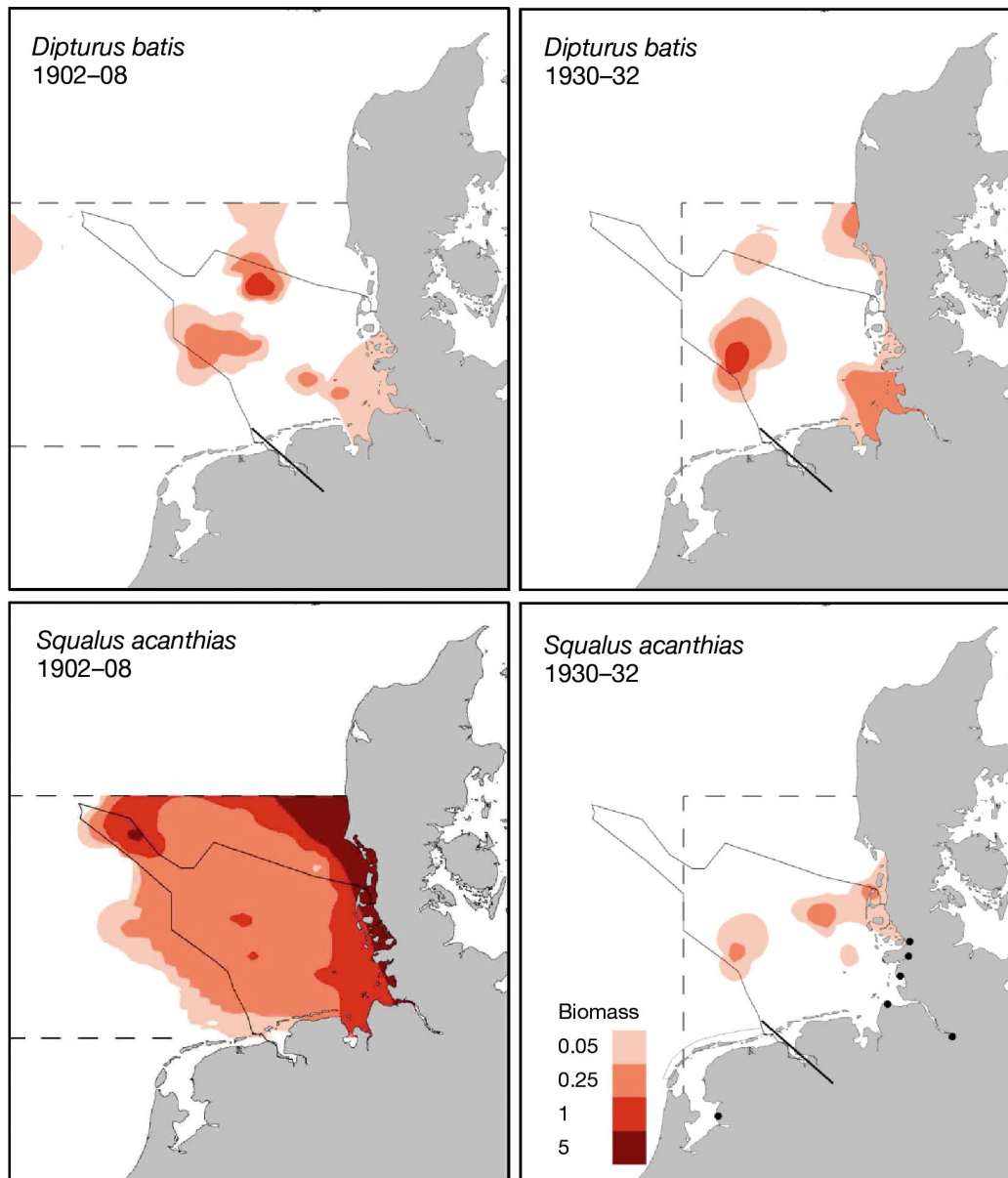


Fig. 4. Historical distribution patterns of common skates *Dipturus batis* and spiny dogfish *Squalus acanthias*. Biomass contours in kg per 30 min trawling (survey catch per unit effort). Left panels cover the period 1902–1908 including the Dogger Bank area, right panels cover the period 1930–1932. Due to low abundances of these species in particular after 2000, no data are shown for the period 1991–2009

ificant for thornback rays and spiny dogfish, but the models for these 2 species in general are of poor fit. The intersection with the time axis (x -axis) indicates that abundance during the migrating phase becomes 0, and that all species are apparently migrating out of the area. This can be interpreted such that connectivity to donor patches by means of negative \hat{C} proxy was lost prior to the collapse of the resident sub-population itself. However, despite significant differences in slopes, differences in the intersection with

the time axis are not significantly different (see Fig. 6C1 as indicated by CIs for both regressions). The opposite is observed for increasing populations. Connectivity by means of \hat{C} proxy increases, and slopes for the migrating stage are steeper than in the resident stage (Fig. 6A,B). In line with the interpretation of the case of population decrease, connectivity is established before the site is effectively populated. There is a further effect related to population density. For starry rays and common skates in the period

Table 2. Long-term average \hat{C} values. Mean abundances are given as n per 30 min. Ratio is winter to summer relationship, except where indicated

| Species | Period | Mean abundance | | Ratio |
|------------------------------|-----------|----------------|--------|-------------------|
| | | Summer | Winter | |
| <i>Amblyraja radiata</i> | 1902–1932 | 0.018 | 0.04 | 1.2 |
| | 1991–2009 | 0.30 | 0.76 | 1.5 |
| <i>Dipturus batis</i> | 1902–1932 | 0.05 | 0.08 | 0.6 |
| | 1991–2009 | 0 | 0 | 0 |
| <i>Raja clavata</i> | 1902–1932 | 0.53 | 3.29 | 5.2 |
| | 1991–2009 | 0.003 | 0.022 | 6.3 |
| <i>Scyliorhinus canicula</i> | 1902–1932 | 0 | 0 | 0 |
| | 1991–2009 | 0.04 | 0.095 | 1.4 |
| <i>Squalus acanthias</i> | 1902–1932 | 0.33 | 0.008 | 40.2 ^a |
| | 1991–2000 | 0.055 | 0.072 | 0.3 |
| <i>Galeorhinus galeus</i> | 1902–1932 | 0.3 | 0 | ∞ ^a |
| | 1991–2009 | 0.134 | 0.001 | 133 ^a |

^aSummer:winter ratio; spiny dogfish migrations are mainly temperature driven (McMillan & Morse 1999)

1902–1932, and lesser spotted dogfish after 1991, wintertime abundances were often smaller than summer abundances or 0, indicating that emigration took place turning \hat{C} proxy into negative values. In turn, when species were abundant (thornback rays in the period 1902–1932, starry rays after 1991), \hat{C} proxy was mainly positive, either declining (thornback ray) or increasing (starry ray).

DISCUSSION

Trends in local elasmobranch abundances and elasmobranch diversity in the German Bight were analyzed in terms of meta-population dynamics,

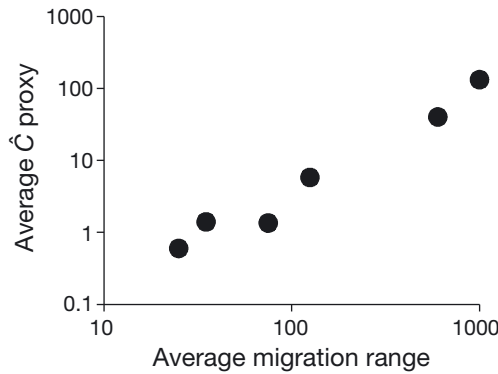


Fig. 5. Interpretation of the relationship between average connectivity (\hat{C} proxy) and mean migration range (nautical miles) according to data from Tables 1 & 2

i.e. as connectivity, by means of a proxy based on seasonal dynamics derived from an incidence function model (IFM) with the aim to understand extirpation and recovery. The applicability of the meta-population approach is scale dependent with regard to the dispersal capabilities of the species and the size relationship between the local sub-population and the regional meta-population (Hanski & Gilpin 1991, Kritzer & Sale 2004). Elasmobranchs exhibit distinctive spatial behavior. Spatial behavior is a prerequisite for the design of spatial models and is evidenced for elasmobranchs either in terms of migratory connectivity (McFarlane & King 2003, Sequeira et al. 2013), aggregation on feeding grounds (Domeier &

Table 3. Analysis of seasonal dynamics assigned to the resident (N_{ir}) and migrating part (N_{im}) of the local population N_i . See Fig. 5 for data used in regressions. Slope parameters also show model significance (*p = 0.95, ***= 0.999); periods of observation are 1991–2009 or 1902–1932

| Species | Part of population modeled | Model fit (r^2) | Intersection on x-axis $y_{N_{ir}}$ $y_{N_{im}}(\text{year})$ | Difference in occurrence (yr) $\Delta yr = y_{N_{ir}} - y_{N_{im}}$ | Slope parameter | Year of first observation in periods | Year of last observation in periods |
|------------------------------|----------------------------|---------------------|---|--|-----------------|--------------------------------------|-------------------------------------|
| <i>Amblyraja radiata</i> | N_{im} | 0.37 | 1899 | | 0.00699*** | 1906 | |
| | N_{ir} | 0.55 | 1924 | 25 | 0.00222 | 1902 | |
| <i>Scyliorhinus canicula</i> | N_{im} | 0.24 ^a | 1983 | | 0.0056*** | 1991 | |
| | N_{ir} | 0.16 | 1989 | 6 | 0.0022 | 2001 | |
| <i>Squalus acanthias</i> | N_{im} | 0.03 ^a | 2004 | | -0.00465*** | | 2002 |
| | N_{ir} | 0.04 ^a | 2007 | 3 | -0.00255 | | 2008 |
| <i>Raja clavata</i> | N_{im} | 0.06 ^a | 1927 | | -0.2214* | | 1923 |
| | N_{ir} | 0.07 ^a | >2000 | >50 | -0.00114 | | 1932 |

^aModels with higher tolerance to outliers

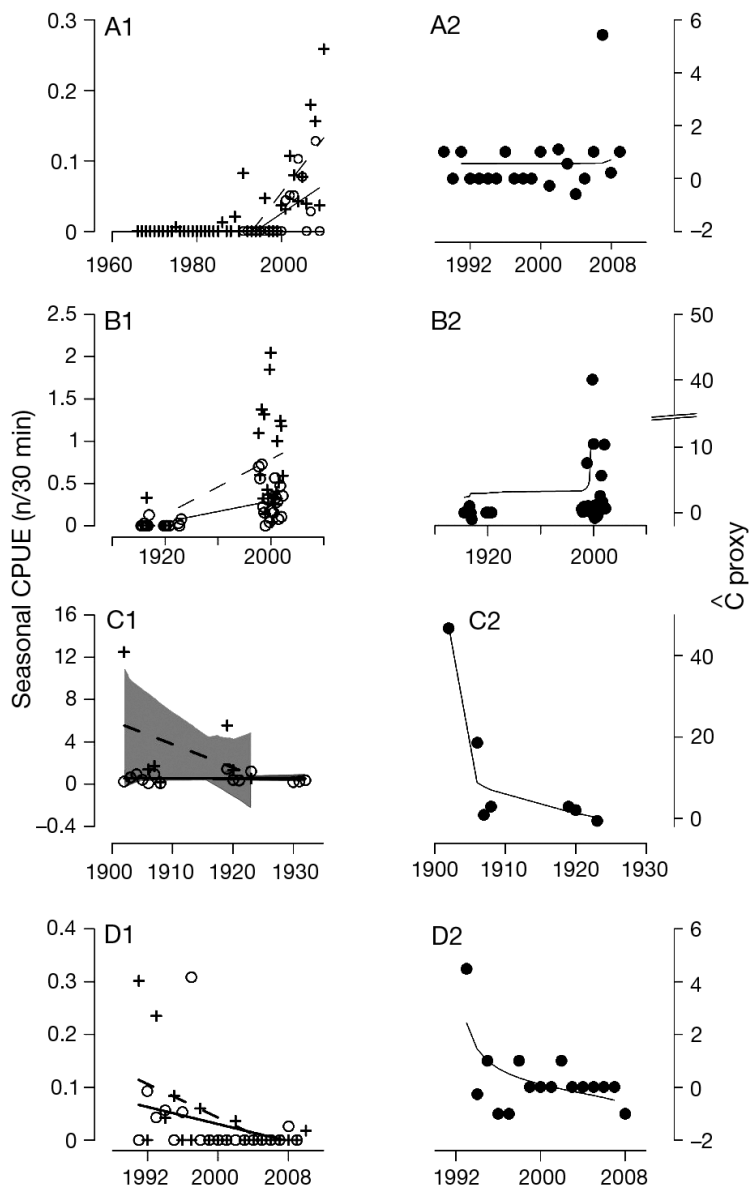


Fig. 6. Analysis of connectivity for (A) lesser spotted dogfish *Scyliorhinus canicula*, (B) starry ray *Amblyraja radiata*, (C) thornback ray *Raja clavata*, (D) spiny dogfish *Squalus acanthias*. Left panels: trends in seasonal abundances (circles, bold line: summer; crosses, dashed line: winter), right panels: connectivity parameter \hat{C} proxy and modeled trend according to Eq. (8). CPUE: catch per unit effort

Nasby-Lucas 2008), in marine reserves and over reefs (Man et al. 1995, Robbins et al. 2006), or in nurseries (Garla et al. 2006, Franks 2007). In turn, sharks in particular show a range of variability in terms of migration and dispersal (Benson et al. 2001, and references therein), and features such as strong site fidelity to mating grounds (white shark: Jorgensen et al. 2010; stingray: Le Port et al. 2012) would infringe on exchange processes between sub-populations

and thus limit the applicability of the meta-population approach. The low migration range of common skates has also been reported in terms of site fidelity (Wearmouth & Sims 2009), and this species likely indicates the transition between species with migratory connectivity and those with high site fidelity (see average \hat{C} proxy in Table 2). Strong site fidelity refers to the case of 'closed populations' according to Kritzer & Sale (2004) with almost no inter-population exchange. On the other hand, meta-population dynamics also do not apply to populations with large migration ranges and high migration rates, for which tope sharks may be the linking species between species with high migratory connectivity and species with extraordinary migration capabilities. In the latter case, overall 'mixing' overrules local population dynamics, reducing the capabilities of the IFM to predict connectivity (see Kritzer & Sale 2004).

The home range of fish species increases with body size (Kramer & Chapman 1999) or planktonic larval duration (PLD, Bradbury et al. 2008). PLD does not apply to elasmobranch species with an oviparous or viviparous mode of reproduction (see Table 1). Taking into account the strong correlation between migration range and average \hat{C} , the body size rule applies fairly well to lesser spotted dogfish, spiny dogfish, and tope sharks. In turn, for the 3 skates, it is likely that their benthic living mode makes them an exception to the rule (see Table 1).

Applying linear methods to the analysis of seasonal trend components may be regarded as tentative, but appears appropriate for the purpose of detecting patterns. In fact, model fits for 2 species with declining population trends, i.e. spiny dogfish and thornback rays, were not good (Table 2), probably indicating stochastic influences that are not accounted for. As mentioned earlier, the 'rescue' effect was incorporated into Levin's model in terms of a quadratic term that penalizes the extinction parameter with increasing probability of patches being occupied (Hanski & Gilpin 1991). In turn, it could be possible that depensating effects at low densities also need to be considered, i.e. Allee effects (thornback ray: Whittamore & McCarthy 2005; cod:

Swain & Chouinard 2008). However, IFMs according to Eq. (2) neither account for the rescue effect at high nor the Allee effect at low densities (Etienne et al. 2004), which could in part explain the poor model fit for the above-mentioned species. \hat{C} proxy is definitely non-linear (see Fig. 6A2,B2,C2,D2), and similarly, sighting records have been modeled for declining populations (Solow 2005, McPherson & Myers 2009).

For thornback rays, declines were linked to fishing pressure (Wolff 2000, Fock 2014b). Declines in abundance were also associated with reductions in spatial distributions which apply to common skates, thornback rays, and spiny dogfish in the period 1902–1932, coinciding with a significant decline in elasmobranch species diversity (Fig. 3). Likewise, for lesser spotted dogfish, increases were linked to range extensions, since this species was not encountered in the period until 1932 but after 1990. Because \hat{C} proxy for lesser spotted dogfish has been relatively stable since 1991 with 1 exceptionally high value (Fig. 6A2), the increase in range took place before 1991.

The interpretation of connectivity depends on the correct understanding of immigration and emigration, which in turn is confined by the availability of data in terms of summer and winter surveys. It also depends on the time period analyzed. With the exception of starry rays, processes were either analyzed in the historic period or in the period after 1990. The increase in starry rays as indicated over both periods is in line with the interpretation of their trend in the North Sea, where this species benefited from the decline in thornback rays in terms of competitive release (Stevens et al. 2000). Besides consistent changes in \hat{C} across the 4 species investigated in detail, a consistent pattern appeared for slopes, in that slopes assigned to migrating components either increased faster with increasing resident populations or decreased more steeply for decreasing resident populations. The effect of selection of the time period analyzed can be shown for lesser spotted dogfish: the slope of the migrating population would be smaller than that of the resident population if the entire period of the IBTS Quarter 1 survey were considered (see Fig. 6A1), but then slopes for the migrating and resident populations would not be fully comparable.

Migration aspects have been widely ignored in conservation planning for migratory species, and migration parameters should be treated as key life-history traits (Small-Lorenz et al. 2013). The relationship between migration range (see Table 1) and the long-term average of the connectivity parameter in the meta-population model enables us to consider as-

pects of migration in line with life-history traits to analyze local dynamics in terms of migration effects between inhabited patches in an area. Warm-water, i.e. Lusitanian, species such as lesser spotted dogfish and thornback rays have the potential to cope with climate-change-induced warming of the southern North Sea. Starry rays and spiny dogfish exhibit a widely boreal and temperate distribution pattern and penetrate well into subarctic waters (Fock 2008, H. Fock unpubl. data). Thus, environmental warming could dampen the prospect for boreal species in the southern North Sea and German Bight and could be responsible for the overall stagnant trend in starry rays for the North Sea (ICES 2012), even if fishing pressure could be reduced significantly. Species' vulnerability to fishing pressure is mainly compensated through earlier maturation rather than through changes in fertility (Frisk et al. 2005). In this respect, starry rays with their small size at maturity and early age at maturity have an advantage over thornback rays (Table 1). However, if fishing pressure could be reduced, fecundity in terms of litter size and Lusitanian affiliation would offer thornback rays an opportunity to recover. Wolff (2000) stressed that over-exploitation was the main driver for extirpations of lesser spotted dogfish, thornback rays, common skates, and smoothhound *Mustelus* spp. in the southeastern North Sea up until 2000. The recovery of lesser spotted dogfish after 2000 despite a lack of fisheries management shows that these extirpations due to overexploitation should be reversible with appropriate management (Lotze et al. 2005).

Connectivity was analyzed in terms of the surrogate parameter \hat{C} for which approximations were developed for intra-annual as well as inter- and long-term dynamics derived from IFMs. IFMs appear robust in the analysis of connectivity relationships, even for highly fragmented habitats with explicit consideration of local (N_i) and source (N_j) populations and considering their separating distance D_{ij} (Moilanen & Nieminen 2002). The application of \hat{C} was due to constraints of sampling design, mainly in the historical period, and circumvents complications from different concepts of connectivity either including donor and recipient patch sizes (Hanski & Ovaskainen 2000) or only donor patch sizes as shown here (Eq. 2) (Etienne et al. 2004). Average values for \hat{C} (Table 2) were apparently stable between the early period and 1991–2009 for starry and thornback rays and are interpreted as being proportional to migration range; differing conditions for small sharks were suggested to be a density-dependent effect in relation to schooling. This could indicate that schooling

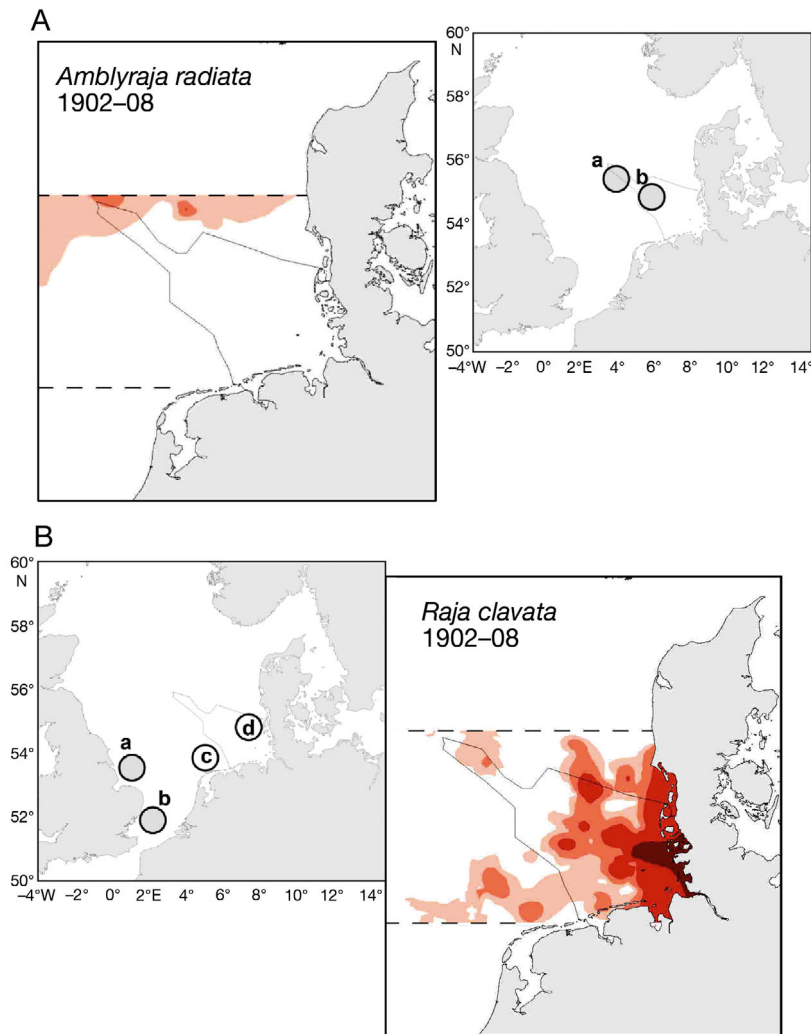


Fig 7. Distribution in 1902–1908 for (A) starry ray *Amblyraja radiata* and (B) thornback ray *Raja clavata*, and the corresponding interpretation of population patches in the southern North Sea and German Bight for both species. a, b: existing patches; c, d: patches known from historical distributions. Biomass contour levels as in Fig. 4

behavior generates a positive feedback loop in migrations between successfully occupied patches. With regard to \hat{C} , extirpations were associated with a decline in \hat{C} and vice versa. These observations may be interpreted as changes of \hat{C} in relation to the distance parameter $D_{i,j}$ and donor patch size N_j : (1) Prior to an extirpation (common skates, spiny dogfish, thornback rays), connectivity is lost before resident populations collapse. This was evidenced by steeper slope parameters and earlier intersections with the time axis (Table 3). This loss of connectivity can be due to a collapse in adjacent donor patches and accordingly increased distances D . For thornback rays, a collapse of the early donor patch off the Dutch coast (Fig. 7B, patch c) as evidenced by ICES (2002)

resulted in an increase in D from about 150 nautical miles (n miles) to about 300 n miles from the patches off the English east coast (Fig. 7B, patches a and b). Accordingly, the value of the exponential term in \hat{C} (Eq. 2) would drop from 0.22 to 0.05, in the case of a migration range R of 100 n miles (Table 1). Thus, the loss of 1 intermittent sub-population could only be compensated for by a 5-fold increase in size in the remaining substitute patches, which is not likely to have occurred at that time (see Fig. 2 with the declining trend). (2) In turn, an increase in one of the parameters $D_{i,j}$ and N_j , would increase \hat{C} , resembling the patterns found for lesser spotted dogfish and starry rays. Lesser spotted dogfish increased in abundance in the North Sea while not changing their distributional pattern between 2010–2011 and 2005–2009, i.e. forming hotspots in the Channel and along the English east coast (ICES 2012). Thus, $D_{i,j}$ is much larger than the small migration range of about 50 n miles buffering the increase in N_j , since in the first stage of immigration from distant patches the exponential term increases only little. Starry rays populate the central and northern North Sea directly adjacent to the German Bight (ICES 2012). From the 1980s to 2006, starry rays concentrated over the central North Sea (ICES 2007), where they were also abundant in the period 1902–1908 (Fig. 7A, patch a).

The concentration is shown as the ratio of regional to overall normalized abundances (Fig. 8). This concentration led to an effective decrease of $D_{i,j}$ in relation to the part of the population living in the German Bight (Fig. 7A, patch b) now being fairly equal to the migration range and to an apparent increase in donor patch size N_j . This decrease in $D_{i,j}$ and increase in N_j led to a positive immigration tendency into the German Bight over a short distance and increasing \hat{C} proxy (Fig. 8) despite decreasing overall abundance since 2001 (ICES 2012). This rationale applies to other species as well, e.g. an increase in N_j led to a recolonization of the Wadden Sea for grey seals (Reijnders et al. 1995). For thornback rays, establishing stepping stones in line with historical patches

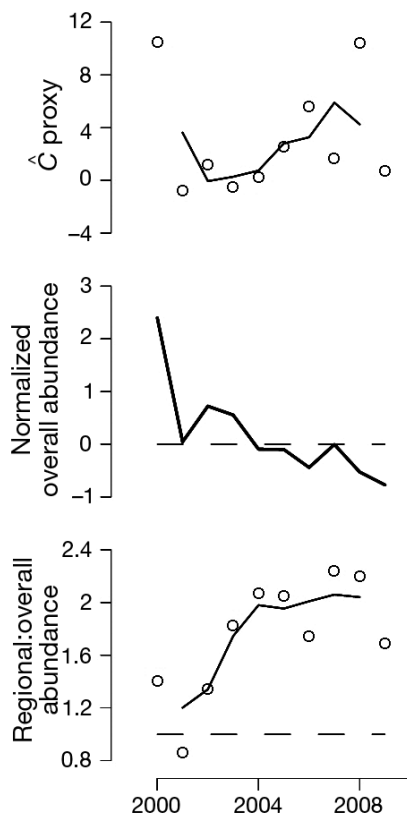


Fig. 8. Relationship between connectivity (\hat{C} proxy), declining overall abundance, and increased concentration in the central North Sea for starry ray *Amblyraja radiata*. Concentration is indicated as the ratio of regional vs. overall abundance. Values >1 (dashed line) indicate a concentration in the Doggerbank/German Bight as compared to the trend for the entire North Sea. The concentration in the Doggerbank/German Bight leads to an apparent increase in N_j and shortening of dispersal distance D_{ij} . Abundances were normalized to 0 mean and unit variance for the entire time series available

(Fig. 7B, patch c) could facilitate reintroduction to the German Bight.

This analysis shows how seasonally resolved survey information can be used to deduce migrations and principal mechanisms in meta-population dynamics in the sea, even if supporting tagging information is lacking (see Metcalfe 2006). The analysis based on trend slopes for seasonal abundances, \hat{C} proxy, and migration range provides a reasonable interpretation of local dynamics in terms of meta-population dynamics with regard to parameters N_j and $D_{i,j}$. This allows planning for stepping stones to recover extirpated sub-populations (e.g. for thornback rays, Fig. 7) or clarification of complex regional shifts in abundance (e.g. for starry rays, Fig. 8). The theoretically derived relationship between average \hat{C} proxy and migration range further augments the applicability of

the meta-population approach (Fig. 5, Eq. 7a,b). However, the best fit for the comparison of average \hat{C} proxy and migration range was obtained for a power function with a power of 1.4 (Fig. 5), indicating that the form obtained in Eq. (7b) is only an approximation given the correct interpretation of the underlying data. The merits of the meta-population approach in the interpretation of local abundance dynamics were underlined by Kritzer & Sale (2004, and references therein), who stressed the potential of the meta-population approach for analytical purposes rather than as a set of fixed criteria and definitions.

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