Investigation into the ecology of the ormer (*Haliotis tuberculata* L.), factors influencing spatial distribution

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Abstract

The factors affecting spatial distribution of the ormer (*Haliotis tuberculata* L.) in the vicinity of Saint-Malo (northern Brittany, France) are analyzed using a multivariate approach. A correspondence analysis is applied to a contingency table based on 200 samples. Ormers are always absent from smooth rocky substrata, exposed to a strong current or deeper than 8 m below low chart datum. Abundance and biomass of *H. tuberculata* are distributed along a gradient correlated with an increasing complexity of habitat and a reduction of current. Otherwise, no correlation has been found between characteristics of ormer distribution and surge, depth or large and turf algae.

Keywords : *Haliotis*, Brittany, ecology, spatial distribution, correspondence analysis.

Étude écologique de l'ormeau (Haliotis tuberculata *L.*), *paramètres influant sur la répartition spatiale.*

Résumé

Les facteurs influençant la répartition spatiale des ormeaux (*Haliotis tuberculata* L.) dans la région de Saint-Malo (Bretagne nord) ont été étudiés à l'aide d'une analyse factorielle des correspondances. Cette dernière a été appliquée à un tableau de contingence (population × milieu) défini à partir de 200 stations. Les ormeaux sont toujours absents des zones rocheuses sans anfractuosité, à courant fort et à profondeur importante (>8 m). Les densités et les biomasses évoluent proportionnellement à la complexité du substrat mais décroissent lorsque le courant s'intensifie. Enfin, l'espèce marque une nette indépendance vis-à-vis des macrophytes dressées, de la houle et de la profondeur.

Mots-clés : *Haliotis*, Bretagne, répartition spatiale, analyse factorielle des correspondances.

INTRODUCTION

The ormer (*Haliotis tuberculata* L.) occurs along the rocky shores of the eastern Atlantic from south of the English Channel down to western Africa (Gaillard, 1958). However, it occurs in sizeable densities only off the north of the Armorican peninsula and in the Channel Islands, where the species was exploited until 1973 (Forster *et al.*, 1982). Ormer gathering using SCUBA is prohibited along the French coast and the presumed abundance of the subtidal stock aroused the interest of local fishermen. Therefore, scientific investigations were undertaken in Brittany to estimate the potential for the commercial exploitation of these gastropods.

Information on the ormers and their environment was collected during stock assessment in the vicinity of Saint-Malo (Clavier and Richard, 1986*a*). The main factors affecting the distribution of this species were determined from these data and are presented in this paper.

The role of some ecological factors is already well known and we do not re-examine the fact that ormers live exclusively on shallow rocky bottoms (Crofts, 1929; Forster, 1962). In this study, we consider the characteristics of the environment e. g. the range of habitat or the intensity of surge and currents. We also consider the algal community and the population size structure of the ormers. The influence of these factors are assessed by multivariate analysis.

MATERIAL AND METHODS

Data were collected by SCUBA diving utilizing a stratified sampling survey with optimum allocation calculated on biomass data (Cochran, 1963). The sampling area was divided into three strata according to the nature of rocks (schist, granulite and sandstone). A total of 200 units of 10 m² were investigated. Critical comments on the sampling are given in Clavier and Richard (1986*a*).

The shell length (Li) of each specimen collected was measured to the nearest millimeter and the individual fresh total weight (Wi and grams) was calculated using the allometric relationship $Wi = 6.586\ Li^{3.177}$ derived from 986 pairs of measurements (Clavier and Richard, 1986*a*). The available information for the ormer population in each sample consists of density (Ni), biomass (Bi) per 10 m² and size frequency distribution. In order to provide a simple view of the demographic pattern of the population, size frequencies are grouped into four classes with corresponding ages. The legal minimum size of ormers in France is 80 mm.

Table 1. — Coding of the demographic structure of the ormers.

	Code	Size (mm)	Age (yr)
Very young	Vy	<40	0-3
Young	Yg	40-80	3-5
Adult	Ad	80-100	5-9
Old	Od	>100	>9

For each sampling unit, the ormer population is defined by two types of parameters, global population (density, biomass) and demographic parameters (density of each age class). Moreover, on the same sample, available environmental information is provided by eight factors: Z, depth in meters for interval 0-10; Ha, potential habitat corresponding to any shelter with at least one firm side (crevice, underside of boulder...), habitat was defined according to an ordinal scale; Ea, crustose algae (% of coverage); Sa, algae less than 25 cm high (% of coverage); La, algae higher than 25 cm (% of coverage); Cu, accounts for both current speed and length of still water period; Wa, index related to surge exposure. As quantitative information on Cu and Wa is not available for each sampling site, these parameters are defined according to an ordinal scale with only four classes and based upon information provided by coastal trap fishermen who are familiar with local hydrodynamic conditions.

The original data are expressed in either nominal, ordinal or interval scales and, in order to provide homogeneous information, the data are transformed. Population and environmental parameters are coded in a limited number of classes (3 to 5) with each class having a similar number of observations. *Tables* 2 and 3 give the limits of these classes.

An inertia analysis is performed on a multidimensional contingency table "population × environment". The main reason for a contingency table analysis is to assess directly the links between population and environment, which is the main objective of the present study. Such an investigation goes beyond the conventional scope of a simple ordination. Moreover, using a contingency table is of particular interest in the case of simultaneous analysis of mixed data and non-monotonic distributions (Legendre and Legendre, 1984). Within this context, correspondence analysis (Benzecri *et al.*, 1973) also called reciprocal averaging (Hill, 1973) and primarily developed for the analysis of contingency tables, appears to be the most appropriate technique.

We also established the 28 contingency tables between the envionmental parameters themselves in order to estimate their amount of redundancy.

RESULTS

Correspondence analysis makes it possible to plot simultaneously the projections of the line attributes (environmental parameters) and column attributes (population parameters). In order to keep graphics legible, the two types of projection are given separately but our comments will describe the links between these two structures (*fig.* 1, *A*, *B*).

The three first inertia axes extracted by the analysis explain 83.5% of the total variance, with 59.3%, 17.7% and 6.5% for axis 1, 2 and 3 respectively. Our comments will be restricted to the plane 1-2 because of the small part of the variance explained by axis 3. The projection of the population attributes (*fig.* 1 *A*) suggests a 'horseshoe effect' (Kendall, 1971), also known as Guttman effect (Benzecri *et al.*, 1973). The Guttman effect reveals the existence of a predominant factor expressed, here, through the two first axes. For every parameter, ordination of the population attributes reveals a clear gradient from the nil and low indices in the negative scores of axis 1, to high indices in the positive scores of the same axis. It suggests a general factor of abundance for the population. The closeness of density (Ni) and biomass (Bi)

Table 2. – Double entry array used for coding population parameters. For example, Yg3 corresponds to the ormers less than 40 mm long with more than 7 individuals/10 m^2. N: density; B: biomass; Vy: very young; Yg: young; Ad: adults; Od: old ormers.

Code	N N/10 m^2	B g/10 m^2	Vy N/10 m^2	Yg N/10 m^2	Ad N/10 m^2	Od N/10 m^2
0	0	0-100	0	0	0	0
1	1-2	100-400	1	1-2	1-2	1-2
2	3-7	400-1,000	2-3	3-7	3-7	3-7
3	8-21	1,000-2,400	3	>7	>7	>7
4	21-60	2,400-6,400	–	–	–	–

Table 3. – Double entry array used for the coding of environmental parameters. Z: depth; Ha: habitat; Ea: crustose algae; Sa: small algae; La: large algae; Cu: current; Wa: surge exposure.

Code	Z (m)	Ha	Ea (%)	Sa (%)	La (%)	Cu	Wa	Substratum
0	0-2	null	0	0-20	0-10	low	null	sandstone
1	2-4	low	0-25	20-40	10-30	mean	low	granulite
2	4-6	mean	25-50	40-60	30-50	strong	mean	schist
3	6-8	strong	50-80	60-80	50-60	very strong	strong	–
4	>8	–	80-100	80-100	60-100	–	–	–

attributes exhibits a strong relationship between these two parameters and suggests some constancy of the age structure in our samples. The relative closeness of the projection of demographic attributes with the same code supports this statement. Very young individuals (Vy) are therefore preferentially located towards high scores of axis 1 and are not consistent with this.

In the case of correspondence analysis, the relationship between environmental parameters and population attributes may be considered as the distance between their projections on the plane 1-2. Parameters contributing the most to plane 1-2 are habitat, current and depth (*fig.* 1 *B*). Absence of ormer (NO, BO) corresponds to a null potential habitat (HaO), a strong current (Cu3) and a depth below 8 m (Z4). In the same way, the general factor of abundance is closely related to an increase in potential habitat (Ha1 to Ha3) and a decrease in current (Cu2 to Cu0). The vegetation index also follows this gradient. High ormer densities occur with mean and high crustose algae indices (Ea2, Ea3, Ea4) and low coverage of large macrophytes (La1). Lastly, the geological nature of the bottom follows the general trend of abundance. Schist bottom (Schi) is located in the same factorial area as high biomass or high density, while sandstone (Sands) bottom is associated with the low values of these parameters. The granulitic (Gran) substrate stands in an intermediate position with regard to the global population attributes.

DISCUSSION

The widespread distribution of the ormer is mainly dependent on larval settlement at metamorphosis, whereas densities are related to subsequent survival of individuals (Breen, 1980). The mean range of displacement of the ormer does not exceed a few metres a year (Clavier and Richard, 1984) and the occurrence of an abundant population on a suitable substratum cannot be related to migration from a recruitment area. Larval settlement, as well as the abundance of population, are induced by environmental factors and biological interactions whose combined effects are observed.

Factors influencing larval settlement cannot be assessed directly from our results. We consider only the distribution of individuals smaller than 40 mm and less than 3 years old (Clavier and Richard, 1986 *b*). Our results suggest that habitat is a relevant factor for juvenile abundance as for general population abundance, but it is likely to have no direct effect on larval settlement. Habitat rather provides a shelter from predators and will be discussed later. Pink crustose algae (mainly *Lithothamnium* species) are generally considered to be a preferential substratum for larval settlement of *Haliotis* at metamorphosis (Morse *et al.*, 1979; Morse and Morse, 1984; Shepherd and Turner, 1985). *H. tuberculata* data are consistent with this (Clavier and Richard, 1986 *b*). Forster (1962) also observed high densities of adults on rock surfaces encrusted with pink algae. Our data suggest a link between this kind of algae and the highest densities of ormers. Examination of *table* 4 indicates that this is mainly due to juveniles. Conversely, our analysis suggests an inverse relationship between current velocity and general abundance, including juveniles. According to our data, young ormers are found preferentially in places where the flow becomes zero or negligible over extended periods during the tidal cycle. To support this hypothesis, we present in figure 2 the densities and the length frequency distribution of the ormers around Fort Dugesclin. Juveniles are located only in the eastern cove sheltered from the main tidal currents. As they grow, individuals progressively diffuse on the neighbouring grounds and some large

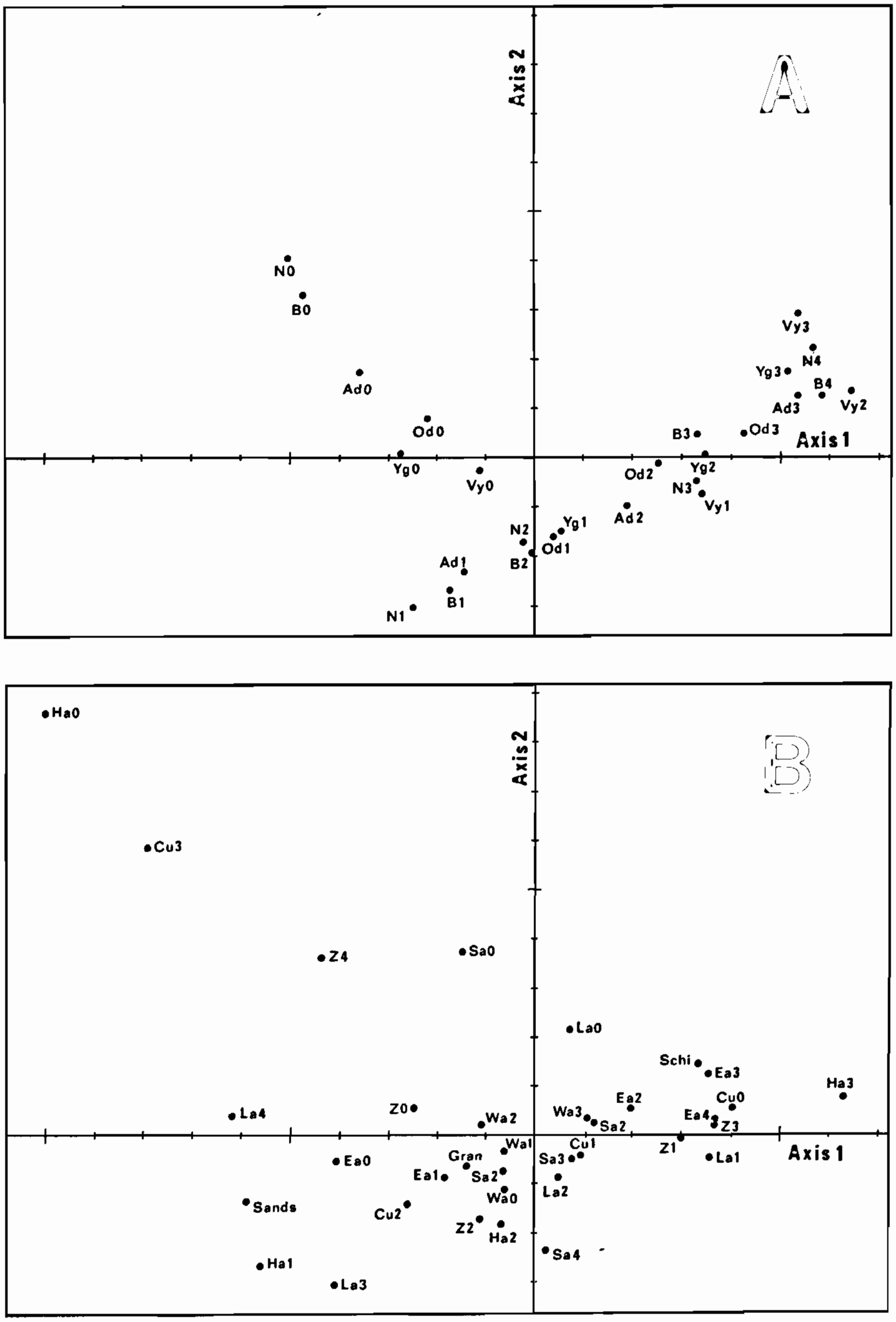

Figure 1. – Correspondence analysis. Ordination of the population attributes (*A*) and of the environmental parameters (*B*) in the plane 1-2.

Table 4. – Proportions of samples with or without very young (Vy) and old (Od) ormers according to five classes of crustose algal (Ea) cover.

Crustose algae (% of coverage)	0	0-25	25-50	50-80	80-100
% of samples with Vy	5	11	26	28	39
% of samples without Vy	95	89	74	72	61
% of samples with Od	44	52	62	59	56
% of samples without Od	56	48	38	41	44

specimens may be encountered in less sheltered places. Slow currents were also observed by Tanaka *et al.* (1986) on the nursery grounds of the Japanese species, *Haliotis discus*.

With respect to biological interactions, there is an obvious correlation between densities of juveniles and adult ormers. This link may be related to the lack of real migration. The species being essentially sedentary (Clavier and Richard, 1984), an adult individual never moves more than a few hundred meters from its

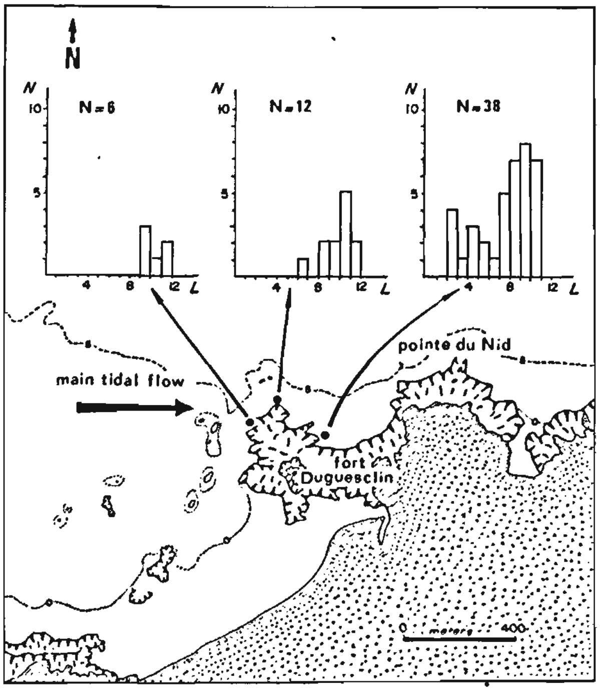

Figure 2. — Densities on 10 m² (N) and size frequency distributions observed at three locations distributed along a hydrodynamic gradient. L: shell length in centimeters.

settlement area. However, it is possible that adults may influence larval settlement in a manner similar to the Japanese species *H. discus hannai* (Seki and Kan-No, 1981. According to these authors, mucous tracks left by moving adults induced larval settlement and metamorphosis.

When environmental conditions are suitable for larval settlement, population abundance is related to individual survival. The results of our study underline the close relationship between ormer density or ormer biomass and the number and size of durable anfractuosities on hard bottoms. We define these rugged grounds as the habitat of the ormer. *H. tuberculata* is absent from places with a smooth substratum, whereas its abundance increases with substratum complexity. Such a relationship has been found for several Japanese abalones (Inoue, 1976). The preferred habitat of the ormer consists of fissures and crevices on bedrock (Forster, 1962; Forster *et al.*, 1982), rock ledges (Inoue, 1976) and the underside of boulders lying on bedrock or sand (Stephenson, 1924; Forster, 1962; Forster *et al.*, 1982). Such a habitat provides a firm substratum allowing for an optimal adherence of the pedal sole (Breen, 1980) to resist predators and firm enough to avoid shifting by waves and surge (Crofts, 1929). It also offers shade from direct illumination (Crofts, 1929) and shelter from predators.

The complexity or unevenness of the bottom differs according to rock type. Schist naturally splits into narrow crevices and forms numerous elongated boulders which are very suitable as a habitat for ormers. In the study area, the most abundant ormer populations are actually located on schist bottoms. In contrast, granulitic and sandstone rocks form scattered large round boulders or solid bedrock, with wide and shallow crevices less suitable for the establishment of an abundant population.

The present study does not consider potential predators or competitors of ormers as they are absent or scarce in the Saint-Malo region. The main ormer predators are *Octopus* species (Stephenson, 1924; Crofts, 1929) and starfishes [*Asterias rubens* (L.), *Marthasterias glacialis* (L.)] (Stephenson, 1924; Crofts, 1929; Forster, 1962). The former disappeared during the 1963-1964 cold winter and the latter are absent from the study area (Retière, 1979). The crab *Macropipus puber* L.) and various wrasses (*Labrus bergylta* Ascanius, *Symphodus melops* L.) are likely to take young ormers but not adults (Clavier and Richard, 1985). In the study area, natural predation controls juvenile density and adult ormers are threatened only by humans. However, this feature is not characteristic of the whole distributional area of the ormer.

In the Saint-Malo region, and in particular in the study area, *H. tuberculata* is the only large grazer living on rocky bottom. Elsewhere in the world, *Haliotis* species may compete with other species, especially with sea urchins (Shepherd, 1973*a*; Breen, 1980). Likewise, in places where several *Haliotis* species coexist, each of them is restricted to a particular sub-habitat (Shepherd, 1973*b*). On suitable substrata, densities of ormers are dependent on intraspecific competition, and limiting resources (space and food) set the upper limit for populations.

H. tuberculata is essentially herbivorous but will occasionally ingest other organic particles (Stephenson, 1924). In this study, we consider the effect of three algal classes as a possible influence of algal community on ormer distribution. Abundance of large algae (*Laminaria* species) varies inversely with the density and biomass of ormers. A contingency table of large algae versus population attributes shows that there is no direct relationship. The contingency table Ha x Sh reveals a strong inverse relationship between these two parameters and may explain the observed structure. Small algae (turf) have no relation with ormer abundance and biomass gradient and are also missing where strong currents and great water depths occur. On the other hand, crustose red algae are positively related with ormer abundance and, as previously quoted, larvae of *Haliotis* show preferential settlement on such algae.

In fact, as with several other *Haliotis* species, the distribution of *H. tuberculata* is largely independent of the surrounding algal community (Cox, 1960; Leighton and Boolootian, 1963; Olsen, 1968; Inoue, 1976; Poore, 1972). However, ormer habitat is closely tied to a regular supply of drifting algae carried by currents. The quantity of such detrital algae determines ormer density where habitat is suitable. The deposition of algal fragments is inversely related to flow intensity and duration, as are the density and biomass of ormers.

Surge is an irregular event in the study area and our data suggest that it is not important in determining for ormer distribution and abundance. Ormer breeding occurs during summer (Girard, 1972; Hayashi, 1980) and larvae settle during the period of low frequency of storms. As the ormer grows, adherence of the pedal sole and cryptic habitat enable the animal to resist strong hydrodynamic conditions. However, on a small scale, surge may have an influence on the range of individual movement when the habitat is disturbed (Poore, 1972) or individuals have been knocked loose from the substrate (Minchin, 1975). Surge may also induce natural mortality when ormers are crushed by rocks during storms (Mottet, 1978).

In the study area, ormers are distributed from the intertidal zone down to about 8 m below chart datum. The intertidal segment of the population is actively harvested from the shore and is almost depleted, with only a few juveniles to be found up to 2 m above chart datum. In the subtidal zone no general relationship can be found between global density or abundance of various size classes and depth. Maximum depths occupied by ormer are of little importance in the Saint-Malo region but differ along the coast of Brittany and may go beyond 20 m in the western regions.

In conclusion, the distribution of the ormer on shallow rocky bottom is the net outcome of a number of factors which differentially affect different sizes of ormer. These various factors may be of interest to fisheries management and aquaculture development of the ormer.

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