



Maintenance of long-term equilibrium in a perturbed metacommunity of sub-arctic marine fishes

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ABSTRACT: The theory of island biogeography (TIB) predicts that species richness in isolated areas is determined by the processes of colonization and extinction, and, in turn, governed by island size and isolation. Metacommunity models extend the TIB, predicting that both habitat and species interactions are important drivers of community vital rates and structure, and that marine metacommunities will exhibit higher extinction/colonization rates relative to terrestrial ecosystems. Here we demonstrate that oceanic banks can be considered islands, and document how application of these theories advanced our understanding of the dynamics of these submarine islands following the fishery-induced collapse of predatory groundfish populations. We employed a 48 yr dataset of fish communities on 10 offshore banks of the Scotian Shelf, Northwest Atlantic Ocean to examine colonization and extinction rates before and after the collapse. Bank-specific colonization, extinction and turnover rates were quantified using the *island* R package to correct for imperfect detectability, inherent to all sampling of natural systems. Colonization and extinction events were briefly unbalanced following the predator collapse, and reflected in increases in species richness and turnover, most notably on the largest banks. However, over the longer term, a dynamic equilibrium of colonization and extinction events prevailed on 8 of the 10 banks. This resulted in a generally time-invariant species richness, and a negative relationship between species turnover and bank area, as predicted by theory. Our study provides support for the relevance of island biogeography and metacommunity theories in guiding exploration and understanding of the mechanisms governing marine community vital rates and structure.

KEY WORDS: Theory of island biogeography · Ecology · Marine · Fishes · Banks · Metacommunity · Turnover · Colonization · Extinction · Dynamic equilibrium

1. INTRODUCTION

The theory of island biogeography (TIB; MacArthur & Wilson 1967) found its basis in the widely observed pattern of species richness (number of species) being positively related to habitat size, with larger habitats providing more space/habitat types (niche diversity)

and resources, thereby supporting a greater number of individuals (MacArthur & Wilson 1967, Rosenzweig 1995). The TIB was also the first to assume that mature ecological communities are not static (Case & Cody 1987, Akatov 2013), but rather experience repeated local extinctions and colonizations that, being relatively equal in number per unit time, yield a tempo-

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rally invariant species number. MacArthur & Wilson (1967) further hypothesized that the rate of local extinction would vary inversely with habitat area and that the rate of habitat colonization would be an inverse function of the degree of isolation of an island or habitat from the species pool or source community (Fig. 1) due to the reduced potential for influx of replacement individuals (i.e. rescue effects, Brown & Kodric-Brown 1977), and that colonization rates would increase with habitat area due to the greater niche space available (Fig. 1).

In the 54 yr since the publication of the TIB (MacArthur & Wilson 1967), ecological theory has evolved to incorporate the dynamism and complexity of natural systems. Acknowledgement of variation in the strength and shape of species–area relationships (SARs) among ecosystems and species groups (Connor & McCoy 1979, Drakare et al. 2006, Dengler 2009, Hachich et al. 2015, Stortini 2020) led to extensions of the TIB linking life history traits and species interactions to variations in the relative insularity of communities (e.g. Jacquet et al. 2017, the allometric and trophic theory of island biogeography). The strength of the core concepts of colonization and extinction rates being related to habitat area and isolation have also led to extensions of the TIB, including metacommunity theory, which predicts that in addition to habitat area and isolation, species dispersal, niche space, and species interactions will impact community turnover (Leibold et al. 2004, Holyoak et al. 2005). Metacommunity theory also predicts that highly interconnected communities such as marine metacommunities, linked by ocean currents and motile species, should exhibit higher rates of extinction and colonization (in sum, higher ‘turnover’) than those typically seen in terrestrial habitats. However, the frequency of colonization and extinction events should remain greatest in smaller habitats where local extinction rates are higher (MacArthur & Wilson 1967, Simberloff 1969, 1976, Rosenzweig 1995).

Recently, in acknowledgement of the fact that most ecological communities have not reached (and will not reach) ‘maturity’, ‘saturation’, or carrying capacity, it has been suggested that ecological theories and corresponding biodiversity models should be adapted to account for the following duality: communities should be considered as unsaturated, but also constrained by various scale-dependent drivers of biodiversity (Mateo et al. 2017). This concept facilitates the application of traditional ecological theories to the exploration of the drivers and constraints of community assembly without the need to assume saturation.

Within marine ecosystems, the drivers of local colonizations and extinctions have rarely been examined within the framework of TIB, as it has been assumed that the theory would not apply to these potentially highly dispersive, dynamic, unsaturated communities (Angel 1993, Carlton et al. 1999, Gislason et al. 2000). However, recent applications of ecological theories first formulated in terrestrial environments to marine environments have yielded advanced insights into both the ecology of marine systems in general and of marine community dynamics and assembly (Leggett 1977, Larkin 1978, Rothschild 1986, Frank & Shackell 2001, Link 2002, Francis et al. 2007, Webb 2012, Hachich et al. 2015, Dawson 2016, Jacquet et al. 2017, Stortini 2020).

The 10 offshore banks of the Scotian Shelf, North Atlantic Ocean (see our Fig. 2) may be considered as unsaturated (*sensu* Mateo et al. 2017) underwater islands. They host unique and productive fish and invertebrate assemblages that differ dramatically from off-bank habitats (Shackell & Frank 2000, Breeze et al. 2002, Stortini 2020) and they serve as important summer feeding and spawning grounds for many species (Ricard & Shackell 2013, Smith et al. 2015, Boudreau et al. 2017). In this respect, they are of similar significance in the life history of fish as oceanic islands are in the life cycles of migratory birds. There is also evidence of cohort retention of younger haddock on banks through the action of local gyres, and genetic differentiation in Atlantic cod populations

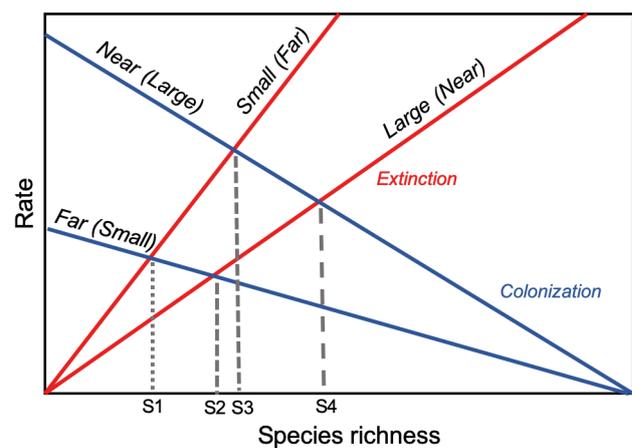


Fig. 1. Schematic representation of the classical theory of island biogeography (TIB; MacArthur & Wilson 1967) in which species richness ($S1 < S2 < S3 < S4$) is determined by the point at which colonization (blue) and extinction (red) rates are at equilibrium (intersecting lines). Colonization rate (or immigration) and extinction rate are negatively and positively related to the size of a habitat, respectively. Colonization rate and extinction rate are negatively and positively related to the distance of a habitat from the source of species (isolation), respectively

among these banks (Ruzzante et al. 1998, Shackell et al. 1999).

The banks of the Scotian Shelf were severely overfished in the 1970 and 1980s, which led to a shelf-wide collapse in the abundance (up to 95% loss; Myers & Worm 2005) and average body size (Shackell et al. 2010) of large-bodied predatory groundfish species in the early 1990s, including Atlantic cod *Gadus morhua*, pollock *Pollachius virens*, haddock *Melanogrammus aeglefinus*, American plaice *Hippoglossoides platessoides*, and Atlantic halibut *Hippoglossus hippoglossus*. One consequence of this collapse of the predator complex was the first ever documented trophic cascade in a large marine ecosystem (Choi et al. 2004, Frank et al. 2005, Petrie et al. 2009, Shackell et al. 2010), reflected in an explosive increase in the biomass (~900%; Bundy et al. 2009, Frank et al. 2011) and diversity (Ellingsen et al. 2015) of smaller prey fish species. The biomass of macroinvertebrate prey species also increased by ~200% (Bundy et al. 2009). The predator collapse and resulting trophic cascade were most striking in the northeastern portion of the shelf (Frank et al. 2005, 2011, Shackell et al. 2010, Ellingsen et al. 2015).

Here we report on the colonization and extinction dynamics of this bank archipelago/metacommunity of marine fishes prior to, during, and following the regime shift that occurred on the Scotian Shelf as viewed through the lens of TIB and metacommunity theory. In particular, we examined the temporal evolution of colonization, extinction, and turnover rates and their relationships with bank area and isolation (interbank distance).

2. MATERIALS AND METHODS

2.1. Study area and physical data

The 10 offshore banks of the Scotian Shelf (Fig. 2) range in depth from 60 to 90 m and area from 534 to 10 537 km². Average interbank spacing (boundary to boundary) is ~280 km. Interbank distance between the nearest neighbouring bank pairs ranges from 0 km (banks separated only by shallow troughs such that their boundaries were defined at the center of the trough) to 26 km from one another (Doubleday & Rivard 1981).

Bank area and isolation (distance to nearest neighbour) were calculated, using bank delineations as defined by the 100 m isobath (our Fig. 2; Doubleday & Rivard 1981), in ArcMap 10.5 (ESRI 2016). Polygon surface area was quantified using the calculate geometry function. Given high interconnectivity and low retention relative to fish species pelagic larval durations and adult motility (Cong et al. 1996, Stortini et al. 2020), and similarities in fish assemblage structure among the banks (Stortini et al. 2018), distance to the nearest neighbouring bank was expected to be an effective measure of isolation from the species pool. This was calculated by measuring the length of a straight line drawn between nearest vertices of bank boundary polygons. The banks are distributed along the trajectory of the northeast-to-southwest-flowing Nova Scotia Current (Brickman & Drozdowski 2012), with some banks exhibiting recirculation features that serve to retain eggs and larvae of both fish and invertebrates (Loder et al. 1988, Cong et al. 1996).

2.2. Ecological data

We employed a 48 yr (1970–2017) standardized ecological dataset, the product of ongoing monitoring of the Scotian Shelf ecosystem by Fisheries and

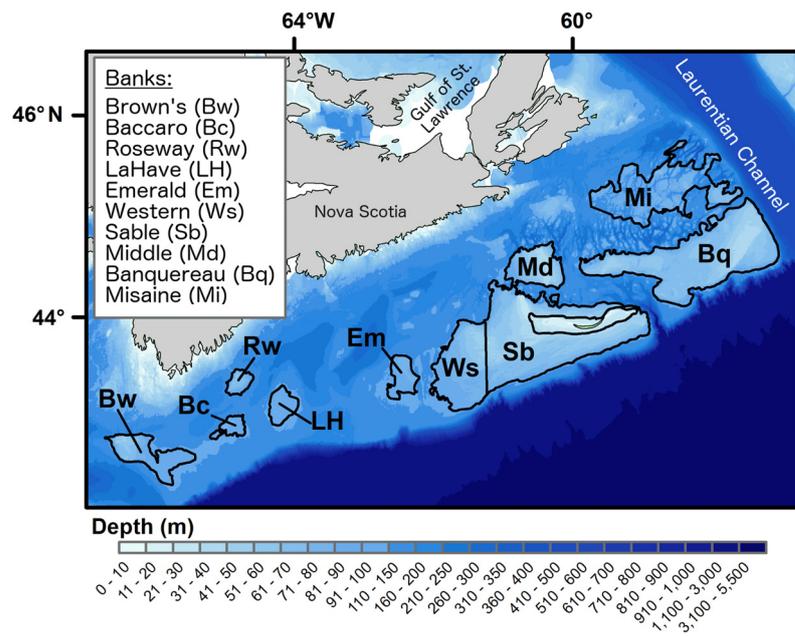


Fig. 2. Ten offshore banks of the Scotian Shelf. Bathymetric (depth below surface) data obtained from the Canadian Hydrographic Service. White areas: missing data. Bank boundaries defined by the 100 m isobath

Oceans Canada (DFO) (DFO 2017). The fishery-independent survey has been conducted annually, at the same time of year (July–August), and employing the same sampling design (Doubleday & Rivard 1981) since 1970. Changes in gear have been corrected for by DFO database managers. Full details of the sampling methodology, which yields equal sampling effort in relation to the planar area of each bank, can be found in Doubleday & Rivard (1981). See also Fig. S1.2 in Supplement S1 at www.int-res.com/articles/suppl/m675p081_supp.pdf. The average number of samples per year per bank were as follows: Baccaro: 2, Roseway: 2, LaHave: 2, Emerald: 2, Brown's: 6, Middle: 5, Western: 6, Misaine: 4, Banquereau: 12, and Sable: 15. The average coverage equated to ~1% of each bank's total area annually. While a sampling coverage of 1% may seem small, this survey is one of the most consistent and comprehensive marine ecosystem surveys in the world (Maureaud et al. 2021). Further, the low percentage sampled is not unique to the Scotian Shelf, and indeed, routine under-sampling of species across ecosystems has led to the growth of an entire field of statistical techniques to infer species richness and account for detectability issues (Colwell & Coddington 1994, Colwell et al. 2012).

The 48 yr (1970–2017) survey dataset was quality-controlled to include only individuals identified to the species level, with the single exception being redfish, which constitutes 2 species that are not easily distinguished, *Sebastes mentella* and *S. fasciatus*. Duplicate species records that resulted from the recording of different common names were combined ($n = 1$, *Triglops murrayi*). Fourteen non-species-level records were removed by this filtering to further reduce the influence of rare species that might otherwise induce uncertainty in estimates of colonization and extinction. The final dataset included only those species that were detected more than once within 3 yr windows over the 1970–2017 time series (Supplement S1). In total, 42 species fit the above criteria and were included in the analyses that follow (Table 1). The resulting annual detectability of the species within this dataset averaged 0.52, which exceeded the 0.25 detectability threshold that was found to yield reliable estimates of colonization and extinction rates in models that account for imperfect detectability (Ontiveros et al. 2019).

All species sampled were categorized as either large-bodied predators, mesopredators, or prey based on their average body size (marine fish tend to eat organisms that are, on average, 50% or less of their own body size; Scharf et al. 2000, Costa 2009)

and diet as in Stortini et al. (2018). All analyses were conducted using R version 3.6.1 (R Core Team 2019).

2.3. Estimating colonization and extinction rates

Nichols et al. (1998) argued that estimators of species richness and colonization/extinction rates based on probabilistic modelling would be more effective than criteria-based approaches (as in our Supplement S1; e.g. Cisneros 1993, Arnott et al. 2006) in studies of spatial and temporal community dynamics. Following this logic, Kéry et al. (2006) argued that maximum likelihood estimates derived from probabilities of detection (e.g. MacKenzie et al. 2003) can be unbiased and effective. This interest in probability-based modelling and maximum likelihood estimates of colonization and extinction rates led to the development of a statistical package in R called *island* (Ontiveros et al. 2019). This analysis framework follows the stochastic implementation of Simberloff & Wilson (1969) model of time-variant species richness in which the species present in a site is related to the number of species arriving from the greater species pool minus the number of species lost.

Before proceeding with our analyses, we first evaluated 6 methods to account for detectability when estimating colonization and extinction events: 1 employed the use of raw data not corrected for detection; 3 were derived from criteria-based approaches, 2 of which used species presence/absence data, and 1 of which employed species abundance data (Supplement S1); and 2 involved the use of functions within the *island* R package ('*sss_cedp*', which accounts for imperfect detectability, and '*regular_sampling_scheme*', which assumes perfect detectability). The resulting time series of colonization and extinction events derived from the 6 methods were strongly related (Supplement S1). Most surprisingly, results from the abundance-based method were nearly identical to results derived from the presence/absence-based methods. The *island*-based methods were most effective at correcting for detectability (Supplement S1). To streamline our results and highlight key temporal trends, we here discuss only results from the *island* function '*sss_cedp*' (Ontiveros et al. 2019; our Box 1). Supplement S1 details the results derived from the 5 other methods evaluated and provides a discussion of the relationships among all methods.

The *island* '*sss_cedp*' function employs a maximum likelihood approach to correct for imperfect

Table 1. Species observed on the banks at least 3 times in at least one 5 yr time interval between 1970 and 2017. When a species met this criterion for a particular bank, it was listed as present (1) and when it did not, it was listed as absent (0). Banks listed from smallest (Baccaro, Bc) to largest (Sable, Sb) and abbreviated as in Fig. 2. Species organized by trophic group (top predators = pred, mesopredators = meso, prey = prey; as defined by Stortini et al. 2018) and frequency of occurrence

Trophic group	Scientific name	Common name	Bc	Rw	LH	Em	Bw	Md	Ws	Mi	Bq	Sb	Banks occupied
pred	<i>Anarhichas lupus</i>	North Atlantic wolffish	1	1	1	1	1	1	1	1	1	1	10
	<i>Gadus morhua</i>	Atlantic cod	1	1	1	1	1	1	1	1	1	1	10
meso	<i>Amblyraja radiata</i>	Thorny skate	1	1	1	1	1	1	1	1	1	1	10
	<i>Glyptocephalus cynoglossus</i>	Witch flounder	1	1	1	1	1	1	1	1	1	1	10
	<i>Hemitripterus americanus</i>	Sea raven	1	1	1	1	1	1	1	1	1	1	10
	<i>Hippoglossoides platessoides</i>	American plaice	1	1	1	1	1	1	1	1	1	1	10
	<i>Melanogrammus aeglefinus</i>	Haddock	1	1	1	1	1	1	1	1	1	1	10
	<i>Myoxocephalus octodecemspinosus</i>	Longhorn sculpin	1	1	1	1	1	1	1	1	1	1	10
prey	<i>Clupea harengus</i>	Atlantic herring	1	1	1	1	1	1	1	1	1	1	10
	<i>Triglops murrayi</i>	Moustache sculpin	1	1	1	1	1	1	1	1	1	1	10
pred	<i>Hippoglossus hippoglossus</i>	Atlantic halibut	1	1	1	1	1	1	1	0	1	1	9
	<i>Pollachius virens</i>	Pollock	1	1	1	1	1	1	1	0	1	1	9
meso	<i>Sebastes</i> spp.	Redfish spp.	1	1	1	1	1	0	1	1	1	1	9
	<i>Limanda ferruginea</i>	Yellowtail flounder	1	1	0	1	1	1	1	1	1	1	9
	<i>Merluccius bilinearis</i>	Silver hake	1	1	0	1	1	1	1	1	1	1	9
pred	<i>Leucoraja ocellata</i>	Winter skate	1	0	0	1	1	1	1	1	1	1	8
prey	<i>Aspidophoroides monopterygius</i>	Alligatorfish	1	0	1	0	1	1	1	1	1	1	8
meso	<i>Lophius americanus</i>	Monkfish/goosefish	1	0	0	1	1	1	1	0	1	1	7
	<i>Malacoraja senta</i>	Smooth skate	1	1	0	1	0	1	1	0	1	1	7
pred	<i>Squalus acanthias</i>	Spiny dogfish	1	1	1	0	1	0	1	0	0	1	6
	<i>Urophycis tenuis</i>	White hake	0	0	0	1	1	1	1		1	1	6
prey	<i>Ammodytes dubius</i>	Northern sand lance	0	0	0	0	1	1	1	1	1	1	6
meso	<i>Urophycis chuss</i>	Red hake	0	0	0	1	1	1	1	0	0	1	5
prey	<i>Scomber scombrus</i>	Atlantic mackerel	0	0	0	0	1	1	1	0	1	1	5
meso	<i>Pseudopleuronectes americanus</i>	Winter flounder	0	0	0	0	1	1	1	0	0	1	4
prey	<i>Eumicrotremus spinosus</i>	Atlantic spiny lumpsucker	0	0	0	0	0	1	0	1	1	1	4
	<i>Mallotus villosus</i>	Capelin	0	0	0	0	0	1	0	1	1	1	4
meso	<i>Leucoraja erinacea</i>	Little skate	0	0	0	0	1	0	1	0	0	1	3
prey	<i>Peprilus triacanthus</i>	Butterfish	0	0	0	0	1	0	1	0	0	1	3
meso	<i>Zoarces americanus</i>	Ocean pout	0	0	0	0	1	0	1	0	0	1	3
	<i>Brosme brosme</i>	Cusk	1	0	0	0	1	0	0	0	0	0	2
prey	<i>Citharichthys arctifrons</i>	Gulf Stream flounder	0	0	0	1	0	0	1	0	0	0	2
	<i>Myoxocephalus scorpius</i>	Shorthorn sculpin	0	0	0	0	0	1	0	0	1	0	2
	<i>Leptagonus decagonus</i>	Atlantic sea poacher	0	0	0	0	0	0	0	1	1	0	2
	<i>Lumpenus maculatus</i>	Daubed shanny	0	0	0	0	0	0	0	1	1	0	2
pred	<i>Dipturus laevis</i>	Barndoor skate	0	0	0	0	1	0	0	0	0	0	1
meso	<i>Lycodes terraenovae</i>	Newfoundland eelpout	0	0	0	0	0	0	0	1	0	0	1
prey	<i>Scophthalmus aquosus</i>	Windowpane flounder	0	0	0	0	0	0	0	0	0	1	1
	<i>Tautoglabrus adspersus</i>	Cunner	0	0	0	0	0	0	0	0	0	1	1
	<i>Liparis atlanticus</i>	Atlantic snailfish	0	0	0	0	0	0	0	0	1	0	1
	<i>Lumpenus lumpreteaformis</i>	Snake blenny	0	0	0	0	0	0	0	1	0	0	1
	<i>Lycodes vahlii</i>	Shorttailed eelpout (Vahl)	0	0	0	0	0	0	0	1	0	0	1
Total species richness			29	21	17	15	21	29	32	26	28	23	

Box 1. Description, strengths, and weaknesses of the *island* method (function 'sss_cedp'; Ontiveros et al. 2019) used to quantify colonization and extinction events of fish species on the Scotian Shelf offshore banks 1970–2017. TIB: theory of island biogeography

Description

- Function 'sss_cedp' in *island* R package (Ontiveros et al. 2019)
- Based on likelihood function by MacKenzie et al. (2003) to estimate site occupancy, colonization and local extinction when species are detected imperfectly
- Relies on replicate observations (trawl sets within banks each year): here, calculated probabilities for 5 yr sliding windows
- Rates, and therefore transition probabilities, are estimated heuristically from the sum of probabilities of all possible detection histories (between consecutive sampling periods)

Strengths

- Estimated from the original stochastic implementation of equations of TIB
- Rates based on probabilities of all presence/absence combinations
- Less interannual variability than raw data or criteria-based methods (clear, smoothed temporal trends). See Supplement S1 for details

Weaknesses

- Assumes equal detectability among species, which may not be correct
- Assumes species are independent from one another
- Low replication (sites, number of transects) prevents species-specific characterization of vital rates and detectability

detection across a range of sampling periods (MacKenzie et al. 2003), here defined as 5 yr sliding windows (Box 1). The function was used to calculate bank-specific annual rates of community-level colonization and extinction (relative to bank-specific total species richness, S_p) across the 1970–2017 time period, by averaging across 5 yr sliding windows. The 'sss_cedp' function cannot estimate rates based on single years, and accuracy increases with the number of years used as input; we found that 5 yr was the minimum number of years after which results were generally consistent. Average colonization and extinction rates were also estimated for pre-collapse (1970–1991) and post-collapse (1992–2017) time periods using the 'sss_cedp' function. The 'cetotrans' function was then used to translate these rates into average annual probabilities of local colonization (PC) and extinction (PE), from which bank-specific annual numbers of colonization (C_t ; Eq. 1) and extinction (E_t ; Eq. 2) events, and annual species richness (S_t ; Eq. 3) were estimated.

$$C_t = (PC \times [S_p - S_{t-1}]) \quad (1)$$

$$E_t = (PE \times S_{t-1}) \quad (2)$$

$$S_t = S_{t-1} + (PC \times [S_p - S_{t-1}]) - (PE \times S_{t-1}) \quad (3)$$

Annual per-bank turnover (T) was then estimated as follows:

$$T = \frac{C_t + E_t}{S_{t-1} + S_t} \quad (4)$$

2.4. Testing for equilibrium of annual colonization and extinction events

The core concept underlying all hypotheses derived from TIB was the presence of equilibrium (i.e. a balance) of colonization and extinction events, leading to temporal stability of species richness in mature/saturated, undisturbed island or island-like communities. Simberloff & Wilson (1969) demonstrated in their community reassembly studies that, following a planned disturbance, community species richness experienced a short-term 'overshoot' and a subsequent 'levelling off' to equilibrium. However, a large literature base supports the idea that most ecological communities are unsaturated (reviewed in Mateo et al. 2017), constantly undergoing immigrations and emigrations of species from and to the larger regional species pool, the magnitude of which are controlled by environmental drivers and species interactions (Leibold et al. 2004, Mateo et al. 2017). Given the near-complete predator collapse that occurred in the Scotian Shelf ecosystem (Frank et al. 2011), and evidence that these banks remain unsaturated after 48 yr of data collection (Stortini et al. 2018), we explored the possibility of a disruption of equilibrium/community stability following that collapse.

We used the bank-specific 1970–2017 time series of colonization and extinction events (Eqs. 1 & 2) to evaluate the ratio of colonization to extinction (C:E) events per year (under the assumption of equilibrium, this ratio should, on average, be close to 1). Average C:E ratios, and corresponding standard errors, were calculated for the pre- and post-collapse time periods. Confidence intervals (95% CI) for the average ratios were generated using the corresponding standard errors (SE) to determine whether the average C:E values were statistically different from 1 (i.e. CIs not overlapping 1), which would indicate disequilibrium.

We further evaluated whether annual species richness on each bank was temporally stable, i.e. with no

directional change across the 1970–2017 time frame. We calculated the pre-collapse (1970–1991) and post-collapse (1992–2017) average rates of change in species richness and their standard error (time-invariance indicated by the overlap of 95% CIs with zero) for each bank.

2.5. Evaluating relationships of colonization, extinction, and turnover rates to bank area and isolation

MacArthur & Wilson (1967) hypothesized that the rate of local extinction should vary inversely with habitat area, and positively with habitat isolation from a species source. Conversely, TIB predicted that the rate of local colonization should be an inverse function of isolation and positively related to habitat area (Fig. 1). Due to higher rates of extinction in smaller habitats (MacArthur & Wilson 1967), combined with the relatively high interconnectivity of the bank assemblages, by extension, small less isolated banks should also exhibit higher turnover rates than larger more isolated banks.

While we explored the potential for unsaturation and disequilibrium, we also acknowledged the potential for duality (sensu Mateo et al. 2017), in that even unstable or unsaturated bank communities may still be constrained by area and isolation, although perhaps to varying degrees depending on the state of disturbance. The relationships of average colonization, extinction, and turnover rates to bank area and isolation (distance to nearest neighbour) were assessed using least-squares regression, and compared between pre- and post-collapse time periods. The trophic identity of species involved in annual turnover dynamics were also evaluated using a criteria-based method that produced similar results to *island* (PA3/5, described in Supplement S1, employed here due to the inability of *island* functions to characterize species-level colonization and extinction dynamics), the expectation being that prey species would be largely responsible for any increases in turnover following the 1991 regime shift.

3. RESULTS

3.1. Testing for equilibrium of annual colonization and extinction events

Time series of colonization and extinction events mirrored one another, with 2–3 species colonizing and

becoming locally extinct per year across the 10 banks (Fig. 3). The C:E ratio was not significantly greater than 1 (95% CIs consistently overlapped with 1) on any of the 10 banks, in either pre- or post-collapse time periods (Table 2), and time series of species richness varied only slightly in relation to the long-term mean (Fig. 4), providing strong support for the TIB prediction of an equilibrium state. However, all banks except Emerald and Western banks experienced a short-term (5 to 10 yr) increase in the number of colonizations relative to extinctions in the early 1990s following the predator collapse (Figs. 3 & 5). Following this brief increase, equilibrium (balance) of colonization and extinction events was generally regained (Figs. 3 & 5). Similarly, all but 2 banks (Emerald and Western) exhibited short-term increases in species richness directly following the predator collapse (Fig. 4). These brief overshoots were generally followed by returns of species richness near to the long-term mean (Fig. 4), which led to low (and in many cases, slightly negative) rates of change in both time periods across the banks (Table 2), supporting the equilibrium prediction. While half of the regime-specific rates of change in species richness were statistically significant (slopes > 0, at $\alpha = 0.05$; Table 2), they ranged from -0.25 to $+0.35$ species per year, or less than 3 species per decade.

There was substantial variation in the annual C:E ratios among the banks (Fig. 5), with low (ranging from 0 to 0.46) between-bank correlations (Pearson) of C:E time series (Table 3). Collectively, there was a minor peak (indicating more colonizations relative to extinctions) in the early 1980s, a trough (indicating more extinctions than colonizations) in the later 1980s, a major peak in the early 1990s, a trough in the late 1990s to mid-2000s and a second major peak in the late 2000s (Fig. 5). However, the magnitude of these peaks and troughs varied depending on whether a bank was located in the northeast (generally larger in size) or the southwest (generally smaller in size). The most evident difference was a more dramatic peak (>1) in the immediate post-collapse years, followed by a rapid return to equilibrium (~ 1 on average, amidst greater interannual variability) in the early-to-mid 1990s on the small southwest banks (Fig. 5).

While the larger northeast and smaller southwest banks exhibited differences in the magnitude of temporal changes in the C:E ratio, the time series tended to follow similar trends across all 10 banks. These findings suggest that the early 1990s regime shift appears to represent a short-term disruption to the long-term equilibrium on the smaller banks (long

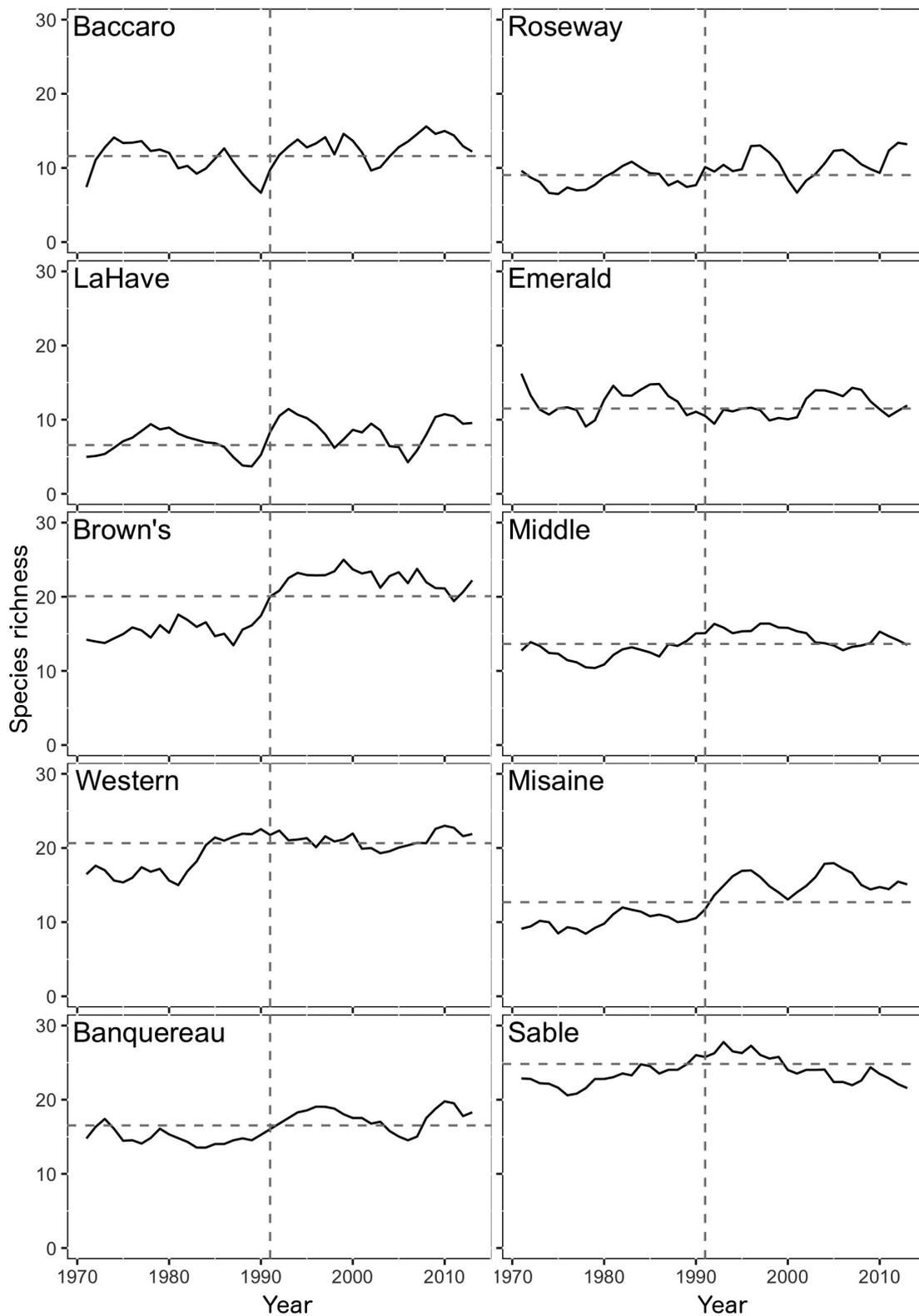


Fig. 3. Time series of annual colonizations (solid lines) and extinctions (dashed lines). Vertical grey dashed lines indicate 1991, the approximate year of the predator collapse and consequent ecosystem regime shift. Horizontal grey dashed line marks zero (i.e. no colonizations or extinctions). Banks listed from smallest (top left) to largest (bottom right)

Table 2. Mean and SE of species richness (SR), rate of change in species richness (Spp. yr⁻¹), and ratio of colonization to extinction events (C:E) for (A) pre-collapse and (B) post-collapse time periods. * Significant rates of change (Spp. yr⁻¹ > 0) and C:E ratios significantly ($p < 0.05$) larger than 1. Banks listed from smallest to largest and abbreviated as in Fig. 2

Time period	Bank	Area (km ²)	SR		Spp. yr ⁻¹		C:E ratio (95% CI)	
			mean	SE	mean	SE	mean	SE
(A) Pre-collapse (1970–1991)	Bc	534	10.95	0.47	-0.17*	0.07	1.27 (0.89–1.39)	0.23
	Rw	551	8.45	0.28	0.06	0.05	1.13 (0.89–1.39)	0.13
	LH	908	6.71	0.37	-0.04	0.06	1.23 (0.92–1.55)	0.16
	Em	1034	12.39	0.40	-0.01	0.07	1.36 (0.77–1.96)	0.30
	Bw	2243	15.61	0.34	0.14*	0.05	1.10 (0.95–1.25)	0.08
	Md	2253	12.66	0.29	0.10*	0.04	1.04 (0.94–1.14)	0.05
	Ws	4442	18.45	0.57	0.35*	0.05	1.08 (0.94–1.22)	0.07
	Mi	4513	10.20	0.23	0.11*	0.03	1.17 (0.95–1.39)	0.11
	Bq	10 496	14.92	0.22	-0.05	0.03	1.02 (0.90–1.14)	0.06
Sb	10 537	23.21	0.32	0.19*	0.03	1.05 (0.95–1.15)	0.05	
(B) Post-collapse (1992–2017)	Bc	534	13.08	0.33	0.06	0.05	1.11 (0.92–1.30)	0.10
	Rw	551	10.73	0.39	0.08	0.06	1.29 (0.90–1.69)	0.20
	LH	908	8.64	0.41	-0.05	0.07	1.27 (0.90–1.64)	0.19
	Em	1034	11.82	0.32	0.09*	0.05	1.15 (0.89–1.41)	0.13
	Bw	2243	22.43	0.27	-0.09*	0.04	1.09 (0.96–1.22)	0.07
	Md	2253	14.76	0.24	-0.12*	0.03	1.01 (0.92–1.09)	0.04
	Ws	4442	21.08	0.22	0.03	0.04	1.03 (0.93–1.14)	0.05
	Mi	4513	15.47	0.29	0.01	0.05	1.12 (0.94–1.31)	0.09
	Bq	10 496	17.59	0.31	-0.01	0.05	1.07 (0.95–1.19)	0.06
Sb	10 537	24.31	0.39	-0.25*	0.03	1.00 (0.89–1.10)	0.05	

term C:E ratios not statistically different from 1; Table 2), reminiscent of the patterns observed by Simberloff & Wilson (1969) in their experimental island studies.

3.2. Evaluating relationships of colonization, extinction, and turnover rates to bank area and isolation

Noting the clear increase in the number of colonizations relative to extinctions directly following the predator collapse (Fig. 5), we assessed the relationships between colonization and extinction rates, bank area and isolation in pre- and post-collapse regimes independently. Colonization rate was not significantly related to bank area in either time period (Fig. 6A), while both extinction rate (Fig. 6B) and overall species turnover (Fig. 6C) were significantly related to bank area (a result consistent with the predictions of TIB) in the pre-collapse time period only. In the post-collapse time period, decreased extinction rates and turnover on the smaller banks, coinciding with zero change or slight increases in turnover on the largest banks, led to a weakening of these relationships (Fig. 6B,C).

Bank isolation was not a significant predictor of colonization rate in either time period (Fig. 6D), but

was a significant predictor of pre-collapse extinction and turnover rates (Fig. 6E,F). This suggests that, despite the interconnectivity of the system, the spatial structuring of this bank archipelago constrains community assemblage to some degree. However, multivariate regression and model comparison using Akaike Information Criterion (AIC) indicated that bank area was the dominant predictor of these rates, particularly in the post-collapse time period.

An investigation into the trophic identities of colonization and extinction events (using the PA3/5 criteria-based method; see Supplement S2) revealed that the heightened turnover on the 4 largest banks (Western, Misaine, Banquereau and Sable) in the post-collapse regime (Fig. 6) was due to increases in the number of colonizations and local extinctions of prey species (Fig. 7). The number of prey colonizations and extinctions increased from pre- to post-collapse on most banks except for Brown's, Emerald and Middle (Fig. 7). In the post-collapse time period, the total number of prey colonizations exceeded extinctions by 1.5 events on average, with the exception of Emerald Bank (Fig. 7).

On the 4 smallest banks (Baccaro, Roseway, LaHave, Emerald), the number of colonization and extinction events were higher in the mesopredator group than in the prey group, but mesopredator colonization events increased between time periods

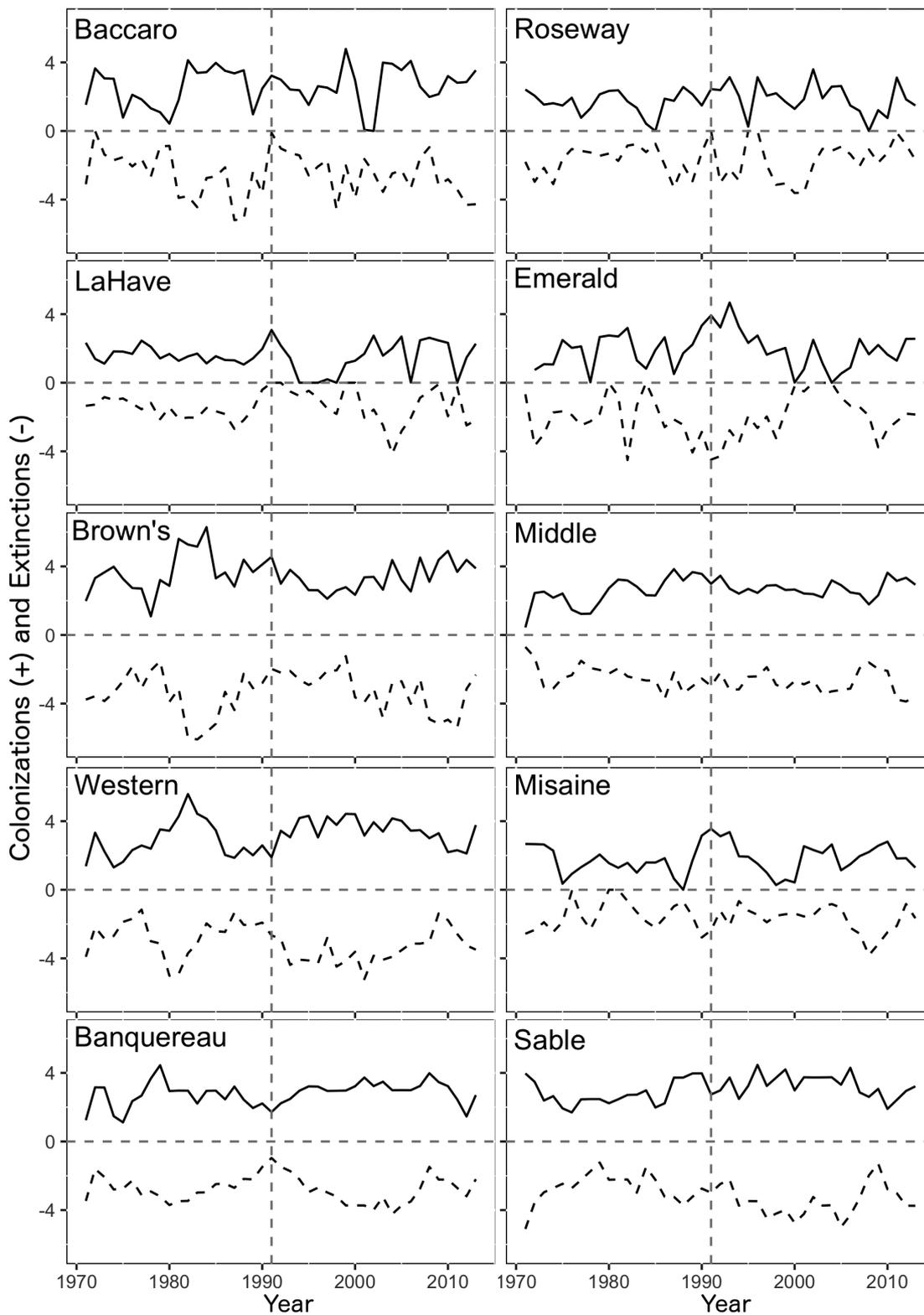


Fig. 4. Time series of annual number of colonization events (solid black lines) and extinction events (dashed black lines) estimated using the island method, for each bank. Vertical grey dashed lines and ordering of banks as in Fig. 3. Horizontal grey dashed lines mark the reference of 0 (no colonizations or extinctions)

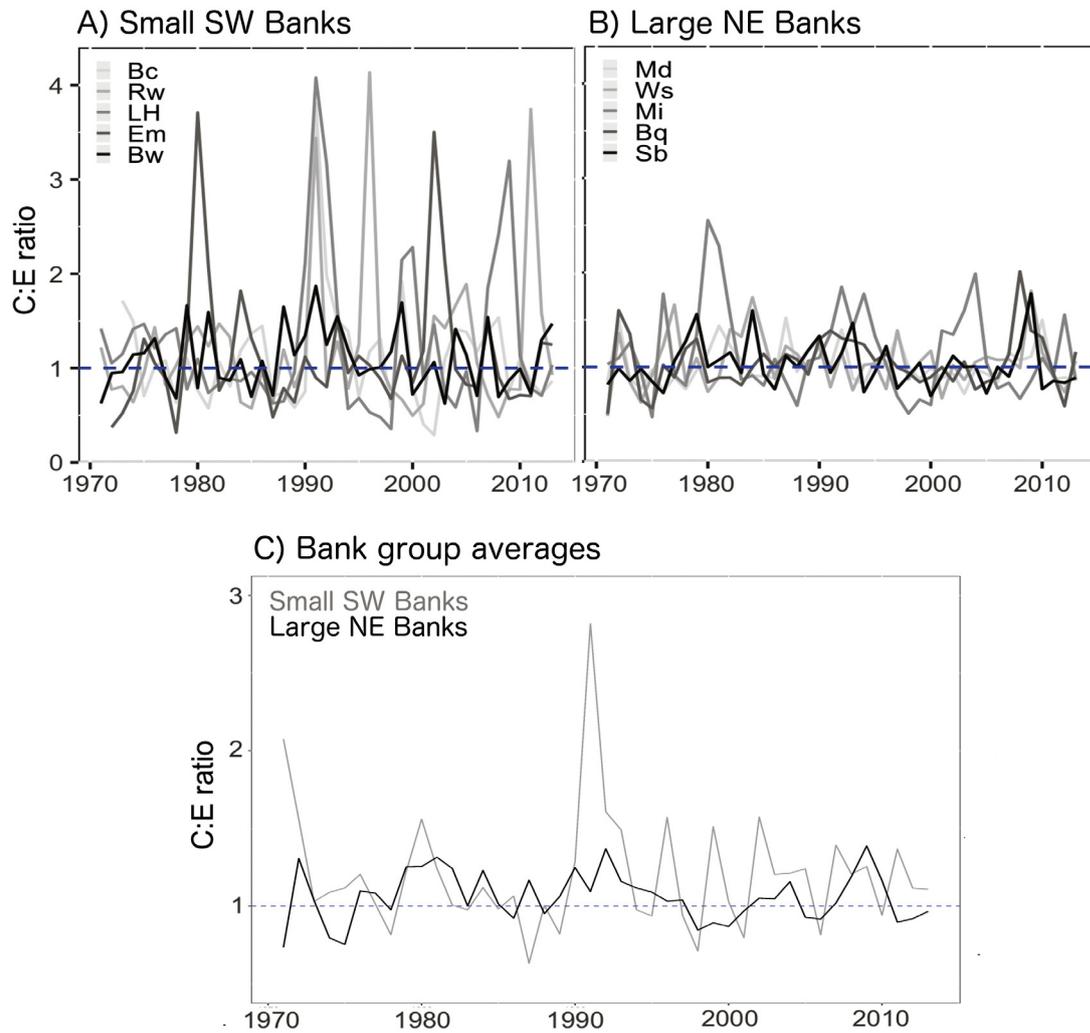


Fig. 5. Annual ratios of *island*-derived colonization events to extinction events (C:E ratio) per year for each of the (A) southwestern (SW) banks and (B) northeastern (NE) banks, arranged from smallest (light grey) to largest (black); (C) average annual C:E ratio anomalies (SD) of the 5 smallest (SW) banks (Bc, Rw, LH, Em, Bw; grey), and the 5 largest (NE) banks (Md, Ws, Mi, Bq, Sb; black). Dashed line at C:E = 1 represents perfect equilibrium. Banks abbreviated as in Fig. 2

only on Roseway and LaHave banks (Fig. 7). Relative to prey and mesopredator trophic levels, top predators contributed little to the turnover dynamics of the banks in either pre- or post-collapse time periods (Fig. 7).

4. DISCUSSION

We found support for the foundational prediction of TIB as it relates to temporal ecosystem dynamic; colonization and extinction events were at equilibrium across a 48 yr time frame, despite a major perturbation. There

Table 3. Pearson correlation coefficients of bank time series of annual ratio of colonization to extinction events (C:E) ratio. Banks abbreviated as in Fig. 2

	Bc	Rw	LH	Em	Bw	Md	Ws	Mi	Bq	Sb
Bc	1									
Rw	0.13	1								
LH	0.37	0.01	1							
Em	-0.30	0.04	-0.01	1						
Bw	0.24	0.12	0.22	-0.10	1					
Md	0.20	-0.10	0.10	-0.20	0.02	1				
Ws	0.08	-0.30	0.09	-0.40	-0.10	0.32	1			
Mi	0.03	0.18	-0.05	0.28	0.18	0.11	-0.20	1		
Bq	0.46	-0.10	0.37	-0.40	0.03	0.30	0.23	-0.10	1	
Sb	-0.10	0.00	0.25	0.00	0.10	0.11	0.35	0.00	0.34	1

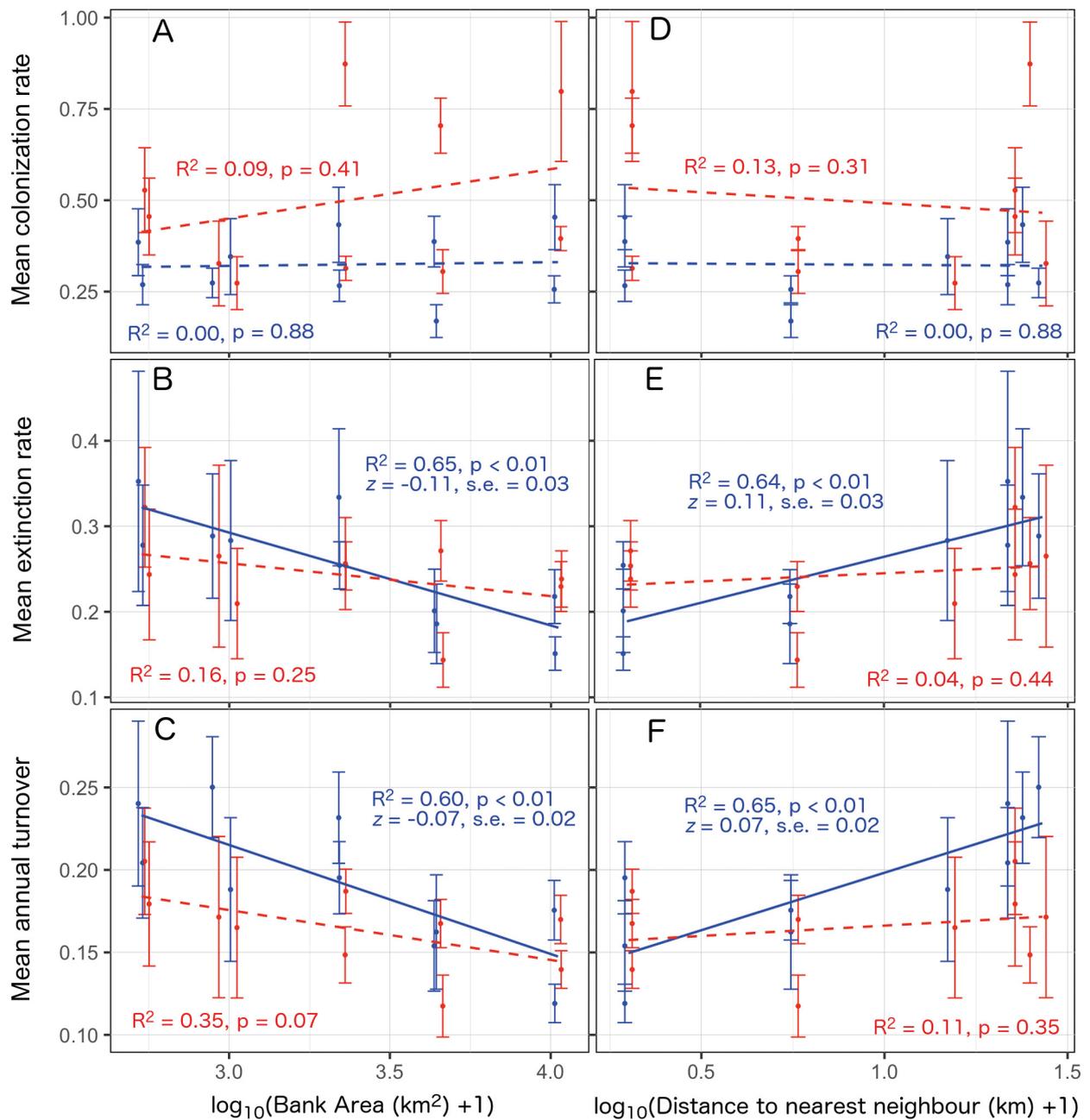


Fig. 6. Relationships of colonization rate, extinction rate, and species turnover (colonizations and extinctions relative to species richness) to bank area (A, B, and C, respectively; $n = 10$) and bank isolation (D, E, and F, respectively) in the pre-collapse (blue) and post-collapse (red) time periods. Significant ($\alpha = 0.05$) fits are shown as solid lines, non-significant fits are shown as dashed lines. Error bars: 95% confidence intervals of estimated rates; s.e.: standard error

was no appreciable long-term change in average annual species richness, despite changes in community structure (Frank et al. 2011), regional beta diversity (Shackell et al. 2012b, Ellingsen et al. 2015), and cumulative species richness (Stortini et al. 2018). Species local extinction and turnover rates were also negatively related to bank area, and positively related to bank isolation, as predicted by TIB and

metacommunity theory. The effect of a major perturbation, the collapse of large-bodied predator species and consequent shift to a mesopredator and prey-dominated system (Shackell & Frank 2007, Shackell et al. 2010, Frank et al. 2011, 2016), was a short-term disequilibrium reminiscent of the patterns of reassembly of invertebrate communities on perturbed islands documented by Simberloff & Wilson (1969).

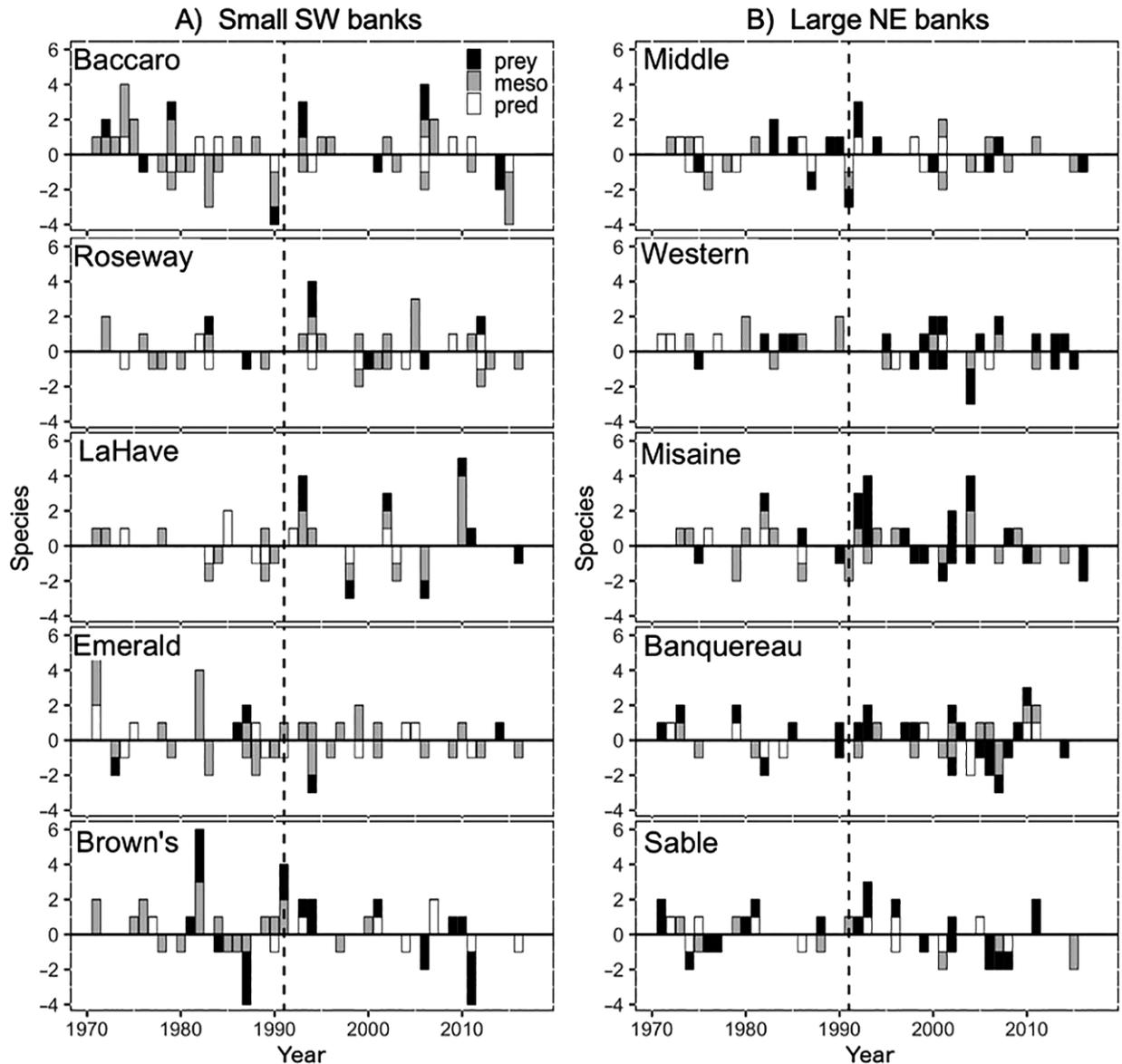


Fig. 7. Annual colonizations (positive, species gains) and extinctions (negative, species loss) within each of the 3 trophic groups (prey: black, mesopredators: grey, large-bodied predators: white) on each of the (A) small southwestern (SW) banks and (B) large northeastern (NE) banks, listed from smallest (top) to largest (bottom), derived using the criteria-based method (PA3/5) described in Supplement S1, which produced similar results to *island*. Pre- and post-collapse time periods divided by vertical dashed line at 1991

This post-collapse destabilization of the Scotian Shelf bank assemblages manifested differently on the large northeast and small southwest banks. The post-collapse increase in colonizations relative to extinctions was most dramatic on the small southwestern banks, where interannual variability in colonizations and extinctions and magnitude of annual turnover were highest. However, the small southwest banks recovered to a dynamic equilibrium more rapidly following this early 1990s disturbance, while the large northeast banks exhibited a more pro-

longed period of increased colonizations, followed by an increase in the number of extinctions relative to colonizations (and subsequent decrease in species richness), a potential second colonization event, and finally a return to equilibrium in the late 2000s. In fact, the small southwest banks experienced reductions in average turnover rates following the predator collapse, implying an increase in community stability (supported by an analysis of temporal changes in community structure, provided in Supplement S3), while the large northeast banks experienced either

no change or an increase in turnover rate, on average, over the post-collapse time period.

It is generally agreed that the northeast region of the Scotian Shelf was more strongly and more persistently perturbed by the predator collapse than was the southwest (Choi et al. 2004, Shackell & Frank 2007, Ellingsen et al. 2015). The southwest region and associated banks are characterized by warmer water temperatures, higher population growth rates and stronger compensatory dynamics among the predator and mesopredator species functional groups relative to the northeast banks (Frank et al. 2005, Shackell & Frank 2007, Petrie et al. 2009, Shackell et al. 2012a). These attributes are consistent with the rapid response and recovery of equilibrium, and the more prominent role of mesopredators in post-collapse turnover dynamics observed on the small southwest banks.

It is probable that the rapid turnover dynamics associated with the prey complex during the post-collapse regime, particularly on the most disrupted large northeast banks, was conditioned by the higher vital rates associated with small-bodied fish species (Mora et al. 2003, Jetz et al. 2004, Luiz et al. 2013, Stier et al. 2014), and by the increased potential for competitive interactions among increasingly abundant and diverse prey species under conditions of reduced predation pressure (McCann 2000, Leibold et al. 2004, Holyoak et al. 2005, Tomášovych & Kidwell 2010). Similar rapid turnover dynamics of *r*-selected species have been reported following dramatic disturbance/mass-mortality events in other marine communities (e.g. Alonso et al. 2015).

This pattern of shifts in community structure across the banks, specifically prey release resulting in reduced temporal stability on the large northeast banks and mesopredator compensation resulting in increased temporal stability on the small southwest banks, is the likely cause of the lack of saturation in species richness previously observed on these banks (Stortini et al. 2018). Our results also offer support for recent developments in theoretical ecology suggesting that ecosystems can be both unsaturated and constrained by environmental (e.g. bank size) and ecological (e.g. trophic interactions, competitive dynamics, stochasticity) factors (Mateo et al. 2017). While bank area was a strong determinant of community stability in the pre-collapse regime (as predicted by the TIB and its extensions), spatial inconsistency of the severity of the predator collapse and consequent prey release (i.e. shifts in ecological constraints) was reflected in the reduced ability of the large northeast banks to sustain stable assemblages in the post-collapse regime.

5. CONCLUSIONS

Dawson (2016) recently suggested, and Stortini et al. (2018, 2020) have demonstrated that TIB can be successfully applied to broaden the understanding of the factors governing the spatial scaling of diversity and assemblage structure in large marine ecosystems, despite these communities often existing in an unsaturated state (Mateo et al. 2017, Stortini et al. 2018). Our previous work (Frank & Shackell 2001, Stortini et al. 2018, 2020) has yielded support for the TIB and its modern derivatives through the presence of positive SARs and species trait- and interaction-dependent variations in the slope of SARs across the 10 banks of the Scotian Shelf. Here, we found support for predictions of the TIB and metacommunity theory that relate to the temporal dynamics of fish assemblages on these same banks.

Our results demonstrate that even in large (~120 000 km²), unsaturated, disturbed, and highly interconnected marine metacommunities, an average long-term equilibrium can occur, and that habitat area can constrain species richness, local extinction rates, and turnover dynamics. However, our findings also reveal that major perturbations can result in significant transient disruptions to equilibrium, and to longer-term shifts in community structure and stability notwithstanding long-term equilibrium states. In this regard, our findings confirm Coulson's (2021) contention that the transient dynamics resulting from omnipresent anthropogenic influences do not negate the utility and/or applicability of the concept of equilibrium in ecosystem science. These results further strengthen the case for the utility of ecological theory in building a greater understanding of the community dynamics of large and complex marine ecosystems, and, conversely, the role of marine-focused studies in testing and expanding theoretical ecology.

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