Progress in Oceanography 156 (2017) 91–103

Contents lists available at ScienceDirect

Progress in Oceanography

journal homepage: www.elsevier.com/locate/pocean

# Can schooling regulate marine populations and ecosystems?

Olivier Maury

*IRD - UMR 248 MARBEC, Av Jean Monnet CS 30171, 34203 SETE cedex, France*

ARTICLE INFO

*Article history:*
Received 9 August 2016
Received in revised form 15 June 2017
Accepted 21 June 2017
Available online 23 June 2017

*Keywords:*
Auto-organized groups
Density-dependence
Phase transition
High fecundity
Population resilience
School, shoal, swarm

ABSTRACT

Schools, shoals and swarms are pervasive in the oceans. They have to provide very strong advantages to have been selected and generalized in the course of evolution. Auto-organized groups are usually assumed to provide facilitated encounters of reproduction partners, improved protection against predation, better foraging efficiency, and hydrodynamic gains. However, present theories regarding their evolutionary advantages do not provide an unambiguous explanation to their universality. In particular, the mechanisms commonly proposed to explain grouping provide little support to the formation of very large groups that are common in the sea (e.g. Rieucau et al., 2014). From literature review, data analysis and using a simple mathematical model, I show that large auto-organized groups appear at high population density while only small groups or dispersed individuals remain at low population density. Following, an analysis of tuna tagging data and simple theoretical developments show that large groups are likely to expose individuals to a dramatic decrease of individual foraging success and simultaneous increase of predatory and disease mortality, while small groups avoid those adverse feedbacks and provide maximum foraging success and protection against predation, as it is usually assumed. This would create an emergent density-dependent regulation of marine populations, preventing them from outbursts at high density, and protecting them at low density. This would be a major contribution to their resilience and a crucial process of ecosystems dynamics. A two-step evolutionary process acting at the individual level is proposed to explain how this apparently suicidal behaviour could have been selected and generalized. It explains how grouping would have permitted the emergence of extremely high fecundity life histories, despite their notorious propensity to destabilize populations. The potential implications of the "*grouping* feedback" on population resilience, ecosystem stability and the persistence of marine biodiversity are discussed. The risk of harvesting marine species with fishing gears that enable catching dispersed individuals (such as longline, gillnet, trawl or using fishing aggregative devices for instance) is underlined. Finally, tropical tunas are used to exemplify the potential importance of schooling in shaping complex life histories and species interaction.



## 1. Introduction

Schooling, shoaling and swarming are pervasive in the oceans where the immense majority of pelagic species and 80% of all fish species aggregate and form dense and labile groups, at least during important periods of their life cycles (Fréon and Misund, 1999). Aggregative behaviour is so common in the aquatic realm that it has to provide very strong advantages to have been selected and generalized in the course of evolution. Auto-organized groups are usually assumed to provide facilitated encounters of reproduction partners, improved protection against predation, better foraging efficiency, and hydrodynamic gains (Brock and Riffenburgh, 1960; Fréon and Misund, 1999; Pitcher, 2010). However, present theories regarding their evolutionary advantages do not provide an unambiguous explanation to their universality. In particular, the mechanisms commonly proposed to explain grouping provide little support to the formation of very large groups (thousands to billions of individuals) that are common in the sea (Rieucau et al., 2014). From literature review, new data analysis and theoretical developments, I show that the emergence and the size of auto-organized groups are density-dependent, and that large groups and clusters of groups (Bertrand et al., 2008) expose individuals to enhanced predation and disease mortality and reduce individual foraging efficiency, while dispersed individuals, isolated or in small groups, largely escape those adverse feedbacks. This would prevent marine populations from outbursts and subsequent extinction due to resource exhaustion at high density, and protect them from predation while maintaining their reproductive capacity at low densities. This process would be a major ecological contribution to the stability and resilience of populations, communities and

*E-mail address:* Olivier.maury@ird.fr

http://dx.doi.org/10.1016/j.pocean.2017.06.003
0079-6611/

ecosystems. It would ensure the viability of extremely high fecundity life histories, despite their notorious propensity to destabilize populations (Mueller and Joshi, 2000). High fecundity is a major evolutionary asset. Its obligatory association with schooling would be the key to understand why schooling and swarming have been so universally generalized in aquatic ecosystems, despite the detrimental effects of large groups on individual fitness. A two-step evolutionary process acting at the individual level is proposed in this perspective, in agreement with standard evolutionary theory.

## 2. Marine populations exhibit density-dependent alternative states

Marine populations, from bacteria to fish, can be composed of up to billions of individuals. Large numbers of elementary interactions between them often lead to the emergence of macroscopic structures such as zooplanktonic swarms or fish shoals and schools (Parrish et al., 2002). Similar phenomena are observed for terrestrial populations with bird flocks, bee or locust swarms, and ungulate herds (Buhl et al., 2006). Field studies (e.g. Fréon et al., 1996) show that marine populations can exist under three different states. Typically, dispersed (scattered layers composed of isolated individuals or micro-groups of few individuals), condensed (swarms, shoals) and organized (schools) phases can be clearly distinguished (Fig. 1).

Condensed and organized phases have been demonstrated to result from complex auto-organization processes (Gautrais et al., 2008) based on simple individual behaviours such as attraction, repulsion and, in the case of schools, alignment (Mirabet et al., 2007; Schellinck and White, 2011). The different states of marine populations are characterized by specific macroscopic properties. Dispersed populations have low individual densities, no individual cohesion and remain poorly detectable compared to condensed phases (cf. Appendix D). Condensed populations show high packing densities of cohesive individuals and enhanced detectability. Organized populations exhibit very high packing densities, individual coordination and polarization and high detectability. The spatial organization of birds in flocks has a structure intermediate between the liquid and gas phases of physical systems (Cavagna et al., 2008). Unlike dispersed state, condensed and organized populations have the ability to transmit information through compressional waves propagating at least one order of magnitude faster than individuals (Gerlotto et al., 2006; Pitcher, 2010; Makris et al., 2009).

Condensed and organized aggregative structures are generally size- and species- specific (Fréon and Misund, 1999; Hoare et al., 2000; Krause et al., 2000), although exceptions exist (e.g. Louw et al., 2014). It has been shown both theoretically (Vicsek et al., 1995; Czirok and Vicsek, 2000; Tu, 2000) and empirically (Becco et al., 2006) that they appear above critical biomass densities. This has also been corroborated by large-scale observations in the field (Makris et al., 2009). Hence, like many physical systems, marine populations exhibit density-dependent (DD) phase transitions between their dispersed, condensed and organized states (Toner and Tu, 1998; Tu, 2000), when their density increases and reaches well-defined thresholds (Fig. 2a red line). Conversely, when the population density decreases, the number of condensed structures and their size decrease (Niwa, 1998, 2004) until they ultimately disappear and the population comes back to a fully dispersed state (Fig. 2a red line). When the population density decreases rapidly however, field observations (e.g. Gutiérrez et al., 2007) suggest that condensed populations might exhibit hysteresis, with sub-critical aggregative structures persisting some time below the critical DD phase transition density (Fig. 2a blue line). In the presence of hysteresis, determining the transition point might become difficult (Albano et al., 2011). This would be particularly true for highly gregarious species such as small pelagic fishes (e.g. clupeidae, engraulidae), which are often referred as obligate schoolers, by contrast to facultative schooling species such as gadidae, carangidae or serranidae. Once obligate schoolers have formed a school,

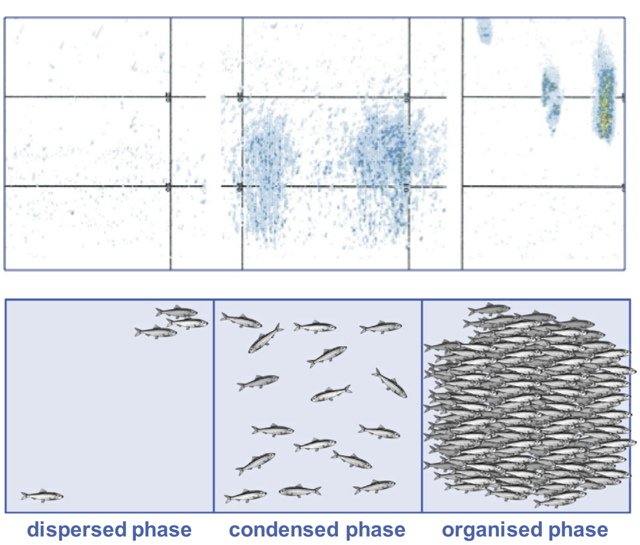


**Fig. 1.** Top: example of three echograms where the interval between the vertical lines corresponds to 0.1 nautical mile (redrawn from Fréon et al., 1996). Left: layer of dispersed fish during the night. Middle: nocturnal layer with two large shoals. Right: typical day schools. Bottom: corresponding schemes for dispersed, condensed and organized phases of marine populations.

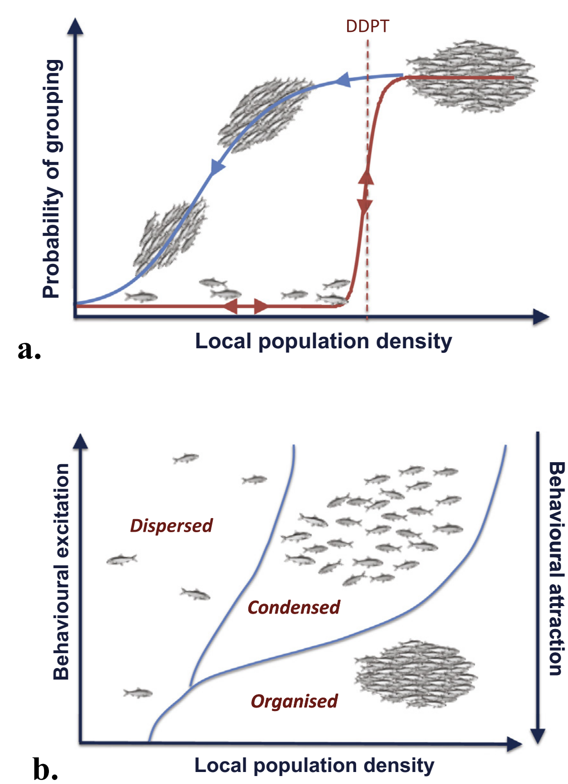


**Fig. 2. a.** Schematic phase transition of marine populations when local density increases (red) and when it decreases without hysteresis (red) and in the presence of hysteresis (blue). **b.** Schematic phase diagram for a fish population exhibiting three phases. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)