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Multi-decadal changes in two co-occurring ophiuroid populations

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ABSTRACT: Mixed beds of *Ophiocomina nigra* and *Ophiothrix fragilis* (Echinodermata, Ophiuroidea) are usually predominated by *O. fragilis* and are reported to be stable over time. The Bay of Brest (Brittany, France) is a highly productive ecosystem where both species co-occur in the main central part. Using a geostatistical approach, we tested for changes in *O. nigra* and *O. fragilis* density and total biomass patterns between 1987 and 2011. Our results highlighted an increase in *O. nigra* population size and the induction of a spatial shift of the co-occurring *O. fragilis*. *O. nigra* increased ~5 times in density and covered almost all the study area, while its density-dependent biomass increased ~3 times (22 t km^{-2}, ash-free dry mass) between 1987 and 2011. Overall, the *O. fragilis* population decreased in density by ~30%, but its total biomass did not change over time. The current distribution pattern revealed a clear spatial exclusion of *O. fragilis* from the central part of the study area toward the southern part, overlapping beds of dead slipper limpet *Crepidula fornicata*, which were formerly considered to be the dominant suspension-feeder species in the bay. The success of *O. nigra* colonization is linked to its biological and functional traits, as well as deep changes in food supply over the studied period. Ecological consequences of such a large change in the benthic compartment of the bay are explored in the light of associated changes in environmental patterns.

KEY WORDS: Echinoderm · *Ophiocomina nigra* · *Ophiothrix fragilis* · Food supply · Kriging method · Suspension-feeder

INTRODUCTION

Echinoderms are reported in many systems to play key structural and functional roles; under a complex set of environmental factors, echinoderms species exhibit high population density fluctuations also called 'outbreak' or 'die-off' events in coastal and deep ecosystems (Uthicke et al. 2009). Indeed, occasional outbreaks are a feature of some echinoid (Hughes 1994) and asteroid populations (Guillou 1996, Seymour & Bradbury 1999). Conspicuous echinoderm outbreaks were reported for the sea star *Acanthaster planci* in the coral reefs (Houk & Raubani 2010) and for the green sea urchin *Strongylocentrotus droebachiensis* in kelp beds (Wharton & Mann 1981), as well as numerous other sea urchin species (Andrew & Underwood 1992, Valentine & Edgar 2010). However, little information has been published concerning brittle star (ophiuroid) outbreaks. Few studies report sharp increases in *Ophiura*

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albida (Neumann et al. 2009), *Amphiura filiformis*, and *A. chiajei* populations in temperate shallow habitat of the North Sea and northeast (NE) Atlantic, as well as in the 2 deep-sea ophiuroids *Ophiocten hastatum*, in NE Atlantic, and *Ophiura bathybia*, in the NE Pacific (as reviewed by Uthicke et al. 2009). In European coastal shallow waters, ophiuroids often occur in soft bottom benthic assemblages, accounting for most of the benthic biomass from heterogeneous coarse sediments (Dauvin & Ruellet 2008), to muddy communities (Goransson 2002) where they are playing key functions in the coupling of benthic-pelagic systems (Allen 1998). A few ophiuroid species classically structure those communities, namely *Amphiura filiformis* (Müller) (Bowmer 1982, Bourgoin & Guillou 1988) and *Acrocnida brachiata* (Montagu) (Thiébaut et al. 1997) as well as the 2 common co-occurring brittle star species, *Ophiocomina nigra* (Abildgaard) and *Ophiothrix fragilis* (Abildgaard). The latter has been widely reported and surveyed in the NE Atlantic region where large beds have been reported, with densities reaching >1500 ind. m^{-2} (e.g. Muths et al. 2010 and references therein). Similarly, *O. nigra* distribution covers a broad range of sedimentary features, but its densities rarely exceed those of *O. fragilis* even in mono-specific beds.

Situated in an ecotone between the English Channel and the Atlantic Ocean (Bay of Biscay), the Bay of Brest (Brittany) hosts populations of both *Ophiocomina nigra* and *Ophiothrix fragilis*. As in many systems with a high primary production, benthic assemblages are dominated by suspension-feeders, in general and especially *O. fragilis*, colonizing a large area in this bay. Distribution of *O. fragilis* in the main part of the bay was monitored early in the 1990s, leading to the conclusion that ecological conditions for this species were optimal (Hily 1991). We used the Bay of Brest as a geographical model to test possible expansion or regression mechanisms of the main ophiuroid species, namely *O. fragilis* and the co-occurring *O. nigra*. Using *O. fragilis* published data (Hily 1991) and unpublished *O. nigra* data from the same survey, we aim at investigating changes in density and biomass between 2 distant time periods for ophiuroid populations. Our study shall provide new insights into long-term echinoderm population dynamics and the potential consequences for associated benthic communities and control of phytoplankton biomass. Investigating the same area after a long period of time with similar protocols has proven to be successful for monitoring and detecting long-term changes in benthic assemblages (Reise 1982, Reise & Schubert 1987, Hily et al. 2008). Differences between past and current data were explored according to *O. nigra* and *O. fragilis* biological traits as well as changes in environmental parameters.

MATERIALS AND METHODS

Study area

The Bay of Brest is a shallow semi-enclosed marine coastal system of ~180 km² connected to the Atlantic Ocean by a narrow opening of 1.8 km width (Fig. 1). This bay is a macrotidal system (tidal amplitude: max. 8 m; tidal current: max. 2.6 m s^{-1}) that receives anthropogenic nutrient inputs from rivers which are promoted by high hydrodynamic mixing (Le Pape et al. 1996). This site is characterized by a high diversity in sedimentary features: estuaries and muddy banks, slopes and channels, heterogeneous sediments and rocky area. Biogenic components such as maerl *Lithothamnium corralioides* beds and accumulations of the gastropod *Crepidula fornicata* cover the sediment and create favorable supports and refuge for many benthic species (Hily 1989). Since its introduction in 1950, the slimper limpet *C. fornicata* expanded from 45 km² in 1978 (southern basin) (Coum 1979) to 90 km² in 1995 (southern and central basins) (Fig. 1; Chauvaud et al. 1998) and constitutes the main benthic suspension-feeder in the bay (Chauvaud et al. 1998).

Sampling methods

In February 2011, a video survey was conducted in the main central part of the Bay of Brest, using the same video protocol and the same sampling points as Hily (1991) in 1987 (Fig. 1). A total of 72 video profiles were recorded using an underwater HD video camera (Sony HD CX6) mounted on a weighted structure with a 0.05 m² metal frame welded in its lower part, so that the camera would focus on both the frame and the sediment surface. Two green laser pointers (S2000BLG Subsea) were mounted on each side of the camera and calibrated to provide an accurate scale (1 mm precision) on each picture or video. Instantaneous pictures were taken each time the frame hit the bottom. Subsequent to that first picture, the structure was lifted for 5 s and dropped for the next picture, while the research vessel was in neutral but still moving with the current. For each of the 72 stations, 20 pictures were taken along a transect of

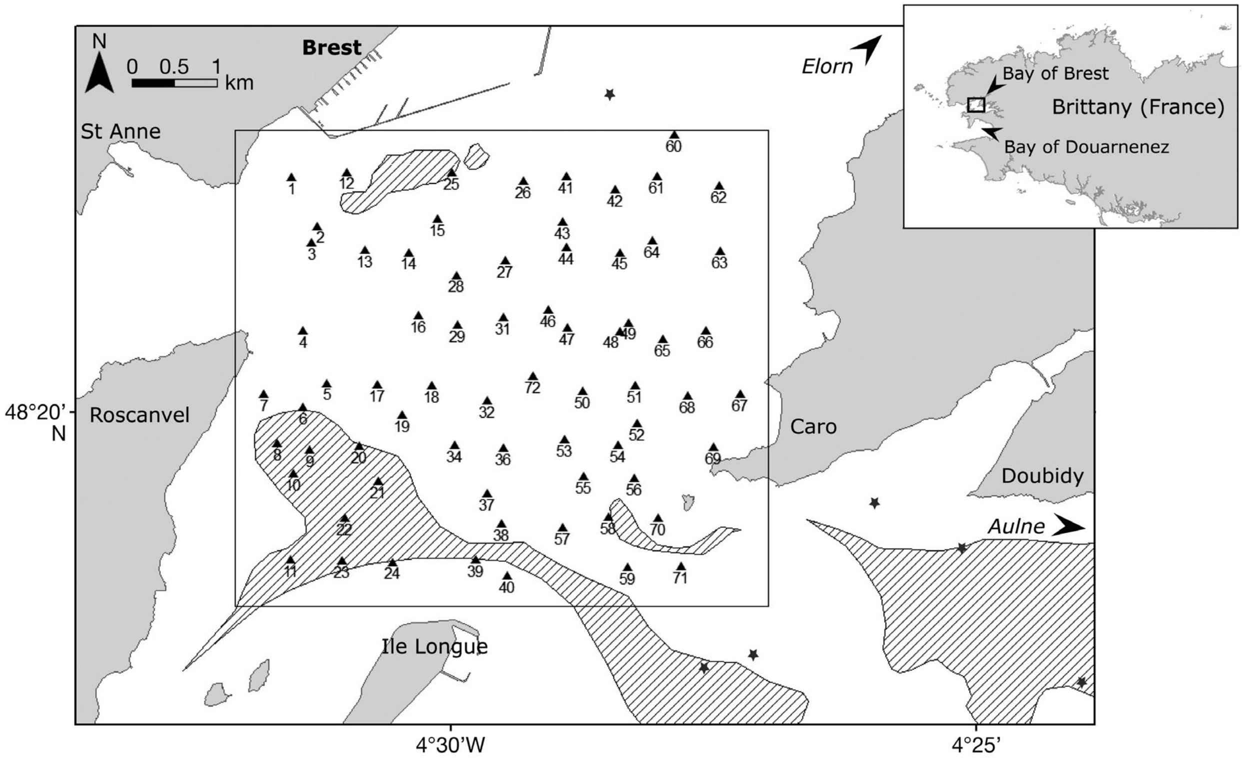

Fig. 1. The 72 sampling stations (▲) from the 1987 and 2011 benthic surveys covering the main central basin of the Bay of Brest, Brittany (France). Square: sampling area. ★: additional stations prospected in 2011 (not included in data analysis). Hatched area: distribution of slipper limpet *Crepidula fornicata* in 1995 (modified after Chauvaud et al. 1998)

~50 m, with a total cover of 1 m². All HD pictures were georeferenced and used to estimate the individual numbers of *Ophiocomina nigra* and *Ophiothrix fragilis*.

We retrieved published densities of *Ophiothrix fragilis* from 1987 (Hily 1991) and added a new set of unpublished density data of *Ophiocomina nigra* from that same video survey, in order to compare both 1987 and 2011 surveys. The sampling occurred in May and February for 1987 and 2011 surveys, respectively. Even if sampling seasons were different, all the specimens sampled by video were >5 mm. A few complementary observations (not used in the 1987 and 2011 surveys comparison) were recorded towards the Aulne and the Elorn estuaries as well as in the westernmost part of the bay, toward the open ocean (Fig. 1).

To calculate the biomass (organic matter) for the whole prospected area for the 2 species, we used the ophiuroid densities from the 1987 and the 2011 surveys. A 2 step process required (1) to measure disc diameters of the ophiuroids from the 2011 survey and link mean diameter and density at each station, and (2) to establish a relationship between individual biomass and disc diameter:

(1) External disc diameters were measured to the closest millimeter with the scale provided by the laser pointer on the HD pictures. To avoid a measure bias, the measure was considered valid when individuals were well-flattened on the bottom. For each species, the disc diameters of 30 individuals were randomly measured among the 20 HD pictures within each station. To strengthen our approach, additional HD pictures were taken from closed areas (Bay of Douarnenez) during the same 2011 survey (Fig. 1). The minimum size of specimens measured by laser pointer was ~5 mm disc diameter for both species. All measurements were used to fit a general model of size vs. density.

(2) Additional samples of the 2 ophiuroid species were taken by scuba divers close to the studied area (Bay of Douarnenez) and brought to the laboratory for further analysis. The external disc diameter of all individuals (n = 183 for *Ophiothrix fragilis* and n = 196 for *Ophiocomina nigra*) covering all size-classes of the population were measured to the closest millimeter. Echinoderms were then ashed in a muffle furnace at 550°C for 4 h. The ash mass was subtracted from the dry mass to obtain the ash-free dry mass (*mass*; mg) for each individual (see 'Data analysis').

Data analysis

Comparisons were made between past (1987) and current (2011) interpolated distributions and total biomasses of both *Ophiocomina nigra* and *Ophiothrix fragilis* from the 72 sampling stations. The 4 interpolations (2 dates × 2 species) were performed using ordinary kriging, a geostatistical method that analyzes the spatial structure of the dataset through semi-variograms to estimate the best interpolation parameters (Kitanidis 1997). Semi-variograms were fitted with a theoretical exponential model (Matheron 1971), for each species separately. Densities (ind. m^{-2}) were interpolated for a regular point grid covering the study area, with the kriging accounting for a minimum of 3 stations to a distance of 1 km from the grid point.

The disc diameter (*diam*) vs. density (*dens*) relationship was estimated from the stations estimates for *Ophiocomina nigra* and *Ophiothrix fragilis* separately as follows:

$$diam = a_1 \times \log(dens) + b_1 \qquad (1)$$

where *diam* are the average disc diameters observed in each station and *dens* are the corresponding densities; a_1 and b_1 are species-specific constants. The coefficients of variations (i.e. standard deviation/mean of disc diameter × 100) were previously calculated for each station to test for the homogeneity in diameter within each station.

The ash-free dry mass (*mass*) vs. disc diameter (*diam*) relationship was estimated from individual observations for *Ophiocomina nigra* and *Ophiothrix fragilis* separately as follows:

$$\log(mass) = a_2 \times diam + b_2 \qquad (2)$$

where a_2 and b_2 are species-specific constants.

Combination of Eqs. (1) and (2) allowed estimating the average individual ash-free dry mass from station densities as follows:

$$\log(mass) = a_3 \times \log(dens) + b_3 \qquad (3)$$

with $a_3 = a_1 \times a_2$ and $b_3 = b_1 \times a_2 + b_2$.

For each grid point, biomass per square meter was calculated from kriged densities ($dens_k$) by multiplying the average individual mass (*mass*, Eq.[3]) with the number of individuals per square meter (i.e. $dens_k$) as follows:

$$\text{Biomass} = \exp[a_3 \times \log(dens_k) + b_3] \times dens_k \qquad (4)$$

The total biomass of the studied area (27 km^2) was summed from grid biomass Eq. (4) for each species and each survey. Eqs. (1) & (2) could not be estimated from the 1987 survey as individual diameters and ash-free dry mass were not recorded. Estimators of the 2011 survey (i.e. a_3 and b_3) were thus used to estimate the 1987 biomasses from kriged densities.

Models and maps were performed with the R-software (R Development Core Team 2012); the 'gstat' library was used for estimating the parameters of the semi-variogram and for kriging.

Seasonality index

A seasonality index was used as a proxy to estimate the grazing pressure of suspension-feeding compartment in the ecosystem (Chauvaud et al. 2000). The seasonality index (α) is defined as $\alpha = 260 - \beta$, where β is the number of days required to obtain half of the integrated chl *a* biomass (Berger & Wefer 1990). We retrieved published data (from 1977 to 1996) of seasonality index (α) assessed over 260 d (from 15 February to 3 November) by Chauvaud et al. (2000), and built up the same seasonality index from 1999 to 2011. The integrated chl *a* biomass was estimated from surface-water chl *a* concentrations collected using data from the Bay of Brest buoy operated by the Service d'Observation en Milieu Littoral, INSU-CNRS, Brest (http://somlit.epoc.u-bordeaux1.fr/; SOMLIT NATIONAL 2005).

RESULTS

Distribution and density

Deep changes were observed in the distribution of the 2 ophiuroid species between 1987 and 2011 (Fig. 2). Data from 1987 showed that *Ophiocomina nigra* was distributed in several patches in the central and in the north-easternmost parts of the study area. The largest patch was located in the central part and reached maximum densities between 150 and 500 ind. m^{-2} (Fig. 2). The interpolations revealed a 5-fold increase in total *O. nigra* densities, between 1987 (1.7×10^9 ind. for 27 km^{-2}) and 2011 (8.6×10^9 ind. for 27 km^{-2}), and reached densities of up and 1500 ind. m^{-2}. The population distribution pattern remained very similar to 1987 (Fig. 2a) but showed that high density levels of between 150 to 500 ind. m^{-2} extended over almost all the study area (Fig. 2b). In 1987, distribution of *Ophiothrix fragilis* showed a similar pattern of distribution, with a central patch reaching maximum densities of between 500 and 1000 ind. m^{-2} (Fig. 2c). The distribution of *O. fragilis*

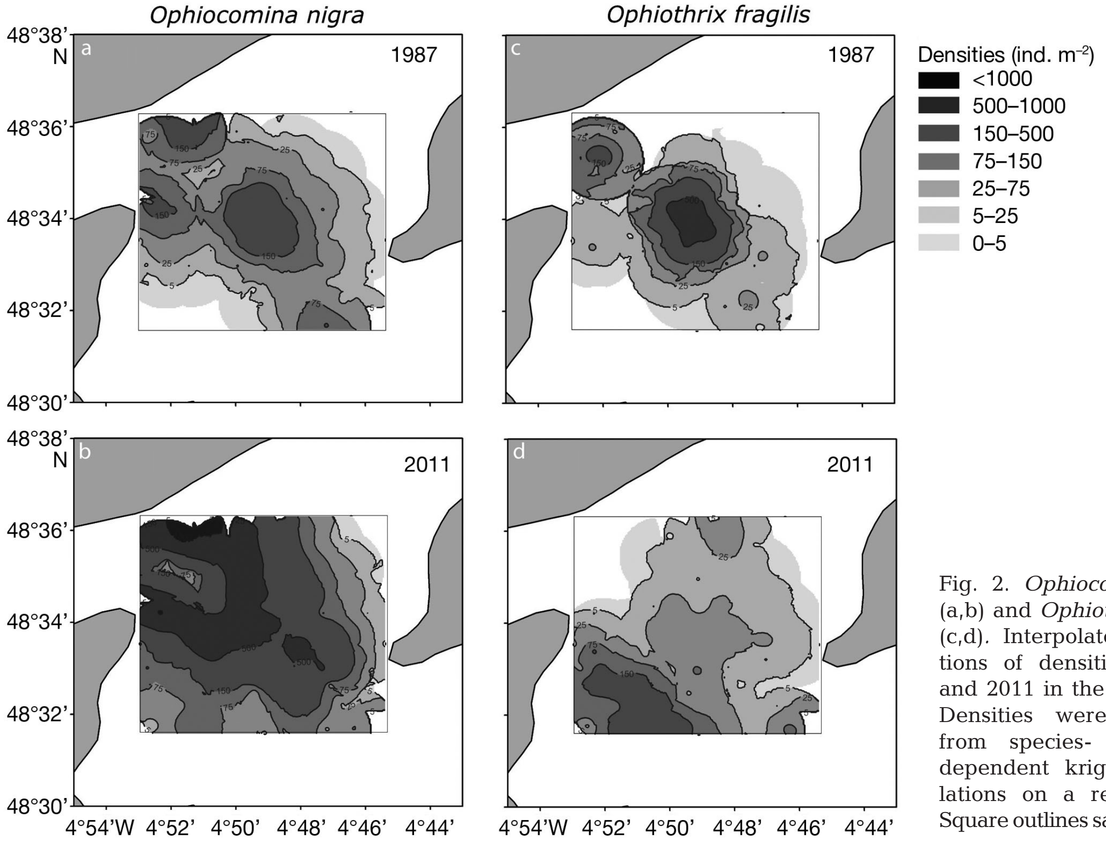

Fig. 2. *Ophiocomina nigra* (a,b) and *Ophiothrix fragilis* (c,d). Interpolated distributions of densities in 1987 and 2011 in the study area. Densities were estimated from species- and year-dependent kriged interpolations on a regular grid. Square outlines sampling area

drastically changed between 1987 and 2011: total densities decreased by ~30 % (from 1.7×10^9 to 1.2×10^9 ind. for 27 km^{-2}) in the study area, and up to 90 % in the central patch of the study area, which highlighted a local shift between ophiuroids. Individuals are now concentrated towards the southernmost part of the study area with the highest densities >400 ind. m^{-2} (Fig. 2d). The spatial distributions of *O. nigra* and *O. fragilis* revealed an important change over 25 yr, with both species having a complementary distribution in space. The high density area of *O. fragilis* seems now to be overlapping the slipper limpet *Crepidula fornicata* beds (shaded contours in Fig. 1). The HD videos revealed that these *C. fornicata* beds mainly consisted of dead shells in this area.

For the 2 species, coefficients of variation were calculated from disc measurements (2011 HD pictures) and showed a mean (± SD) of 17 ± 5 % and 20 ± 7 % respectively for *Ophiocomina nigra* and *Ophiothrix fragilis*, hence supporting a relative homogenous size structure within each station. The relationship between mean diameter and density (Eq. 1) was significantly negative for *Ophiocomina nigra* ($R^2 = 0.58$ with $p < 0.001$; n = 101, Table 1) and *Ophiothrix. fragilis* ($R^2 = 0.73$ with $p < 0.001$; n = 15, Table 1). For both species, these models showed that the higher the density, the smaller the specimens (Fig. 3).

Few observations also showed high densities of *O. nigra* (>1500 ind. m^{-2}) beyond the sampling area, especially in the narrow opening channel, often on rocky area and gravel sediments. Mixed *O. nigra* and *O. fragilis* beds were also observed in stations towards the Aulne estuary, where densities of >150 ind. m^{-2} were calculated (Fig. 1)

Table 1. Estimated parameters of the relationships between individual diameter (*diam*), station densities (*dens*) or individual ash-free dry mass (*mass*) of Eqs. (1–3)

Parameters	*Ophiocomina nigra*	*Ophiothrix fragilis*
Eq.(1) $diam = a_1 \times \log(dens) + b_1$		
a_1	−1.55	−2.06
b_1	18.83	19.50
Eq.(2) $\log(mass) = a_2 \times diam + b_2$		
a_2	0.22	0.25
b_2	2.18	3.03
Eq.(3) $\log(mass) = a_3 \times \log(dens) + b_3$		
$a_3 = a_1 \times a_2$	−0.34	−0.52
$b_3 = b_1 \times a_2 + b_2$	6.26	7.90

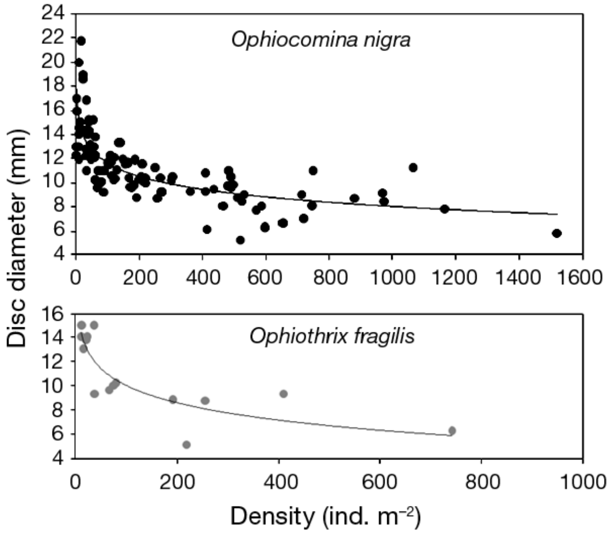

Fig. 3 *Ophiocomina nigra* and *Ophiothrix fragilis.* Relationships between mean disc diameter and density (ind. m^{-2}) estimated from 2011 video pictures

Biomass

The relationships between size and biomass (organic matter, Eq. 2) were significantly positive for *Ophiocomina nigra* ($R^2 = 0.84$ with $p < 0.001$; $n = 196$) and *Ophiothrix fragilis* ($R^2 = 0.70$ with $p < 0.001$; $n = 183$) (Table 1, Fig. 4). The resulting relationships between density and biomass Eq. (4) were positive for *O. nigra* and *O. fragilis* (Fig. 5). The estimate of the total biomass in the study area showed that while the biomass of *O. fragilis* remained similar between 1987 and 2011 (~360 t for 27 km²), *O. nigra* biomass increased 3-fold, ranging from <200 t in 1987 to ~600 t ash-free dry mass in 2011 (Fig. 6).

Seasonality index (α)

The seasonality index (α) decreased between 1980 and 1996, indicating that more days were needed to reach 50% chl *a* biomass. The seasonality index estimated between 1999 and 2011 showed the exact opposite trend, with a decreasing number of days to reach 50% chl *a* biomass (Fig. 7).

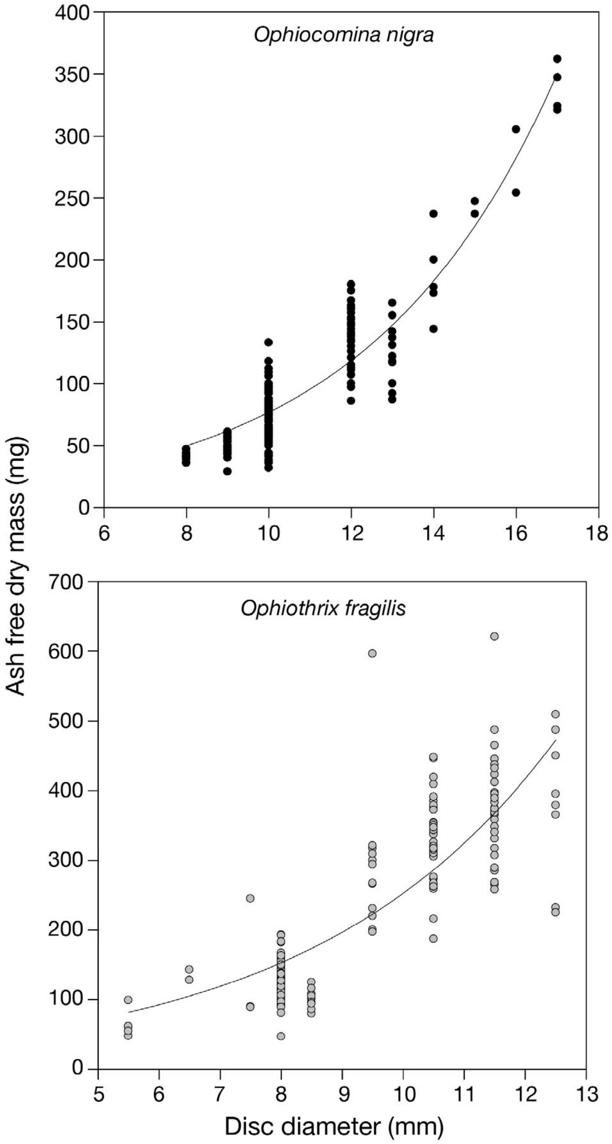

Fig. 4. *Ophiocomina nigra* and *Ophiothrix fragilis*. Relationships (Model 2) between the ash-free dry mass and the disc diameter. Model was fitted from all 2011 data pooled across the study site

DISCUSSION

Changes in ophiuroid dominances

Echinoderms play key ecological roles in ecosystems, where they often exhibit large population densities (Uthicke et al. 2009). We focused on 2 very common ophiuroid species that occur in most European shallow coastal areas in a large variety of sedimentary features. The Bay of Brest was chosen to revisit the population status of *Ophiothrix fragilis* and *Ophiocomina nigra*, 2 very abundant species structuring the benthic compartment (Hily 1989, 1991). We used data collected 25 yr ago and conducted a survey with the same protocol to reveal multidecadal changes in the density and the biomass of the 2 ophiuroid species. The 2011 survey highlighted

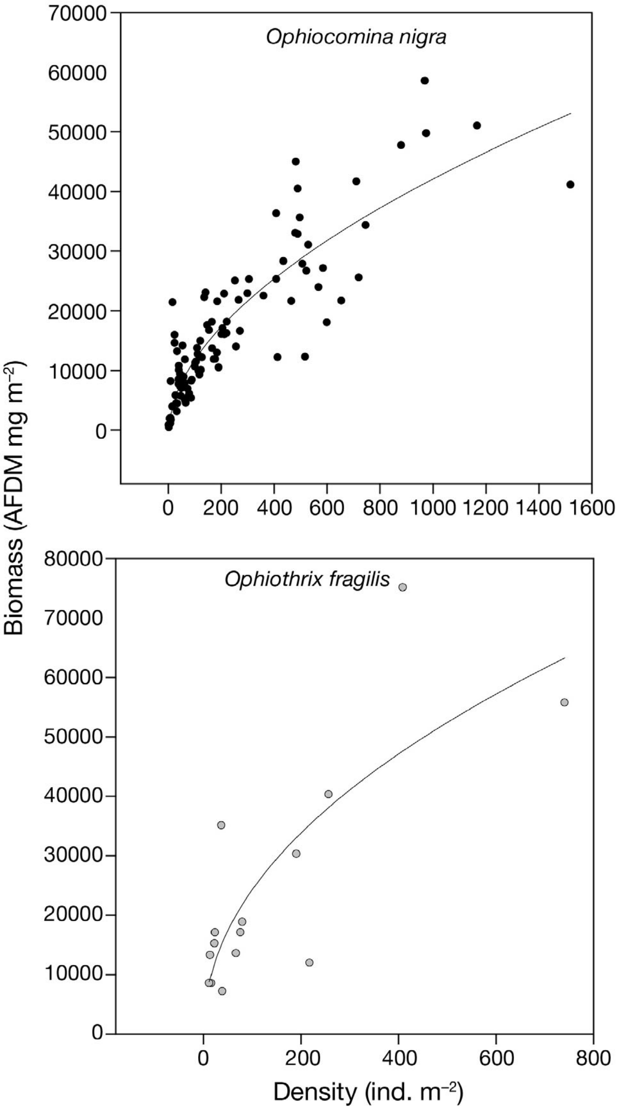

Fig. 5. *Ophiocomina nigra* and *Ophiothrix fragilis*. Relationships (Model 3) between the biomass (ash-free dry mass: AFDM) and the population density. Model was fitted from all 2011 data pooled across study site

that *O. nigra* had spread over and beyond the whole prospected area. Its densities were 5 times higher than the ones estimated for 1987: using the existing relationship between density and size, we showed that *O. nigra* biomass increased 3-fold, reaching 22 t km^{-2} (ash-free dry mass) in 2011. The *O. fragilis* population not only decreased in density but moved to the southernmost part of the study area. The total biomass of this species did not change between 1987 and 2011, and the 2011 distribution pattern revealed a clear exclusion of *O. fragilis* from the central part of the study area, where *O. nigra* is now highly dominant.

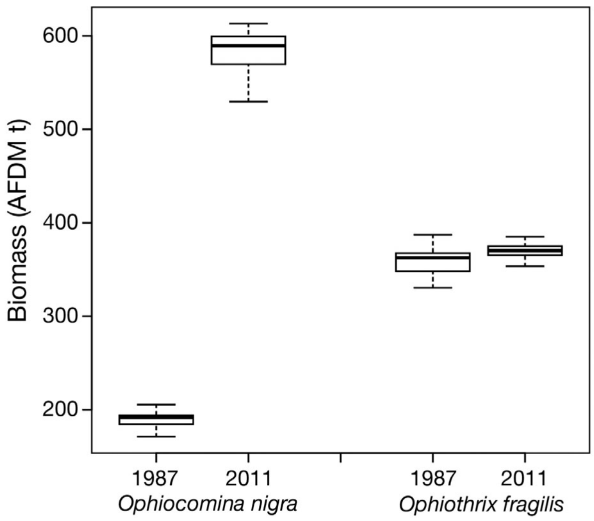

Fig. 6. *Ophiocomina nigra* and *Ophiothrix fragilis*. Boxplots estimates of total biomass (ash-free dry mass: AFDM, t) issued from species- and year-dependent kriged densities on a regular grid and density vs. biomass relationships (Model 4) in the study area. Horizontal line in box indicates the mean of the data, box and whiskers include 20 to 75% and 95% of the data, respectively

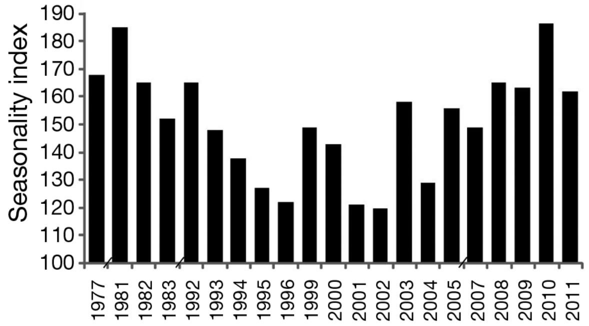

Fig. 7. Variation in the seasonality index $\alpha = 260 - \beta$, where β is the number of days required to obtain half the integrated chl *a* biomass assessed over 260 d (from 15 February to 3 November), as calculated in Chauvaud et al. (2000, from 1977 to 1996) and in the present study (from 1999 to 2011), using data from the Bay of Brest buoy operated by the Service d'Observation en Milieu Littoral, INSU-CNRS, Brest (http://somlit.epoc.u-bordeaux1.fr/; ©SOMLIT NATIONAL 2005) since 1997

To our knowledge, this study reported for the first time such an increase in density for *Ophiocomina nigra*. Mixed *Ophiothrix fragilis* and *O. nigra* beds are a common feature in a variety of sediments in Europe, but are usually largely dominated by *O. fragilis* (e.g. Allain 1974, Vevers 1952, Cabioch 1967, Hughes 1998). While *O. fragilis* densities can peak with >5000 ind. m^{-2} (Davoult & Migné 2001, Méar et al. 2006) because of its gregarious and social behavior (Broom 1975, Brun 1969), *O. nigra* is very rarely reported with high densities, especially when co-occurring with *O. fragilis* where it usually represents <8% of the ophiuroid population (Holme 1984). Our maximum values (e.g. 1500 ind. m^{-2}) matched the only high density of *O. nigra* reported in the literature, in the west coast of Scotland, where this species locally reached 2000 ind. m^{-2} in a mono-specific bed (Aronson 1989). *O. fragilis* populations were reported to be stable over time (e.g. Holme 1984, Lefebvre et al. 2003), and the present investigation supports this population characteristic, when considering the total biomass of this species in the central Bay of Brest. In 1987, Hily (1991) reported the most dense *O. fragilis* beds in the central part of the study area in response to occurrence of optimal habitat features, such as suitable substrata, favorable local hydrodynamic conditions, and a high primary production. Our video survey showed that this species was now mainly reported in close association with dead slipper limpet *Crepidula fornicata* beds.

Echinoderms have previously been identified as a 'boom-bust' phylum, because of notoriously large changes in population density, but most echinoderm models refer to Asteroidea or Echinoidea families (see review by Uthicke et al. 2009). In our study, a 5-fold increase in *Ophiocomina nigra* density fits the definition of a large population density variation (at least doubling in population density), also called outbreaks, as defined by Uthicke et al. (2009). While it is difficult without time series to estimate the level and the tendency of deep changes in ophiuroid population, the present investigation targeted adults of well-known species with a long lifespan (up to 14 yr, as suggested by Gorzula 1977). Similar changes were observed in several embayments (e.g. in the Bay of Douarnenez). Observed changes in population densities were then not local episodic 'boom-bust' events but were very likely due to progressive changes in environmental conditions and/or anthropogenic factors.

Ophiuroid success linked with human-induced environmental changes

In most cases, fluctuations in high density populations are reported for echinoderms with planktotrophic larval development (Uthicke et al. 2009, Valentine & Edgar 2010). Both *Ophiocomina nigra* and *Ophiothrix fragilis* are planktotrophic developers (Stöhr 2005), hence supporting the possibility of 2 outbreaking ophiuroids. Because the 2 species exhibit similar planktotrophic developments, large population density variations in 1 of the 2 species are most likely triggered by the association of biological traits or changes in food supply of adults.

While both adult ophiuroid species are reported to be suspension-feeders, collecting particles from the water-column with their arms (Aronson 1989), *Ophiocomina nigra* exhibits a much wider trophic plasticity and displays a very important versatile feeding behavior (Fontaine 1965), as this species is more mobile at the sediment-water interface and commonly behaves either as a deposit-feeder feeding from the surface film (Magnus 1963), browses from a variety of deposited material (Vevers 1956), or behaves as a carnivorous species, foraging over detritus or carrions (Nagabhushanam & Colman 1959). As demonstrated for other echinoderms (Norkko et al. 2007, Thrush & Cummings 2011), flexibility in feeding habits of *O. nigra* contributes to the success of this species (Fontaine 1965).

Changes in potential food supply in the Bay of Brest has probably resulted in an increase in *Ophiocomina nigra* density and enhanced the fecundity and fertilization success of adults, as demonstrated for other echinoderms (Sewell & Levitan, 1992). For the last decade, green tides and high production of green macrophytes *Ulva* sp. have been an increasing issue in Brittany coastal waters (Dion & Le Bozec 1996, Merceron et al. 2007). The Bay of Brest as well as many other embayments (inshore fringes and estuaries) exhibits frequent macroalgae blooms (Ménesguen et al. 2006), hence providing a large supply of macroalgae detritus for species which may benefit from this. Overall, *O. nigra* and *Ophiothrix fragilis* are widespread and abundant in many embayments in Brittany, especially southward in the Bay of Douarnenez (also impacted by green macroalgal blooms) where *O. nigra* also sharply increased during several decades (M. Guillou & A. Blanchet-Augriny unpubl. data).

Simultaneously, rocky western coasts of France (including the Bay of Brest) have been heavily colonized by wild oysters *Crassostrea gigas* in the last decade (Cognie et al. 2006). Lejart & Hily (2011) investigated the consequences for the Bay of Brest and reported that mass biodeposits from the invasive oyster reefs were washed away from the reefs and sedimented in deeper areas of the bay. Such organically rich inputs could result in a diversified and unusual deposit-feeder fauna (Hily 1991, Lejart & Hily 2011). Because of its higher trophic plasticity, *Ophiocomina nigra* benefited more from those changes than *Ophiothrix fragilis*.

Anthropogenic disturbances in the Bay of Brest could also have induced changes in ophiuroid distribution. Dredging activities in this bay targeted the scallop *Pecten maximus* and more recently the warty clam *Venus verrucosa*. While the landing of scallops remained <25 t yr^{-1} in 1980, it has linearly increased since then to reach >350 t yr^{-1} in 2000 (Fleury et al. 2003). As demonstrated for the starfish *Asterias rubens* in the Barents Sea (Zolotarev 2002) or for the ophiuroid *Ophiura albida* (Gaspar et al. 2003), chronic dredging activities attract mobile scavengers and predators (Kaiser & Spencer 1994). In late 1980, a restocking and sea-ranching program was launched for scallop in the Bay of Brest (Alban & Boncoeur, 2008). The main seeding area perfectly fits within our study area, in the central part of the bay. This seeding program and the ultimately linked dredging activities very likely benefited *Ophiocomina nigra*, which is reported to feed on damaged or weak scallops (Jenkins et al. 2004). Over long-term periods, this could partly explain the success of *O. nigra*.

Ecological consequences of changes in ophiuroid densities

Changes in Echinoidea population densities can have deep consequences in the functioning of the ecosystem, as highlighted in the die-off of the tropical herbivore urchin *Diadema antillarum*, which transformed the coral community into a macroalgal community (Lessios 1988) or in the outbreak of urchin populations adversely affecting the kelp forest dynamic (Steneck et al. 2004). The Bay of Brest is a system where primary production and phytoplankton bloom events are partly regulated by suspension-feeders (Grall & Chauvaud 2002), and where large populations of the invasive slipper limpet *Crepidula fornicata* or the ophiuroid *Ophiothrix fragilis* dominate the benthic suspension-feeding compartment (Hily 1991, Chauvaud et al. 2000, Grall & Chauvaud 2002). In addition to a spatial shift of the population, our video survey revealed that the *O. fragilis* had now colonized *C. fornicata* beds and that this area was the only one left uncolonized by *Ophiocomina nigra* in high densities. In the studied area, video filming revealed that the vast majority, if not all, slipper limpets were dead. We suggest here that the *O. fragilis* beds covering the *C. fornicata* beds had progressively lead to the death of most of the slipper limpets underneath. Whether *O. fragilis* caused the death of *C. fornicata* or not, dead shell beds are a very suitable habitat for *O. fragilis* which commonly live in more or less muddy microhabitats among shell and gravels (Cabioch 1967, Warner & Woodley 1975, Hily et al. 1988). Hence, the present study showed that *O. nigra* has excluded *O. fragilis* from the central part of the bay, leaving dead slipper limpet beds as potential habitat for *O. fragilis* and limiting this invasive gastropod's distribution in the central part of the Bay of Brest.

The first and probably the main consequence of ecological effect of changes in ophiuroid populations in this bay is that the *Crepidula fornicata* beds may no longer have the same grazing impact on the microalgae (phytoplankton) biomass. Indeed, Chauvaud et al. (2000) clearly demonstrated that the seasonality index was decreasing between 1980 and 1996 while the density and biomass of suspension-feeders (and mostly the invasive *C. fornicata*) increased, indicating that the suspension-feeders were controlling the phytoplankton biomass. The opposite trend was observed between 1999 and 2011 (Fig. 7), which indicates that suspension-feeders were probably no longer having the same controlling effect on the phytoplankton blooms in the Bay of Brest.

Ophiuroid beds are known to play an important role in the fluxes of organic matter from the pelagic to the benthic system (Davoult et al. 1991). Sediment reworking through ophiuroid bioturbation also contributes to sediment biochemical processes (Lohrer et al. 2004, Webb & Eyre 2004, McLenaghan et al. 2011). Because of its high densities and its mobility and burrowing activity within the superficial sediment layers, *Ophiocomina nigra* is likely to locally affect nutrient cycling at the sediment surface and ultimately modify the associated benthic assemblages. Ultimately, spreading of ophiuroid species over large areas may affect the habitat diversity. This assumption is supported by several studies and theoretical concepts in biology and ecology suggesting that the replacement of specialist by generalist species, such as *O. nigra*, with a change in functional attributes, is causing functional homogenization at the community level (Thrush et al. 2006, Clavel et al. 2010). Moreover, because of its non-exploitation by humans or predators, *O. nigra* could be considered as a trophic impasse and may decrease the efficiency of overall food web interactions in the ecosystem, as previously showed for *Crepidula fornicata* in other shallow-water systems (Arbach Leloup et al. 2008, Cugier et al. 2010).

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