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CONSERVATION OF LONG-LIVED MARINE SPECIES: SOME HINTS FOR ADOPTING A POPULATION APPROACH

Conservação de espécies marinhas de vida longa: algumas dicas para adotar uma abordagem de populações

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ABSTRACT

Long-lived species, whose life-span can amply exceed one century, play a fundamental role within marine communities. However, due to the short time windows covered by most research our knowledge of their demography is quite limited, consequently severely limiting the possibility of understanding their complex dynamics over the long run. Moreover, several aspects of the life-history of long-lived populations are largely unknown. This short review describes some examples of demographic analyses in terrestrial ecology, which are then applied to long-lived marine species. The ultimate aim is to suggest that wider application of demographic concepts and models could improve our ability to understand how these populations might respond to unusual increases in mortality rates due to Global Climate Changes and other sources of anthropogenic disturbance. In this framework, close, continuous, reciprocal and dialectic interaction between population mathematicians and field marine ecologists could greatly help to both design the necessary research and set out improved population dynamic models for such species. Such models would constitute an important first step in increasing our knowledge, and thereby implementing management plans for fostering the conservation of long-lived marine species, which too frequently have been defined by international authorities as data deficient.

Keywords: demography, mortality tables, life-tables, gorgonian corals, cetaceans.

RESUMO

Espécies de vida longa, aquelas com ciclo de vida superior a um século, têm um papel fundamental dentro das comunidades marinhas. Entretanto, o tempo de duração da maioria das pesquisas é curto e nosso conhecimento da demografia dessas espécies é restrito, o que traz sérias limitações no entendimento da complexa dinâmica no longo prazo. Além disso, diversos aspectos da história de vida dessas populações de vida longa são largamente desconhecidos. Essa breve revisão descreve al-

guns exemplos de análises demográficas em ecologia terrestre, que são então aplicados para espécies marinhas de vida longa. O objetivo principal é sugerir que a aplicação mais ampla de conceitos e modelos demográficos pode melhorar nossa habilidade de entendimento de como essas populações podem responder a aumentos não usuais nas taxas de mortalidade devido às mudanças climáticas globais e outras fontes de distúrbios antropogênicos. Nesse contexto, a interação próxima, contínua, recíproca e dialética entre matemáticos e ecologistas marinhos poderia ajudar a projetar pesquisas necessárias e estabelecer modelos de dinâmicas populacionais aprimorados para essas espécies. Esses modelos podem constituir um primeiro passo importante para aumentar nosso conhecimento e, assim, implementar planos de manejo para promover a conservação de espécies marinhas de vida longa, que muitas vezes têm sido definidos por autoridades internacionais como deficientes de dados.

Palavras-chave: *demografia, tabelas de mortalidade, tabelas de vida, gorgônias, cetáceos.*

INTRODUCTION

Eroding biodiversity

Human activities are eroding biodiversity, consequently reducing the environmental benefits provided to local human populations (Di Minin *et al*., 2021). Habitat loss and unsustainable harvesting are historically the most influential drivers of biodiversity reduction (Dobson, 1999). When practiced irresponsibly, harvesting can lead to population declines and even to their extinction. Prime historical examples of unsustainable harvesting leading to species extinction are the dodo, *Raphus cucullatus*,Linnaeus, 1758, the great auk, *Pinguinus impennis,* Linnaeus, 1758, Steller's sea cow, *Hydrodamalis gigas* (Zimmermann, 1780*)*, the passenger pigeon, *Ectopistes migratorius* (Linnaeus, 1766), and the thylacine, or Tasmanian tiger, *Thylacinus cynocephalus* (Harris, 1808), which was hunted to extinction due to its predation of sheep herds on the island of Tasmania.

Several approaches to conservation can be set out in response to unsustainable harvesting; they range from total protection (no harvesting at all), to limited harvesting and strict prohibitions in response to unsustainable harvesting rates. However, too strict bans prevent locals from benefiting from nature conservation, and the lack of any local benefit can lead to increased wildlife poaching (Dobson, 1999; Di Minin *et al*., 2021). The effects of unsustainable harvesting on marine populations may be nowadays even more dramatic as they act in synergy with GCC.

To avoid species extinction our efforts towards sustainable harvesting and conservation have been based on sound knowledge of the basic demographic features of endangered populations. Demography (with the notable exception of its 13th-century Italian forerunner, Leonardo Fibonacci) was established as a science at the end of the 18th century and was initially dedicated to the study of human populations (Malthus, 1798). Only during the early 20th century was it applied to the study of animal populations.

From community to long-lived species conservation

To date, a large number of conservation plans for terrestrial and freshwater populations have been formulated based on sound demographic data, while far fewer have focussed on single marine species and populations. Programs dealing with marine environments have more frequently focussed on community and ecosystem conservation, sometimes based on short-term monitoring of marine biodiversity, through rarely based on the life-history of single (long-lived) populations. In general, demographic monitoring of populations is quite infrequent, and hence establishing baselines for past population abundance is difficult. Some prime examples of pristine abundance estimates include Jackson's study based on the historical catch proxies of the green turtle (*Chelonia mydas*) in the Caribbean (Jackson, 1997) and Roman and Palumbi's paper on North Atlantic whaling (Roman & Palumbi, 2003). Another notable example is the study of historical catch data of Steller's sea cow, *Hydrodamalis gigas* by means of *Population Viability Analysis* (Turvey & Risley, 2006). Despite these and some other noteworthy exceptions, there are large gaps in our knowledge due to the limited information available on the basic life-history and demographic traits of benthic and pelagic marine animal populations and even more so, due to the lack of long-term demographic data series. One example of this latter is the historical sixty-three years data series on the herring, *Clupea harengus* reported by Yablokov and Larina (1985). More recently, a shorter (16-year) time series of a gorgonian population affected by anomalous mortality associated to anomalous temperature increase, was reported on by Santori and coll. (Santori *et al*., 2021).

Nowadays the bulk of demographic studies deal with fish, with a several dedicated to corals, while examples of research specifically focussed on the demography of cetaceans are less numerous than those dedicated to their distribution, eco-ethology and social behaviour. Moreover, in several cases the demographic information and subsequent modelling are the collateral product of research focussed on other topics. In some other cases the demographic data have also been collected through *citizen science*, which though allowing for large-scale data collection with minimal economic effort, suffers from some limitations in accuracy (e.g. Fujwara & Caswell, 2001; Bramanti *et al*., 2011, Robbins; Babey & Embling, 2020).

It is rather puzzling why specific, ad hoc demographic research devoted to increasing our demographic knowledge, which is so basic to the conservation of emblematic endangered marine species, is seldom funded by national and international institutions. This continues to be the case despite the calls for such data by the IUCN (International Union for the Conservation of Nature), which defines those species whose demography is largely unknown as *data deficient*, a designation applied all too frequently to marine species and populations for which "there is not adequate information to make a direct or indirect assessment of its risk of extinction based on its distribution and population status". For example, the status of 15 out of 90 species belonging to the genus *Epinephelus* (grouper fish) are defined by CITES as data deficient and 53 as having *unknown population trends*. A data deficient taxon may be "well studied and biologically well known, but appropriate data on abundance and distribution are lacking" (IUCN, 2012). Overall, the IUCN underline the need for dedicated studies on population size, life-history, harvesting and natural mortality and population trends for several long-lived marine species.

Developing demography of long-lived marine populations

The time scale for studying marine species is extremely wide, depending on the system under study (Tonelli, 2020). The life-cycle duration of living organisms ranges over several orders of magnitude from protists to large cetaceans. This short review will therefore be limited to the demography of long-lived marine species, some of which are *foundation, engineer, keystone* species within marine communities, typical examples being the long-lived gorgonian corals in tropical and temperate reefs the world over (*e.g*. Gili & Coma, 1998; Rossi, S., 2013; Rossi, S. *et al*., 2017) and the cetaceans in the pelagic environment (e.g. Notarbartolo di Sciara *et al.*, 2003; Matsuoka & Hakamada, 2014). When protected, long-lived species can also play the role of *umbrella species,* fostering the conservation of the whole community in which they live (Bramanti *et al*., 2011, among others).

Several years ago, Bramanti and I tried to sketch out a succinct history of ecology and its evolution over time (Santangelo & Bramanti, 2006). That overview ended with a chapter optimistically entitled: "Population dynamics and Conservation biology; the answers that Ecology can give". This short review will pick up from there and try to point out some basic criteria for a demographic approach to the study of marine populations focussing on the life-history of long-lived species.

The concept of *natural population*, initially formulated for the terrestrial environment, was set out to describe the genetic, evolutionary, and conservation units in which several species are naturally structured. According to Yablokov (1987): "The population is an ultimate, self-reproducing grouping of conspecific individuals, which occupies a definite area over an evolutionary long span of time to form an independent genetic system…".

The complex problem of the genetic definition of the (sometimes) uncertain boundaries between marine populations is beyond the scope of this paper. However, by referring to the wider concept of populations as "groups of conspecifics living in the same area", we are able to suggest what can be done by following a demographic approach to assess the basic features and structures of local populations, and to project their growth trends over time to foster, whenever possible, their survival. The monitoring of species and population abundance and distribution, supported by sound knowledge of their basic demographic features, such as population structure, reproductive output, mortality, life cycle and life span, will enable projecting their trends over time by providing information crucial to wildlife conservation (Dayton, 2003).

As frequently occurs during the evolution of ecology, the demographic approach was initially developed to study endangered terrestrial populations, though in more recent times it has also been applied to the study of long-lived marine populations especially worthly of protection. The concepts of *animal forest*, as well as that of *self-thinning, and shading* have also been derived from terrestrial ecology (Rossi, S., 2013; Nelson & Bramanti, 2020). The techniques of spatial analysis, first developed to study the distribution of trees in a wood (Pielou, 1962, 1974), were also successively applied to the study of gorgonian spatial distribution within the marine animal forest (Giannini; Gili & Santangelo, 2003; Gori *et al*., 2011; Cupido *et al*., 2012; among others).

Knowledge of population and species life cycles and life-history features is basic to developing population dynamic studies and reliable conservation plans. In the following some examples of demographic research on populations of long-lived marine species will be presented. However, some background and reflections on demographic models, their potential and limitations, should be useful.

MODELLING THE LIFE-HISTORY OF LONG-LIVED SPECIES

Demographic models: potential and limitations

According to Fenchel (1987), all sciences apply models to describe, analyse, and understand real phenomena. The formulation of models is basic for our understanding of natural systems' functioning. However, such models are only attempts to represent and understand reality based on observations and data – the hypotheses and models that researchers build must be validated, improved and even changed; they cannot be complacently accepted and applied in an acritical manner by researchers working in the field. To the contrary, a tight feedback loop must be established between field researchers, modellers and mathematicians working on population dynamics. Epidemiology supplied one of the world's first, historical examples of the application of a population model; it regarded a plague epidemic and was based on the vital statistics for the City of Copenhagen in 1711 (Hutchinson, 1978; Fenchel, 1987).

The possibility of projecting population trends overtime through growth laws has long intrigued ecologists. Malthus' writings on human population growth (Malthus, 1798) exerted great influence on Darwin's concept of natural selection. Exponential (Malthusian) and geometric growth laws were used to represent the unlimited growth of populations, while the *deterministic models* developed by Gauss, Pearl and Reel and Lotka and Volterra introduced population density and environmental *carrying capacity* as limits to "regulated" population growth (Scudo & Zeigler,1979; Ricklefs & Miller,1999).

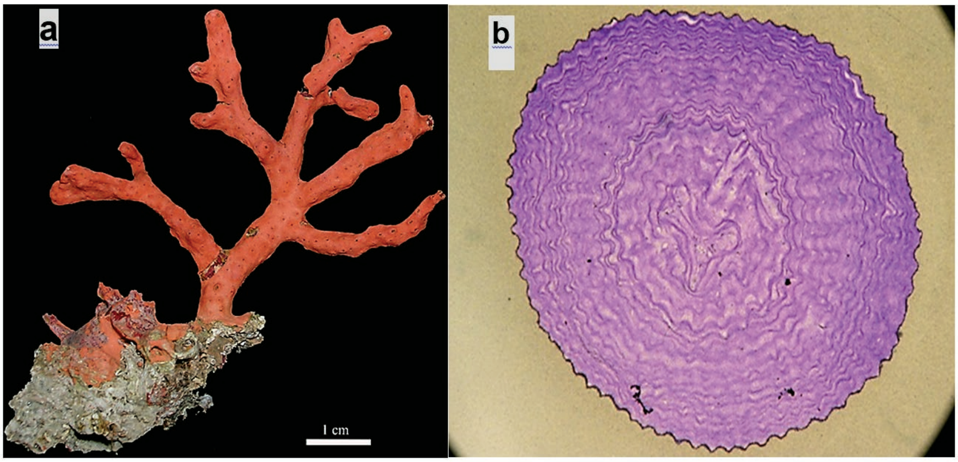
More recently, demographic modelling based on *life-cycle graphs*, *life history tables* and *algebraic transition matrices* (Leslie, 1948) have been developed in order to project population abundance and structure over time (Tupujanupur & Caswell, 1997; Ebert, 1999; Caswell, 2001). Demographic studies thus can furnish useful tools for the management and conservation of threatened and overexploited species. The first step in modelling the population growth of a long-lived species with several *overlapping generations* can be to set out a *static life-history table* (describing the population in a defined timeframe), in which the main population parameters are reported: number of age classes or vital life-stages, number of individuals in each class/vital stage, sex ratio, survival/mortality and birth rates of each age class/life stage. All the data listed in a life-table can be organized into an *algebraic transition matrix*, a *discrete* model suitable to calculate growth in stage/age-class subdivided populations (Ricklefs & Miller, 1999). Algebraic transition matrices enable calculating the number of individuals in each stage/age class and the intrinsic growth rate of the population under study. As different populations may have different age structures, and different classes are provided of different mortality and reproductive rates, they will be also characterised by different growth rates. Population models, based on life-history tables and algebraic transition matrices enable projecting population trends over time and estimating population performance and can thereby foster conservation of the studied populations by suggesting specific measures for their protection (Dobson, 1999; Ebert, 1999; Fujiwara & Caswell, 2001; Morris & Doak, 2002, Santangelo; Bramanti & Ianneli, 2007; Bramanti; Ianelli & Santagelo, 2009; Bramanti *et al*., 2017, 2019). Some examples of the life-history tables and transition matrices set out for long-lived marine species will be given in the following.

What kind of demographic data are necessary for population dynamic modelling?

Taking a *census* of a population can provide information on its size (abundance), sex ratio, population age structure, mortality/survival, and other data basic to the study of population dynamics. These latter data include their size/age at first maturity, fertility, fecundity and birth rates, and finally the population's *reproductive output* and *recruitment* rate (the rate at which reproduction adds new individuals to a long-lived population each year). All this knowledge is fundamental for managing and conserving any population and even becomes essential in the case of rare and endangered long-lived species (*e.g.* Dobson, 1999). Knowledge of the demographic features of single populations constituting the complex species assemblages of marine communities allows researchers to project population trends overtime and to explore the probability of their survival, building up realistic appraisals of the future scenarios facing the actual populations and communities (Margalef, 1997). *Community matrices* may be a suitable tool for such projections (Ricklefs & Miller, 1999). Collecting life-history, demographic data in the marine environment is often a demanding task.

Population growth rates (such the *geometric, discrete population growth rate* $\lambda = N_{t1}/N_{t0}$, and the *exponential, continuous rate of population growth* $r = dN/dt$) are the simplest tools for describing population dynamics. They have to account for both the reproduction and mortality occurring in a population between two successive times or instants. What they do not account for, however, is that some populations (as most of those belonging to long-lived species) are made up of several *partially overlapping,* reproductive generations that may have different mortality and reproduction rates (Ricklefs & Miller, 1999). Therefore, the first step in the study of such populations is to define their age structure by dividing them up according to age classes or vital life stages. Clearly, to do this it is necessary to estimate the ages of individuals.

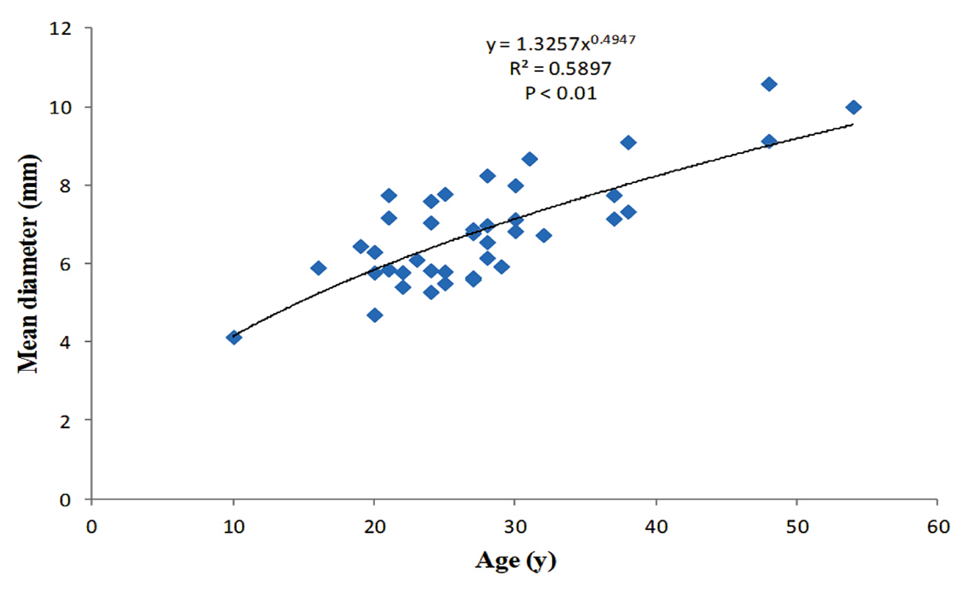
Figure 1 – a) *Corallium rubrum colony*; b) thin section (40 um wide) of a *C. rubrum* colony in which annual growth rings have been stained on thin (40-um) sections. (G. Santangelo and C. Priori photocredits; 20x)



From size to age: a population size/age structure

There are several different methods for assessing the age of single individuals belonging to long-lived species populations. By way of example: otoliths allow determining the age of fish (FAO, 1981); annual growth rings provide an estimate of the age of some gorgonian corals such as those in the genus *Corallium* (Marschall *et al*., 2004; Gallmetzer; Haselmai & Velimirov, 2010; Priori *et al*., 2013; Bramanti *et al*., 2014; Benedetti *et al*., 2016; Lartard *et al*., 2017; Figure 1); teeth growth layers are measured in dolphins and seals (Hohn *et al*., 1989; Cebuhar; Negrete & Botta, 2021), and so on. However, such methods only enable determining the age of a limited number of dead individuals from a population, and clearly is highly unsuitable for species in need of protection. Loosing even a few individuals can be dramatic for a small population in demographic decline, or even near collapse (Dobson, 1999). Thus, any and all destructive methods of sampling must be avoided in such populations. To this end, estimating the age of a larger sample of population components can be carried out by determining a relation between an individual's age and a more easily measured parameter, such as its size. When such a relation actually provides a good fit, it is possible to estimate the age of a larger number of individuals in the population based on their size by applying the resulting relation between size and age (Figure 2). Thus, the whole population can be divided into size classes based on the growth rate measured in the population (e.g. Santangelo; Bramanti & Ianneli, 2007; Cupido *et al*., 2009). Such procedure leads to the dividing up of the population according to so-called "size/age classes", which are annual classes determined on the basis of the average annual growth rate of individuals.

Figure 2 – Non-linear relation between colony age (determined by annual growth rings) and colony diameter in *C. rubrum* (n = 40). The ratio between diameter and age decreases in older colonies (After Priori *et al*., 2013, modified)



In several species the growth rate of individuals decreases with age. In the study case of *Corallium rubrum,* the best fit size/age relation resulted in a *monotonic, power curve* revealing the decreasing growth trend (in the basal diameter of colonies) with age. Using such curves it is possible to estimate the age of colonies from their basal diameter, which can be easily measured on dead as well as living colonies (Priori *et al.*, 2013; Bramanti *et al.*, 2014). Under *steady state* conditions (i.e., the proportion between successive classes remain constant over time; Caswell, 2001), the distribution curve of the different age classes in a population can also furnish information about the mortality/survival rates that the studied population has experienced. Thus, the difference between two successive age classes represents survivorship/mortality, as it shows the fraction of a population surviving from one year to the next, from which the proportion lost can also be derived. Hence, the age distribution curve is also a mortality curve (Figure 3).

Figure – 3 Size/age distribution curve of a gorgonian coral, *Corallium rubrum* (L. 1758) population. Under *steady-state* conditions this curve also represents mortality/survival

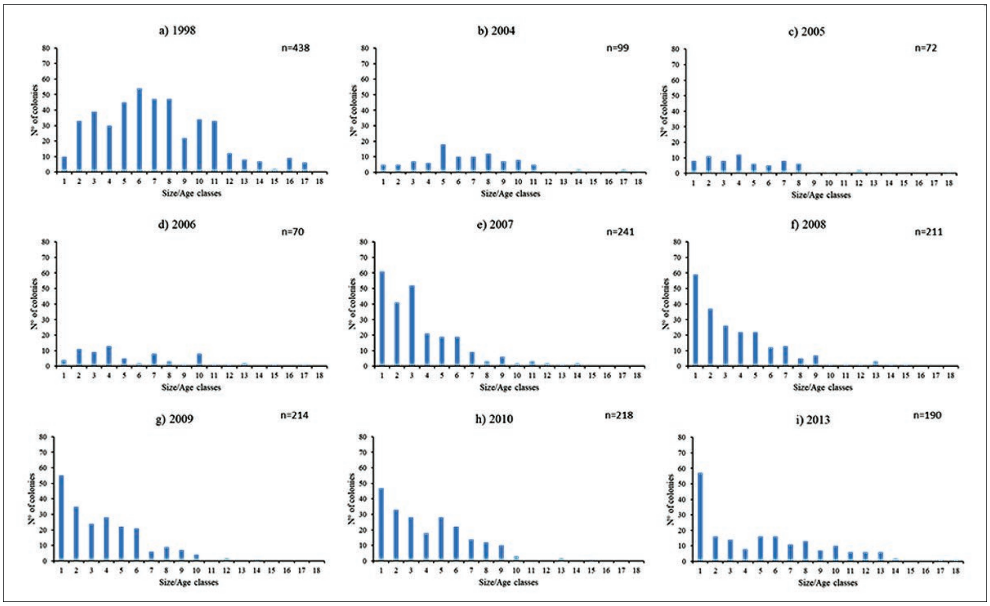
Observing the changes occurring in the population structure over time: the study case of a gorgonian population stricken by mass mortality

Long-term data series can reveal drastic changes occurring in populations of long-lived species. Knowing the population dynamics and, in particular, the size/age structure of populations over long time intervals is crucial to assessing the effect of disturbances on coral communities (Tsounis & Edmunds, 2017; Dietzel *et al.*, 2021). However, such data are scarce, and mostly on deep-sea and mesophotic coral species (Dougly; Quattrini & Cordes, 2014).

The example reported here deals with the *asymbiotic* Mediterranean gorgonian coral *Paramuricea clavata* (Risso, 1826). Gorgonians (Coelenterata, Anthozoa, Octocorallia) are among the main components of the so-called miniature *marine animal forest* (Rossi, S., 2013; Rossi *et al.*, 2017). As *passive suspension feeders*, they collect large amounts of micro-plankton and re-suspended micro-organisms (Gili & Coma, 1998; Tsounis *et al.*, 2006a), allowing an abundant flow of energy and CO_2 from high-turnover systems (the water column and the re-suspended sediment) to the more stable living tissues and mineral scaffolds of gorgonians

(Rossi & Rizzo, 2020), whose life-span can amply exceed a full century in some species (e.g. Priori *et al*., 2013). Gorgonians structure the complex *coralligenous* reefs in the Mediterranean (Ballesteros, 2006). The large, red gorgonian *P. clavata* lives on rocky cliffs exposed to intense currents below the summer thermocline, up to about 120 meters of depth, frequently forming a dense canopy (Carpine & Grashoff, 1975; Ballesteros, 2006). This species is gonochoric at both the polyp and colony level and undergoes *discrete* reproduction, like *Corallium rubrum* and other octocorals (Brazeau & Lasker, 1990, Coma *et al*., 1995). It is an external brooder, its sex ratio does not deviate significantly from 1:1 and it is characterized by high larval output and population stability with low recruitment rates (Coma *et al*., 2004). However, these latter two characteristics have been observed to change drastically after anomalous mortality events (Cupido *et al*., 2012). The following figure (Figure 4) shows an example of the real size/age structure dynamics of a population of this gorgonian that was affected by anomalous mortality events associated to abnormal temperature increases occurring in late summer 1999 and 2003 in the Ligurian Sea (Cerrano *et al*., 2000, Bramanti *et al*., 2005).

Figure 4 – Population structure in annual size/age classes of a *P. clavata* population stricken in 1998 and 2003 by mass mortality: a) pre mortality, b-i) post-mortality (after Santori *et al*., 2021)



The size/age population structure in figure 4 has been determined on the basis of annual size/age classes (Cupido *et al*., 2009; Santangelo *et al*., 2015). This population was followed over 16 years on fixed quadrates (Santori *et al*., 2021). Three different size/age structures can be easily distinguished. In 1998 (Figure 4a) the pre mortality population showed a non-monotonic structure, skewed toward larger/older colonies (reaching class 18), in which classes 5-8 were dominant and *recruitment* (the first size/age class) was low. In the years following the mass mortality events (2004, 2005, 2006; Figure 4b, c, d), the number of recruits and all other classes decreases and larger/older colonies nearly disappeared as a result of the 1999 and 2003 anomalous mortalities. In 2007, and up to 2013 (Figure 4e-i), the population size/age structure changed again, following a regularly decreasing, *monotonic* pattern with dominant recruitment, which indicates a population in a *steady state*. In 2013, the number of larger/older classes increased, and class 18 was again represented (Figure 4i). The population growth rate λ revealed negative trends (λ <1) in the period 2004-2006, a rapid increase in 2007 (λ >>1) and nearly constant growth (λ ~ 1) the following years (Cupido *et al*., 2009; Santangelo *et al*., 2015). Though recovering, this population never reaches its pristine, pre-mortality structure again, probably establishing a new equilibrium point at lower density, whose stability is also likely to be lower (Santori *et al*., 2021) On the basis of these data, an algebraic transition matrix was constructed in order to project the population structure over time, as reported in the following. However, before describing the transition matrix, it seems worthwhile providing examples of *life-cycle transition graphs, mortality tables, life-tables and reproductive tables,* firstly for terrestrial, and then for long-lived marine species.

DEMOGRAPHY OF CETACEANS, A CHALLENGING TASK FOR RESEARCHERS

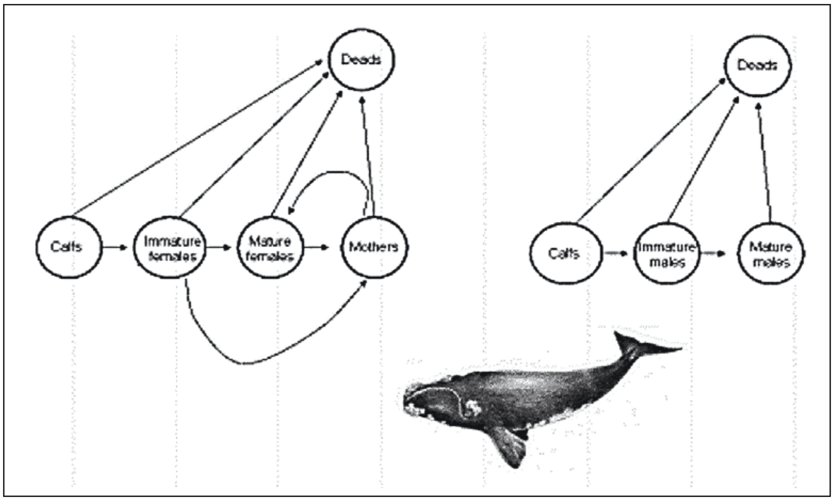
Difficult data collection, vital stages and transition graphs

Cetaceans, including Earth’s largest animals, are apical predators and the largest filter-feeders in the marine environment. Due to a burgeoning whaling industry that lasted some centuries, becoming especially efficient after the 1860s, some populations were driven to extinction and several others to near-extinction (Dobson, 1998). Cetaceans represent a dreadful example of the dangers of overharvesting long-lived, slow reproducing species and are a major target for conservation nowadays. Despite this, little is known about the life-history of several populations. This large gap in our knowledge is due to the intrinsic difficulty posed by collecting data in the vastness of the environment in which they roam, a factor that has made taking a reliable census of their populations a challenging task indeed.

The first, demanding step in studying cetacean demography is to distinguish single individuals in order to take a reliable census of animals; this can be done by photo-identification and comparisons with photo-identification catalogues and mark-recapture methods (e.g. Carrol *et al*., 2011; Rossi, A. *et al*., 2014; Curtis *et al*., 2021). Such comparisons allow avoiding any duplicate counts of animals in the census, thereby providing a reliable estimate of the overall abundance of a population. For the same reason, in order to be reliable, other counting methods, such as aereo-transects, must to be performed within narrow time intervals (Panigada *et al*., 2017). A first *static* life-history table was obtained for the fin whale subpopulation in the Pelagos Sanctuary (NW Mediterranean) by Alessia Rossi and coll. using the photo-identification and mark-recapture method (2014).

The second, difficult step in the study of cetaceans’ demography is determination of the animals’ age. It is difficult to follow the yearly growth of cetaceans based on stranding data and almost impossible by census through sightings and photo-identification. While it is possible to assess the age of stranded individuals through accurate, ad hoc analyses (e.g. Hohn *et al*., 1989; Pribanić; Mioković & Kovačić, 2000, in the bottlenose dolphin), it is impossible to attribute a living animal to a specific, annual size class with data collected by visual census alone. Although this latter method is widely adopted in order to collect a large amount of data, it can provide only a rough assessment of size. Therefore, the structure of living cetacean populations are built on the basis of *life* or *vital stages*, that is to say, particular, easily identifiable phases of their life-cycle (e.g. Fujwara & Caswell, 2001; Caswell & Fujiwara, 2004; Verborgh *et al*., 2020). The *life-cycle transition graph* is a simple dynamic model of the whole species' life-cycle, and accounts for the different life stages and the probability of survival during the transition from one stage to another. Such model was applied to describe the life-cycle of one of the most endangered populations of the right whale (*Eubalaena glacialis*, Müller, 1776), which lives along the North American Atlantic coast (Fujiwara & Caswell, 2001). The life cycle of the population was divided into life stages, whose duration and mortality (i.e., the probability of an individual surviving from one stage to the next) were known (Figure 5).

Figure 5 – *Life-cycle transition graph* for the right whale, *Eubalaena glacialis* (after Fujiwara & Caswell, 2001, modified). A specific survival probability has been calculated for each transition from one stage to the next (arrows)



Living population structure estimated by dead individuals

A life table reports data on the life and death of a population. It summarizes the likelihood that organisms in a population will live, die, and reproduce at different stages of their lives. The life table reported here is of the simplest type, including only mortality/ survival occurring in a population, without data on reproduction. Such tables are also termed *Mortality tables*. The classic example here reported (Table I), as usual from terrestrial ecology, is a mortality table based on deceased big horns, the North American Dall Rocky Mountain sheep, *Ovis dalli* (Deevey Jr., 1947; Berger, 1990). The age of 608 animals was determined based on their skulls and horns, and the entire deceased population was thus divided into annual age classes. Observing the mortality table provides some meaningful insight into the periods during which the bighorns face the greatest risk of death. One high-risk age is between 0 and 1 year (a very young sheep may be easy preyed on). The other period in which the death rate is higher is for older sheep reaching 9-12 years of age (few sheep survival beyond this age).

Table I – Mortality table of the bighorn (*Ovis dalli*, Nelson, 1884) based on the skulls of dead individuals (Bergher, 1990; Ricklefs & Miller, 1999, modified)

Age intervals (years)	Nº dead during age interval	Nº survivals at age interval onset	Nº survivals of original 1,000 cohort (lx)
0-1	121	608	1,000
1-2	7	487	0,801
2-3	8	480	0,789
3-4	7	472	0,776
4-5	18	465	0,764
5-6	28	447	0,734
6-7	29	419	0,688
7-8	42	390	0,640
8-9	80	348	0,571
9-10	114	268	0,439
10-11	95	154	0,252
11-12	55	59	0,096
12-13	2	4	0,006
13-14	2	2	0,003

The fin whale, *Balaenoptera physalus* (Linnaeus, 1758), is the world's second largest cetacean, one of the world's longest-lived mammals, but one of the least-known Mysticetes demographically. This species is defined as *vulnerable* by IUCN (IUCN, 2021). Some demographic studies have been carried out on the Northeast Atlantic population, actively hunted up to 1977 (Aguillar & Lockyer, 1987), while little is known of the demography of the Mediterranean population (Notarbartolo di Sciara *et al.*, 2003). In an effort to reduce this gap in our knowledge, a mortality table similar to that made based on deceased big horns has been set out on the basis of stranding data recorded along the Mediterranean costs over the period 2001-2011 (Arrigoni *et al.*, 2011). The resulting table (Table II), clearly shows that the greatest risk of death (no. dead/stage duration) was for the calves. It is nearly impossible to follow the yearly growth of cetaceans based on either stranding data or census made by sightings and photo-identification. Therefore, differently from the bighorn population, the fin whale population was divided into different life-stages making up its life-cycle. As will be seen in the following for the case of gorgonian corals, in which annual growth rate can be measured, populations of other long-lived species can also be divided into successive annual classes (cohorts).

From terrestrial to marine populations: mortality tables based on cetacean stranding data

Table II – Mortality table of the fin whale, *Balaenoptera physalus,* based on stranding data. The population was divided into life-stages based on size (after Arrigoni *et al*., 2011, modified). (Photocredit: S. Panigada)

 **Life stages**	Nº dead in life stage	Stage duration (yrs)	Nº dead / stage duration	Nº survivals in life-stage	Nº survivals of 1,000 original cohort
Calves	43	0.5	86	134	1,000
Immature	66	0.7	9.42	91	679
Mature	25	82.5	0.30	25	186

As discussed, a mortality table is a simplified life table in which survival/mortality rates alone are reported, thereby omitting reproduction rates. More exhaustive *life-history tables* include both survival and reproduction, and can be constructed from a mortality table by simply adding other columns with the average number of new born delivered by a mother in each age interval. Clearly, this requires information on female reproductive rates. A number of papers, describing the main reproductive features of the common bottlenose dolphin *Tursiops truncatus* populations, have been published. This small Odontocete has a life- cycle about ½ that of the larger Mysticetes discussed above, and some studies have focussed on the reproductive features of its populations worldwide; a *reproductive table,* comparing a population of the North-Western Mediterranean with others of different geographic areas, is reported in the following.

Life-history tables, population age, sex structure and reproduction

To predict if a population will grow or shrink, ecologists need to know the birth and death rates of organisms at different ages, the age at first maturity and the sex ratio of the population (e.g. Ebert, 1999; Cupido *et al*., 2012). Life tables can also summarize birth and death rates of organisms in different stages of their lives, which therefore requires detailed knowledge of the reproduction, reproductive rates and early mortality rates occurring in the population under exam. By way of example, the following presents the results of studies (Manfredi *et al*., 2016; Rossi *et al*., 2017) on female reproductive parameters and early mortality in the Eastern Ligurian Sea (Northwest Mediterranean) population of the bottlenose dolphin (*Tursiops truncatu*s, Montagu, 1821).

According to Alessia Rossi and coll. (2017) the ubiquitous bottlenose dolphin is one of the most well-known cetaceans in the world. It figures in many ancient Greek paintings and myths and was described in the writings of Aristotle, Pliny the Elder and Oppian, becoming an emblematic species in many countries and cultures (Wells & Scott, 2009; Cheney *et al*., 2013). Although an extensive scientific literature is now available, studies have mostly focused on their spatial distribution (Gnone *et al*., 2011), diet (Blanco; Salomón & Raga, 2001) and social behaviour and structure (Connor; Heithaus & Barre., 2001; Stanton

& Mann, 2012, among others), while little remains known about their demography (e.g. Stolen & Barlow, 2003), the information available being limited mostly to the Mediterranean population (Bearzi & Fortuna, 2006), which has been judged vulnerable by the International Union for Conservation of Nature (IUCN, 2021). Population data are fundamental in order to develop the demographic models needed to assess the population status and predict population trends over time, which in turn provide suggestions on specific conservation measures that can be taken.

Life stage and sex determination on living bottlenose dolphins: an exacting task for researchers

In these studies, assigning individual animals to the appropriate life stage was performed through several criteria, including analysis of select images, behavioural observations and available life-history information on previously sighted individuals (Rossi, A. *et al.,* 2017). Only well-marked dolphins that could be consistently identified over long periods were considered adults. To identify immature dolphins, the body size of the young was compared to that of accompanying females (putatively their mothers, as they swim in close formation). Because dolphins generally do not exhibit long-lasting markings on their dorsal fin during the first few years of life (Fruet *et al.*, 2015), juveniles were tracked by following their well-marked mothers up until weaning. Temporary markings and specific behaviours (e.g., sharp dorso-ventral *fetal folds* and infant position) were used for cubs. Each sighted bottlenose dolphin was assigned to one of the following life-stages: Cubs (first stage) – dolphins about 2/3 or less in length than the accompanying adult (the mother), presence of fetal folds, absence of permanent markings, age 0-1 year; Calves (second stage, Figure 6) – dolphins over 2/3 the length of the accompanying adult, but still shorter, absence of fetal folds and permanent markings, age > 1 < 3 years; Juveniles (third stage): dolphins comparable in size to the accompanying adult female or slightly shorter, absence of permanent markings, age 3-7 years; Adults (fourth stage) – dolphins equal in size or larger than the accompanying adult female, presence or even abundance of permanent markings, age 7-57 years (Rossi, A. *et al.*, 2017) . Sex determination was done both directly, by analysing the genital slits in the ventral region in photos, and (for reproductive females only) by observing prolonged associations between the same photo-identified adult individual with a young one (i.e. newborn, cub and calf) throughout repeated sightings and photographic data (Mann *et al.*, 2000; Kogi *et al.*, 2004). These data have been collected over a period of 9 years.

Figure 6 – Mother and calf of *Tursiops trucatus* (Photocredit Alessia Rossi)

Table III – Distribution of bottlenose dolphin, *Tursiops truncatus,* female population and females with cubs or calves in the Ligurian Sea, based on sighted and photo-identified individuals; in parenthesis, the corresponding expected number of sightings assuming a uniform distribution. There are significant differences between observed and expected sightings (* = p < 0.05, ** = p < 0.01, *** = p < 0.001. After Rossi, A. *et al.*, 2017, modified). The table allows the main nursery area to be identified (area B)

Ligurian Sea Sub-areas	Nº sightings females + cubs/calves	Nº sightings females	Encounter rate females+cubs/ calves sighting effort (km)	Encounter rate of females/sighting effort (km)
A	1 (11.7 p***)	7 (44.3 p***)	0.25	1.74
B	51 (28.7 p***)	182 (108 p*)	5.16	18.41
C	25 (17.7 p*)	132 (67 p*)	4.01	21.67
D	32 (50.8 p*	91 (192 p**)	1.83	5.21
Total	109	412	2.91	10.99

The data, collected as explained above and reported in Table III, have allowed identifying the main nursery in the region as sub-area B, as the encounter rate of females with cubs was highest here. Such finding yields indications on where to address major efforts for patrolling and conservation. The data have also enabled compiling the following *reproductive table* for the population (Table IV).

Table IV – Reproductive table for *T. truncatus* in the Eastern Ligurian Sea by sightings and photo-identification and comparison with other worldwide populations; a: Rossi *et al.*, 2017; b: Mitchenson, 2008, c: Fruet *et al.*, 2015, d: Wells & Scott, 1990; e: Anderson, 2004; f: Terzanos Pinto *et al.*, 2015 (Rossi, A. *et al.*, 2017, modified)

	Nº sightings Females +cubs/ calves	Females +cubs/1000 km sampling effort	Annual average fertility and fertility range	Calving interval (years)	Cub/calves yearly mortality
Ligurian Sea (Italy)[a]	109	2.91	$\overline{X}$= 0.343 0.29-0.41	$\overline{X}$= 2.95 2.45-3.45	0.25
Scotland[b]	-	-	0.11	3.18	-
Brazil[c]	-	-	0.11	3	0.16
USA[d]		-	0.144	4	0.19
New Zealand 1[e]	-	-	0.25	4.3	0.34-0.52
New Zealand 2[f]	-	-	-	5.3	0.33

The reproductive table (Table IV) reports the main reproductive parameters for the *Tursiops truncatus* population dwelling in the NW Mediterranean (Eastern Ligurian Sea, Rossi, A. *et al.*, 2017) compared with data collected in different geographic areas. The table includes the *encounter frequency* of females with cubs, the average *annual fertility*, the *calving interval* (i.e., the time interval between two births), and the mortality of calves. This last parameter is quite critical for the survival of many marine mammal populations (Steiner & Bossley, 2008; Hanson, 2013, among others). As can be seen in the table, considerably higher calving interval values were found to be associated with higher cub mortality in two populations (New Zealand 1 and 2). Such a finding may at least partly explain the tendency of these populations to decline (Anderson, 2004; Tezanos-Pinto *et al.,* 2015). By integrating this reproductive table with the life-stage abundance and mortality of the adult populations, suitable life tables can be compiled and simulations of population trends can be carried out.

SOME EXAMPLES OF LIFE HISTORY TABLES, TRANSITION MATRICES AND SIMULATIONS CARRIED OUT FOR OCTOCORALS

Historical harvesting and conservation of a highly valuable, long-lived Mediterranean red coral *Corallium rubrum*

The precious red coral, *Corallium rubrum* (L. 1758), has been harvested for more than 2,000 years. The brilliant red skeleton of this asymbiotic gorgonian coral is carved to produce ornaments and talismans and is traded worldwide (Tsounis *et al.*, 2010, among others). The economic value of this species led to intense harvesting and to the depletion of several populations. Due to the high cultural, economic, nature and emblematic value of this species, several research studies have been dedicated to shedding light on its demography as a precious instrument to reconcile conservation and exploitation (Santangelo & Bramanti, 2010; Santangelo *et al.*, 2015). Within this framework, a number of studies have described the growth rate of colonies and the populations' age structure by annual growth-ring counts (Marschal *et al.*, 2004; Gallmetzer; Haselmai & Velimirov, 2010; Priori *et al.,* 2013; Bramanti *et al.*, 2014). sex ratio, Fertility and fecundity of colonies, and populations' sex ratio, reproductive features and output have been also described (Santangelo *et al.*, 2003; Tsounis *et al.*, 2006b; Gallmetzer; Haselmai & Velimirov, 2010; Priori *et al.*, 2013; Bramanti *et al.*, 2014; Benedetti *et al.*, 2016). Red coral populations living at deeper depths, characterized by lower density and larger size of colonies, possess greater market value (the so called *deep populations* living between 50 and 130 meter's depth (Santangelo & Abbiati, 2001). Some pioneering studies based on sampling of living colonies and by ROV recordings have examined also some basic features of these (for details see Rossi, S. *et al.*, 2008; Priori *et al.*, 2013; Bramanti *et al.*, 2014; Angiolillo *et al.*, 2015; Benedetti *et al.*, 2016; Cau *et al.*, 2016, among others).

The life table reported here (Table V) regards a shallow-water population of red coral living composed of small/young colonies divided into annual size/age classes (after Santangelo; Bramanti & Ianneli, 2007; Bramanti *et al.*, 2017). The table shows the main

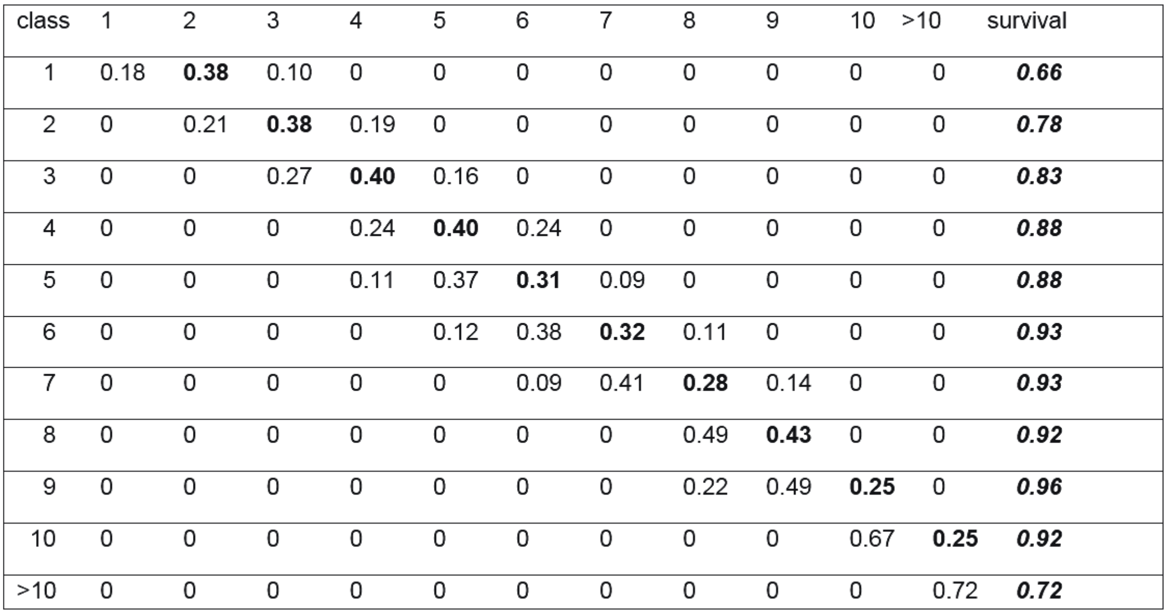
Table V – Life table for a population of the precious Mediterranean red coral *Corallium rubrum* (modified after Santangelo *et al.,* 2015)

Class	Colony number	Survival	Fertility	Planulae per polyp produced	Sex ratio	Nº of polyps In each colony	Planulae produced by each colony	Planulae produced by each class
1	822.00	0.89	0.00	0.87	0.50	0.00	0.00	0.00
2	731.00	0.63	0.00	0.87	0.50	6.20	0.00	0.00
3	463.00	0.70	0.36	0.87	0.50	15.91	2.49	1153.67
4	323.00	0.52	0.64	0.87	0.50	31.06	8.64	2790.72
5	167.00	0.44	0.82	0.87	0.50	52.18	18.61	3108.30
6	73.00	0.29	0.97	0.87	0.50	79.72	33.63	2455.56
7	21.00	0.57	0.98	0.87	0.50	114.06	48.62	1021.10
8	12.00	0.33	0.99	0.87	0.50	155.58	67.00	804.00
9	4.00	0.75	1.00	0.87	0.50	204.24	88.84	355.38
10	3.00	1.00	1.00	0.87	0.50	261.33	113.68	341.03
11	3.00	0.33	1.00	0.87	0.50	326.14	141.87	425.61
12	1.00	1.00	1.00	0.87	0.50	399.23	173.66	173.66
13	1.00	–	1.00	0.87	0.50	480.87	209.18	209.18

reproductive parameters: colony number survival, fertility, fecundity (planulae produced by each polyp), population sex ratio, average number of polyps produced by each colony in each age class and average larval output of each class. The first two classes are sexually immature, while classes 4, 5, and 6, which though bearing a lower number of polyps, are more numerous in the population, and thus produce the major portion of planulae larvae (indicating a trade-off between the effect of colony density and colony size on population larval output). Given that these populations oscillate between higher density of smaller/younger colonies and lower density of larger/older colonies (Santangelo & Abbiati, 2001; Bramanti; Ianelli & Santagelo, 2009), a population growth control function, depending on both colony density and colony size, was included in the model (Santangelo; Bramanti & Ianneli, 2007; Bramanti; Ianelli & Santagelo, 2009). These data enabled carrying out the simulations of population trends over time reported in the following.

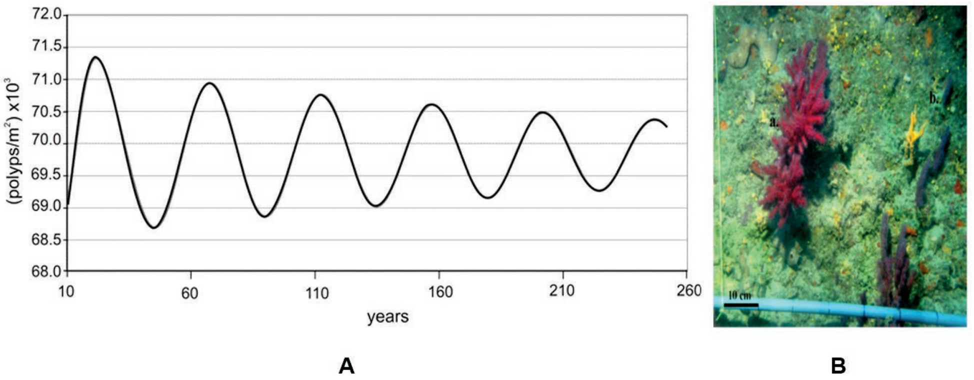
The demographic model reported below (Table VI) is a modified transition matrix based on the time data series of the gorgonian, *Paramuricea clavata,* previously described (Figure 4). Data have been collected over successive years between 2007 and 2010. All the survival values recorded in fixed quadrates on labelled colonies are reported in the matrix, which represents the transition probabilities of each colony: the diagonal of the matrix, in bold, represents the proportion of colonies passing from one class (in the left-most column) to the following (along the top row) from one year to the next; the values along the same rows represent the percentage of colonies that grow most and therefore move up a number of classes each year, the percentage of colonies that do not grow and thus remain in the same size class from one year to the next, as well as the few that lose some fan apices and regress to a lower class. In the last column (bold italics) is the percentage of all colonies that survive (Santangelo *et al.*, 2015). This matrix was used to conduct simulations of population trends over time such as that reported in Figure 7.

Table VI – Transition matrix of a *Paramuricea clavata* population. The matrix presents: the proportion of colonies that rise by one class each year (in bold along the diagonal). The same row also included the proportions of those colonies that rise by a number of classes each year (they grow more), those remaining in the same size class (they do not grow) and the few colonies that loose apices and regress to a lower class. In bold italics in the last column is the percentage of all colonies that survive (modified after Santangelo *et al.*, 2015)



class	1	2	3	4	5	6	7	8	9	10	>10	survival
1	0.18	**0.38**	0.10	0	0	0	0	0	0	0	0	***0.66***
2	0	0.21	**0.38**	0.19	0	0	0	0	0	0	0	***0.78***
3	0	0	0.27	**0.40**	0.16	0	0	0	0	0	0	***0.83***
4	0	0	0	0.24	**0.40**	0.24	0	0	0	0	0	***0.88***
5	0	0	0	0.11	0.37	**0.31**	0.09	0	0	0	0	***0.88***
6	0	0	0	0	0.12	0.38	**0.32**	0.11	0	0	0	***0.93***
7	0	0	0	0	0	0.09	0.41	**0.28**	0.14	0	0	***0.93***
8	0	0	0	0	0	0	0	0.49	**0.43**	0	0	***0.92***
9	0	0	0	0	0	0	0	0.22	0.49	**0.25**	0	***0.96***
10	0	0	0	0	0	0	0	0	0	0.67	**0.25**	***0.92***
>10	0	0	0	0	0	0	0	0	0	0	0.72	***0.72***

Figure 7 – A) Simulation of *P. clavata* population trends. After some damped oscillation, the population is near stabilizing at a polyp density about 1/3 that in the pre-mortality populations (modified after Santangelo *et al.*, 2015). B) A *P. clavata* colony of the studied population in a permanent quadrate plot (photocredit G. Santangelo)

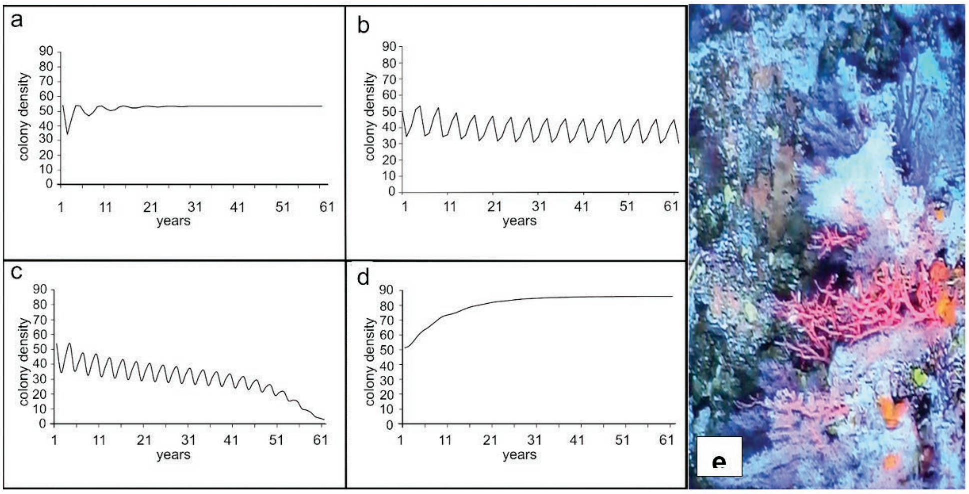


Simulations (How to project population structure over time)

On the basis of data on population density (or abundance), age structure, mortality, reproductive and recruitment rates, various simulations can be performed. As explained above, both models and related simulations are efforts to build reliable scenarios of the future features of a studied population based on our present knowledge. They are thus projections, not predictions, of the configuration that the population would assume in the future (Beissinger & McCullough, 2002). The following presents two simulations of the trends over time for gorgonian populations based on life history tables and the transition matrix previously described. As anomalous mortality events, likely driven by abnormal temperature increases linked to global climate change (GCC), dramatically affected both *Paramuriea clavata* and *Corallium rubrum* populations in 1999 and 2003 (Cerrano *et al.*, 2000; Coma *et al.*, 2004; Bramanti *et al.*, 2005), projections can simulate the effects of such events on their dynamics (Santangelo; Bramanti & Ianneli, 2007; Bramanti; Ianelli & Santagelo, 2009; Linares & Doak, 2010; Santangelo *et al.*, 2015).

In the simulation (Figure 7), the *P. clavata* population (in Figure 4 and Table VI), though recovering after the anomalous mortality events of 1999 and 2003, exhibited wide, damping oscillations, slowly decaying and then stabilizing after several cycles at a density (in polyps/m^2) about 1/3 the pristine, pre-mortality value, which it never attains again. This projection was based on the 2007/2010 field data. Subsequent samplings (Santori *et al.*, 2021) suggest that such stable state (equilibrium point) at lower colony density may actually be reached earlier than the simulations suggest. The main concern regards the stability of such a new equilibrium: repeated mortality events and undamped oscillations may even drive the local *P. clavata* population to extinction.

Figure 8 – a-d. Simulations of a red coral population's trends after mortality events: a) effect of a single anomalous mortality event; b) repeated mortality events occurring every four years; c) effect of increased frequency of mortality events (every 3 years); d) effects of protection by fishing ban: the population reaches saturation in about 30 years (from Santangelo; Bramanti & Ianneli, 2007; Bramanti; Ianelli & Santagelo, 2009, modified). Figure 8e. A red coral colony recorded by ROV at 95 mt depth in the Tyrrhenian sea (North-Western Mediterranean). (Photocredit S. Canese).



Simulations of red coral population trends (Figure 8) suggest that the deleterious effects of a single mortality event may be overcome in a few years, but that repeated mortality events induce non-damping oscillations in a still surviving population, and that mortality events occurring with increased frequency (every 3 years) lead the population to extinction in about 60 years. On the other hand, fishing bans could allow the population to reach saturation in about 30 years. Fortunately, dramatic anomalous mortality events, such as those of 1999 and 2003, have not occurred again (up to now) with similar intensity in the NW Mediterranean, so the studied populations still survive, albeit it with lower densities and different size/age structures.

CONCLUSIONS

Some conclusive remarks

In the framework of this short review I have tried, through a small number of examples, to provide some insights on application of a demographic approach, largely developed for terrestrial plants and animal, to research on long-lived marine species. Many population features, such as life-span, size and age distribution, growth rate, sex structure, reproduction, and recruitment rate are largely unknown for several long-lived marine species. Although collection of such data, mostly in the mesophotic, deep-sea and pelagic environments, is not a simple matter, any advancements in our knowledge of the life-histories of these species will help us to understand the dynamics of their populations.

Nowadays, such knowledge is even more critical, as it enables us to evaluate a population's responses to the dramatic transformations of the marine environment induced by the increasing effects GCC and anthropic disturbances through improved dynamic demographic models and simulations of future scenarios. Moreover, new thermal-dependent diseases may also be the cause of dramatic mortality events in marine benthic suspension feeders such as gorgonian corals in the near future (Bally & Garrabou, 2007). All told, such factors call for specific research dedicated to the demographic trends observable in the affected populations. The sixteen-year-long demographic study on the *P. clavata* population stricken by 78% mortality reported above can serve as a clear example of this approach. The demographic tools reported here will allow identifying critical points in population life-cycles, fostering researchers to set out targeted management plans for the conservation of long-lived marine species based on sound life-history data.

As explained rather summarily herein, research focussing on the demographic features of long-lived marine species will enable compiling dedicated life-tables and transition matrices, and hence performing simulations of future trends of highly endangered populations. Such data and models represent precious tools in the struggle to prevent the occurrence of several extinctions in the marine environment in the near future. Admittedly, collection of the necessary data is by no means an easy or inexpensive task, but the value of the natural heritage we are seeking to protect and pass on to future generations is incomparably higher.

Some specific points to address in future research

1) ROV recordings for studies on deep-dwelling coral populations, as well as Seafloor multi-beam echo sound, multiparametric fibre-optic-cabled videos and other new technologies are emerging tools for standardized ecological monitoring and could allow collection of some important demographic data such as recruitment rate and population structure; 3D photogrammetry modelling may help greatly in determining population size structure and even to estimate the potential larval output of colonies in corals, and can allow for testing the effectiveness of enforcement measures (Rossi, P. *et al*., 2021; Richaume *et al*., 2021).
   Other population features not all directly related to demography have also been measured by ROV recordings: population size and area, colony size frequency distribution, occupancy, encounter frequency, orientation/exposure of colonies (e.g. Rossi, S. *et al*., 2008; Gori *et al*., 2011; Angiolillo *et al*., 2015).
2) Concerning the overharvested, precious octocoral *Corallium rubrum*, there have been recent reports of chimerism (two or more new settlers co-occur to form a new single colony; Giordano & Bramanti, 2021). This peculiar demographic feature should be quantified and included in demographic models for gorgonian corals.
   Self-thinning and density-dependence, suggested by some author as occurring in gorgonian populations (Linares *et al*., 2008; Cupido *et al*., 2012; Cau *et al*., 2016; Nelson & Bramanti, 2020), should be more closely examined and quantified, also in light of previously reported selective mortality towards larger/older colonies (Cupido *et al*., 2009; Santori *et al*., 2021). The contribution of asexual reproduction, recently found in some gorgonian (Pilczynska *et al*., 2017) to population reproductive output, should also be quantified and included in demographic models.
3) Cetaceans, representing another meaningful example of a long-lived species subjected to overharvesting in the past, nowadays are a main target for conservation. Nonetheless, little is known about their life-histories, and detailed demographic

description of several of their populations is still lacking. There is a pressing need for basic demographic data, such as: abundance, calving intervals, reproduction rates, specific life-stage mortality and body growth rates. Calving intervals, in particular, together with early stage mortality (Hanson *et al.*, 2013), is one of the primary determinants of population reproductive success in several long-lived, slowly-reproducing mammals.

Future research on the bottlenose dolphin would likely benefit from reliable estimates of the age/body length relation in individual geographic populations (Pribanić; Mioković & Kovačić, 2000). Such estimates can be based on the dentine layer deposition in dead animals (Hohn *et al.*, 1989).

In the end, an exhaustive knowledge of cetacean life-histories can only be obtained via ad hoc research dedicated to single geographic populations by providing frequent photo and mark-recapture samplings, extended photo-identification catalogues and also by improved aero-surveys (Panigada *et al.,* 2017) and genetic analyses via non-invasive biopsy samples (Marsili *et al*., 2000,). Stranding studies, as previously shown, could also supply precious data on individual growth rates, mortality and population reproductive features.

Long-term research specifically dedicated to life-history data will greatly enhance the prospects for collecting relevant demographic information on long-lived, slowly reproducing populations of marine mammals in the wild, a prerequisite to accurately modelling their dynamics.

Caveat (a cautionary note)

Last, but not least, it should be stressed that all models (including demographic ones) are fundamental for clarifying the actual state of our knowledge – to organise it, to detect gaps and lacks regarding specific species and population life-histories. However, it must be borne in mind that a model is not the reality! Therefore, any model can and must be verified whenever possible, improved with new, more reliable data, compared with the findings obtained by other models, and even changed as necessary. Scientists must never cling to their initial hypotheses or models like a limpet to a rock! In this framework, continuous, close, reciprocal and dialectic interactions between population mathematicians and field marine biologists are imperative. Moreover, better integration between demographic and statistical approaches, as well as deep analysis of spatial structure and scale of population data (McCallum, 2000), is certainly to be hoped for.

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