

# **Ecological and evolutionary effects of harvesting. Lessons from the candy-fish experiment**

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## **Abstract**

Understanding the challenges of sustainable fisheries management is not easy for non-specialists, and even many specialists fail to appreciate the potential evolutionary consequences of harvest. We propose candy-fish experiments as a savoury approach to teaching and disseminating the key principles of applied ecology and evolution to students, practitioners, and the general public. We performed a simple experiment where the resource was represented by fish-shaped candy of distinct colours and flavours (strawberry and liquorice). Typically, harvesting was neither ecologically sustainable (55% of the populations were extinct by the end of the experiment) nor evolutionarily sustainable (most surviving populations had liquorice fish only). This harvest-induced evolution went apparently unnoticed. Somewhat encouragingly, the harvest was most likely ecologically sustainable when a person spontaneously took the role of a stock manager.

**Keywords:** candy-fish, dissemination, education, ecological sustainability, harvest-induced evolution

## **Introduction**

Managing wild fisheries is challenging, and the track record of fisheries management worldwide leaves plenty of room for improvement (Dankel *et al.*, 2008; FAO, 2012; Worm *et al.*, 2009). Superficially, the problem is easy to solve: it is generally accepted that reducing exploitation rate and by-catch, as well as maintaining relatively large fish stocks and low impact on ecosystems are key issues for a sustainable fishery (Hilborn, 2007b). However, there is no consensus on how to achieve these objectives. A major challenge is that managing fish stocks is really about managing people (Larkin, 1988), fishermen in particular, but increasingly a much wider group of

stakeholders too (Hilborn, 2007a; Larkin, 1988; McMullin and Pert, 2010). The situation is further complicated because the concept of success differs between ecologists, economists, policy makers, etc. (Hilborn, 2007a) and because fishery systems are characterized by uncertainty and ambiguity (FAO, 1995; Francis and Shotton, 1997; Moxnes, 1998).

Fish resources are typically common property resources. If nobody controls exploitation, altruistic behaviours are not rewarded and people tend to behave selfishly and overexploit the resource as the costs of selfish actions are shared by all exploiters. This is commonly known as “the tragedy of the commons”, after Hardin’s (1968) seminal paper. Avoiding the tragedy requires closing the commons by restricting individual access and exploitation (Basurto and Ostrom, 2009; Hardin, 1968). However, the top-down practice of managing (fishermen are told when, where and how to fish) is destined to fail (Kraak, 2011) as it results in uncooperative behaviours and unexpected and creative ways to circumvent the rules (Hilborn, 2007a). Therefore, studying the behaviour of the exploiting agents, as well as their motivation and incentives, is the key to a successful fishery, complementing the study of ecological outcomes (Hilborn, 2007a).

An additional challenge to sustainability is that fishing may drive unwanted evolution in fish populations. Fishing is purposely selective, commonly directed towards larger individuals. Fishing can also be directly selective for behavioural patterns, activity, sex, morphology, and maturity (Heino and Godø, 2002; Nelson and Soulé, 1987; Smith, 1994). If a part of the phenotypic variation in selected characteristics is genetic, fishing drives genetic change (Law, 2000). There is increasing evidence that fisheries-induced evolution is contributing to the phenotypic changes commonly documented in fish stocks (Jørgensen *et al.*, 2007; Kuparinen and

Merilä, 2007; Law, 2000). This could have negative effects on the utility humans derive from fish stocks (Jørgensen *et al.*, 2007), not least on the fisheries yield (Conover and Munch, 2002; Edley and Law, 1988).

Given these challenges for developing appropriate management systems, we believe there is a need in better communicating the interplay of human behaviour and ecological and evolutionary feedbacks to the general public, and to students and practitioners in fisheries science and applied ecology. Traditional, lecture-based learning methods have been criticized for leading to low motivation, while active learning keeps the students involved and is more effective (Mitchell *et al.*, 2013). Thus, games, as a form of active learning, have been developed for teaching purposes in a wide range of disciplines from health education, science, and technology to social change (Sherry 2013). Learning through own experience is powerful (Kolb, 1984; McCarthy and McCarthy, 2006), especially when relatively abstract phenomena like the tragedy of the commons and fisheries-induced evolution can be made tangible. Therefore, we designed a simple, easily-repeated experiment to illustrate the key principles of applied ecology and evolution. We used a bowl of candy-fish as a resource as we needed a model system where assessing the cause-effect relationships of exploitation would be both straightforward and rewarding. Specifically, we used the candy-fish system to test two main hypotheses: 1) exploitation is selective and leads to changes in populations' genetic composition (clonal composition, in our particular case), and 2), formal training in fisheries biology and management improves ecological, but not evolutionary sustainability.

## **The experimental set-up**

Eleven groups of people (at the University of Bergen, Institute of Marine Research, and Fisheries Directorate in Bergen, Norway) were each provided with one ‘fish stock’, a bowl with fish-shaped candy, from which anyone could harvest. The groups were defined by coffee tables at three different working places. Each bowl contained two types of candy-fish, initially at the same frequency (total  $N = 50$ ). The two types were similar in size and appearance, except for their colour and flavour: liquorice fish were black and strawberry fish were red. The bowl was accompanied with a note informing that the candy-fish will be available if harvested sustainably and the fish would reproduce daily (Figure 1).

We considered our candy-fish as clonally reproducing populations with two genotypes, corresponding to the black and red phenotypes. Population dynamics followed a Beverton-Holt model, where black fish gave birth to black fish, and red ones to red (see the Supplementary Materials for details). However, the two candy types shared a common source of density-dependent population regulation. We set carrying capacity and a maximum population growth ratio ( $K = 50$  and  $\lambda = 3$ , respectively) such that populations were small enough for the participants to readily see the consequences of their actions. The maximum sustainable yield was around thirteen candy-fishes per day, i.e., similar to average number of participants in each group (approximately 12); this gave on average one fish for each participant every day.

The abundance of fish was assessed daily, and the appropriate number of fish was added according to the model. Beyond this daily census, we did not systematically monitor the coffee tables. However, coffee tables were in the daily

working environment of the persons taking care of the populations, and we could often make informal observations; the participants were unaware of the role of the experimenter in the study. The experiment lasted eight candy-fish generations in each population.

The eleven exploiting groups were categorized according to:

1) Their formal knowledge in fisheries science. We hypothesized that training in fisheries science would facilitate sustainable harvesting. Five groups had training in fisheries biology, and the remaining six groups did not. We hypothesized that training in fisheries science would facilitate sustainable harvesting. The theory of fishing (Clark, 1990) suggests that when harvesting a virgin stock, the optimal solution is to immediately reduce it to the level that produces the maximum sustainable yield (MSY). Here, the exploiters could not know which level produced MSY as the model underlying population renewal was unknown to them. However, from basic lectures in fisheries biology one learns that in the Schaefer model, MSY is obtained when the population is kept at half of its carrying capacity, and that this is a conservative rule of thumb for many other situations too (Shepherd, 1982; Worm *et al.*, 2009). In contrast, even though awareness about evolutionary consequences of fishing is increasing, this has yet to influence practical fisheries management, and we did not expect that the exploiters would notice that evolution was taking place in the experimental populations. After all, fisheries management is primarily focused on maintaining sufficiently large stocks (e.g., sufficient spawning stock biomass), and only secondarily on composition.

2) The treatment they experienced (anonymity or writing names). The experiment was repeated twice for each group. One time the participants were asked

to write their names down if they were participating; the other time there was no such request but only a note explaining the common “rules of the game” (Figure 1). We hypothesized that this treatment would result in a reduced harvest rate because humans are known to be less selfish when given even subtle cues of being watched (Bateson *et al.*, 2006; Haley and Fessler, 2005; Kraak, 2011). In the first round of the experiment there were six randomly selected groups with the “writing names” treatment and five groups with the “anonymity” treatment; the treatments were swapped in the second round of the experiment. In addition, this set-up allowed us to assess the effect of experience, as we could compare the outcome of the first round (candy experiment-naïve participants) with the second round (experienced participants). However, we had no means to ensure that all participants wrote down their name, and it is likely that many did not.

3) The presence of a “manager” in the group. In some groups a person emerged during the experiment and took responsibility for the stock. This manager controlled the harvest, by regulating the harvest of the other group members, aiming at ensuring sustainability; their role ranged from merely informing that the candy had a purpose and was not for free to implementing a moratorium. This happened spontaneously and independently from the original study design, and we do not have precise knowledge about when a manager started nor how managers were respected. There were four groups controlled by a manager, and seven groups unmanaged. There were managers in groups both with and without fisheries knowledge (respectively 3 and 1 groups)..

We did not explicitly explain to the participants that they were part of an experiment, but the note in the bowl implied that the candy were not just a gift. The note hinted that there was a purpose on the candy bowl as it described the simple

“rules of the game” (Figure 1). The lack of detailed information was on purpose in order to mimic an unregulated fishery.

## Results

The abundance of candy-fish decreased over time (Figure 2a), and on the last day of the experiment, 55% of the populations and 63% of the clones were extinct. The average daily extinction rate was 11%. Only 4% of the daily harvest rates of our replicate populations were in accordance with the harvest rate that would have provided the maximum sustainable yield. The harvest rate did not differ between the anonymity treatments (writing names or anonymity; odds ratio = 0.93,  $z = -0.83$ ,  $df = 1$ ,  $p = 0.41$ ), or between the groups with and without formal fisheries knowledge (odds ratio = 0.48,  $z = -1.22$ ,  $df = 1$ ,  $p = 0.22$ ). Among the potential explanatory variables, the factor that had the strongest effect on the harvest rate was the presence of a controlling person who would look after the stock. The groups with spontaneous “stock manager” had a significantly lower harvest rate compared to groups without such manager (odds ratio = 0.28,  $z = -2.11$ ,  $df = 1$ ,  $p = 0.04$ ; Figure 3). The average harvest rate declined between the first and the second round of the experiment (odds ratio = 0.80,  $z = -2.31$ ,  $df = 1$ ,  $p = 0.02$ ; Figure 4), suggesting that the participants learned from their past experience, but this effect was weaker than the effect of a “manager”.

Harvesting over MSY (thirteen candies per day) on the first day was associated with a higher overall harvest rate (odds ratio = 2.54,  $z = 9.17$ ,  $df = 1$ ,  $p < 0.001$ ). It seems that groups that harvested strongly on the first day maintained that strategy over the course of the experiment and depleted the stock faster (Figure 1).



The strawberry fish declined in abundance more dramatically compared to the liquorice fish (Figure 2b). Exploitation of the stock was selective on colour or/and flavour: the harvest probability of the two types of candy differed, being higher for the strawberry type (odds ratio = 1.59,  $z = 5.77$ ,  $df = 1$ ,  $p < 0.001$ ; Figure 3). Consequently, the relative frequency of liquorice fish increased over time, and fewer liquorice than strawberry fish clones were extirpated (Figure 2b).

## **Discussion**

The candy experiment was aimed to illustrate human behaviour when exploiting a shared resource. Even our simple system illustrated that common pool resources are a complex system to manage, as uncertainty and the effect of the commons problem are coupled. While the predicted evolutionary effects indeed took place, they were overshadowed by a more dramatic consequence of harvesting: extinction was the most typical outcome in our experimental populations. The exploiters also showed unforeseen behaviours. In one case, the harvest was so intense than even the bowl itself hosting the candy-fish disappeared. In the other extreme, we witnessed an introduction of an “alien” species: one bowl was supplemented with a new type of candy, after the candy-fish population went extinct.

In addition to assessing the value of the experiment as an educational tool, we were able to obtain interesting insights to conditions that could lead to lower harvest rates. Sadly, formal knowledge on fisheries biology did not have a significant effect on harvesting. It seems that fisheries scientists did not put their knowledge into practice when confronted with a problem outside their professional realm. This result is in accordance with a more complex experiment (Moxnes, 1998) where the participants (researchers, fishermen and bureaucrats) could exploit a resource with

exclusive property rights; 74% of the participants harvested over MSY, independently of the category they belonged to. Moxnes (1998) concluded that the participants, regardless of their background, relied on current measures of benefits, instead of long-term ones.

On a more positive side, good governance seemed to help: emergence of a person (independently from the original experimental set-up) who started to manage the stock resulted in lower harvest rates compared to populations that remained open-access. This person talked to other group members about the possibility of extinction and the “rules of the game” and—in one occasion—even established a moratorium. This result agrees with the conclusion of Ostrom *et al.* (1992) that the tragedy of the commons is not inevitable with common pool resources because self-governance can emerge. Ostrom *et al.* (1992) performed an experiment where participants could invest on a common pool resource under different conditions for communication and sanctioning. In Ostrom *et al.*'s (1992) experiment, as in our experiment, harvesting was most prudent when there was some kind of communication between the participants, and a controlling method was established within the group (see Kraak, 2011, for a thorough discussion on this topic in the fisheries context). Indeed, a few fisheries have recently implemented self-governance approaches, and despite appearing in very different contexts (e.g., orange roughy in New Zealand, scallops in France, and pollock in Alaska, just to name a few), these approaches have often been successful (Townsend and Shotton, 2008). Moreover, exploiters learned from their past failures: harvest rates declined from first to the second round of the experiment. It seemed that the experience of a depleted stock acted as a kind of sanction that improved future outcomes. Notice, however, that contrary to expectations (e.g., Kraak, 2011), reduced anonymity did not improve the outcome. It is likely that

writing down ones name or nickname did not reduce anonymity enough to have a detectable effect.

Exploitation is not just a demographic phenomenon. Our candy-fish experiment showed, as we hypothesized, that exploitation is selective and has evolutionary consequences, albeit in one of the simplest possible experimental settings. In general, harvesting is a selective process that can act on different traits. In this case there was selection over candy flavour that resulted in shifts in the clonal composition of the experimental populations. Exploitation-induced evolution can have important implications for the exploiting agents. In our experiment, the liquorice candy type became to dominate the populations. As we knew a priori that most people prefer the strawberry flavour, this outcome was negative from the majority perspective. This evolutionary change seems to have gone largely unnoticed: change in population composition was not mentioned in the discussions that we witnessed, and surviving populations became dominated by one flavour. Avoiding evolution would have required maintaining equal harvest pressure on both candy types, or in the case of skewed distribution, active harvest of the more frequent type, thus maintaining the composition of the populations similar to the pristine conditions. Even though single participants might have realized that evolution was taking place, there is no evidence to suggest that this influenced behaviour of the groups.

Our simple experiment is far from being the first one to experimentally study harvest-induced evolution (e.g., Conover and Munch, 2002; Edley and Law, 1988; Philipp *et al.*, 2009; van Wijk *et al.*, 2013). Among these, Edley and Law's (1988) experiment on water fleas, *Daphnia magna*, was similar to ours in that it showed evolution in a clonal system: populations where large individuals were removed became dominated by slow-growing clones. Admittedly, our experiment is even

further removed from real-life fisheries than Edley and Law's (1988) experiment—which already was largely ignored by fisheries scientists, perhaps because it was based not on fish but on a tiny crustacean. However, in one respect our experiment was more realistic than other experiments on harvest-induced evolution so far: selection was not artificially imposed, but it naturally emerged from preferences of individual exploiters.

Our study has several limitations. The relatively low potential yield of the candy-fish populations per exploiter (only about one fish per day) perhaps made sustainable exploitation particularly hard. No doubt a sufficiently productive population would have resulted in satiation and ecologically sustainable exploitation, but we wanted to have populations that were small enough such that the consequences of exploitation were clear and directly visible (flooding coffee tables with candy is not ethical either). However, we do not expect that our evolutionary results would have been qualitatively affected. It is also not clear whether many groups failed to attain sustainability because they did not take the experiment seriously enough to even bother to try, or because they tried but did not succeed. However, informal interactions with some participants suggested that at least some of them took the study seriously and tried their best to achieve a sustainable candy-fishery.

We propose candy-fish experiments as a powerful tool for teaching and disseminating basic principles of applied ecology and evolution in schools, science fairs and universities (flavours can be adjusted to local taste). Experiential learning techniques, such as games, have been shown in many disciplines (e.g., biology, psychology, marketing, mathematics, etc.) to increase student learning (Mitchell *et al.*, 2013). We have already used different candy-fish experiments in teaching, allowing students to experience the selective nature of exploitation, harvesting for

MSY, and how this can be altered by population demographics (see the Supplementary Materials for an example). A classroom setting facilitates learning by allowing a tighter interaction with the participants, both before, during, and after the experiment, something we did not attempt during the experiment described here. However, the advantage of the uncontrolled setting of our experiment is that it allowed for a greater spontaneity in how the resources were exploited, perhaps revealing more instinctive behaviours than what carefully briefed participants might have done (cf. Moxnes, 1998; Ostrom *et al.*, 1992). Either way, a candy-fish experiment is fun and rewarding for the participants, illustrates the fundamental challenges in sustainable population management in a tangible way, and is open to countless variations.

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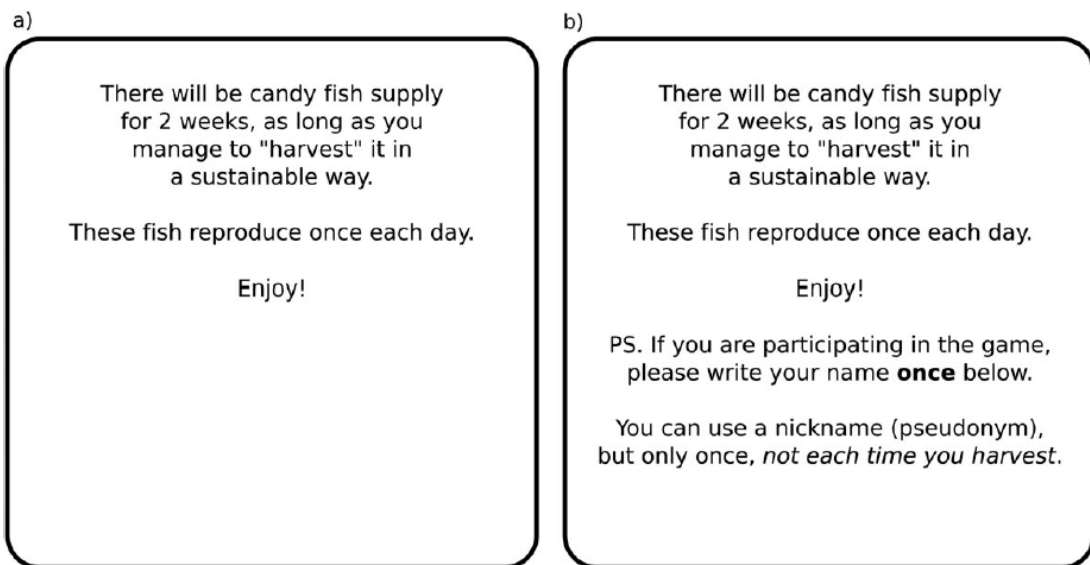


Figure 1. Labels that were placed next to the experimental candy-fish populations. Label a) was used for the treatment with full anonymity. Label b) was used for the treatment where participants were encouraged to register.

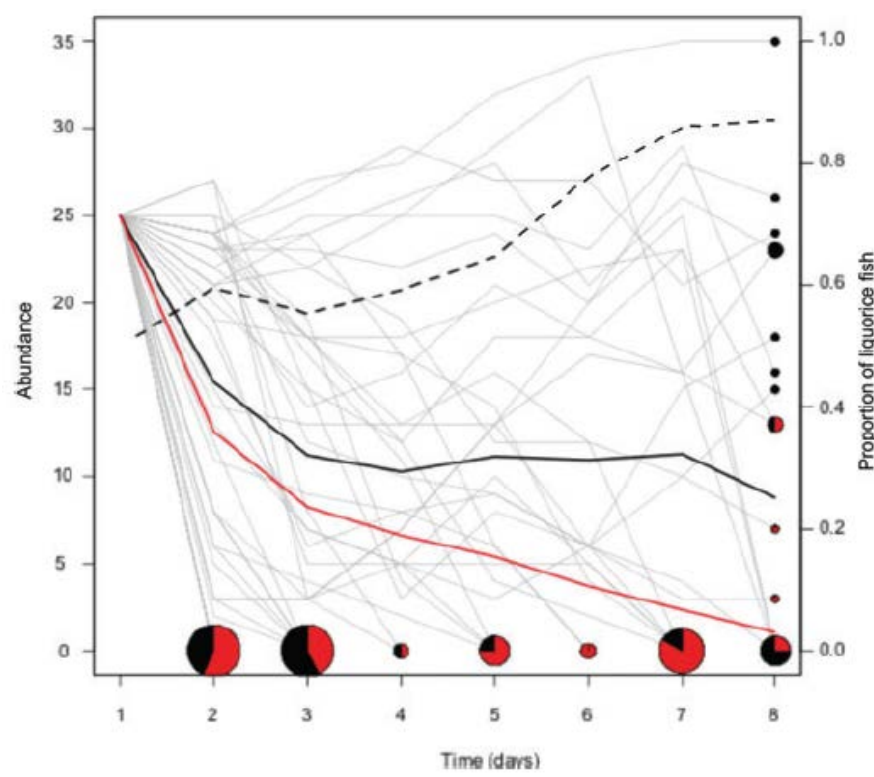
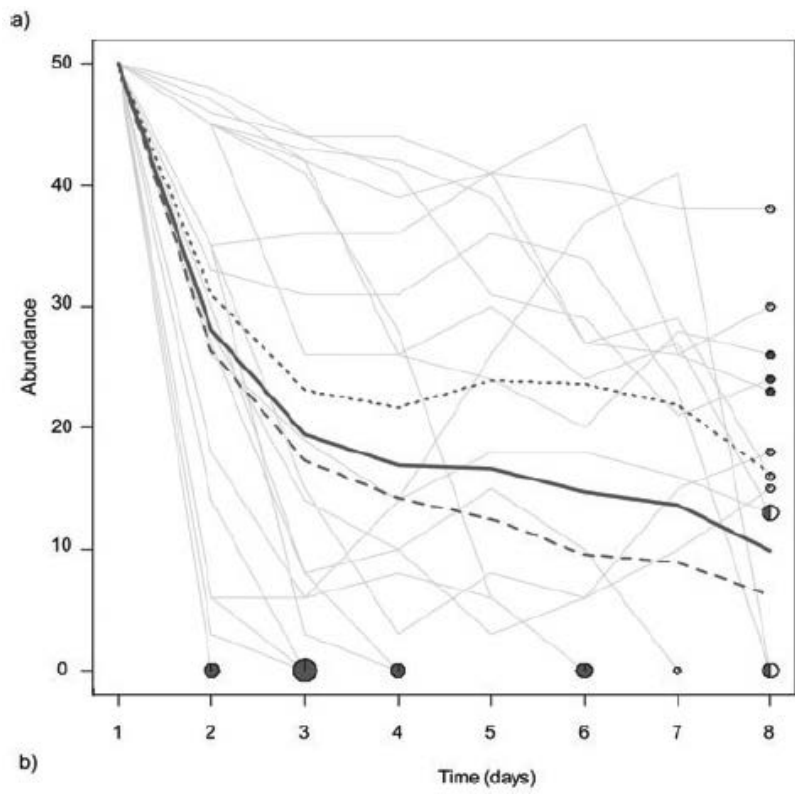


Figure 2. Trends in candy-fish abundance for (a) populations and (b) clones. In (a), the thick continuous line shows mean abundance over all populations, and the dotted and dashed lines show the mean abundance for “managed” and “unmanaged” populations, respectively. In (b), the black and red lines show the mean abundance for liquorice and strawberry clones, respectively: over time, the mean proportion of liquorice clone in populations increase (dashed line). The gray lines show abundance trajectories of individual (a) populations or (b) clones. The diameters of the pie charts along the margins indicate the total number of cases characterized by a particular endpoint, with grey and white sectors depicting respectively unmanaged and managed populations in (a); black and red sectors representing respectively liquorice and strawberry clones in (b).

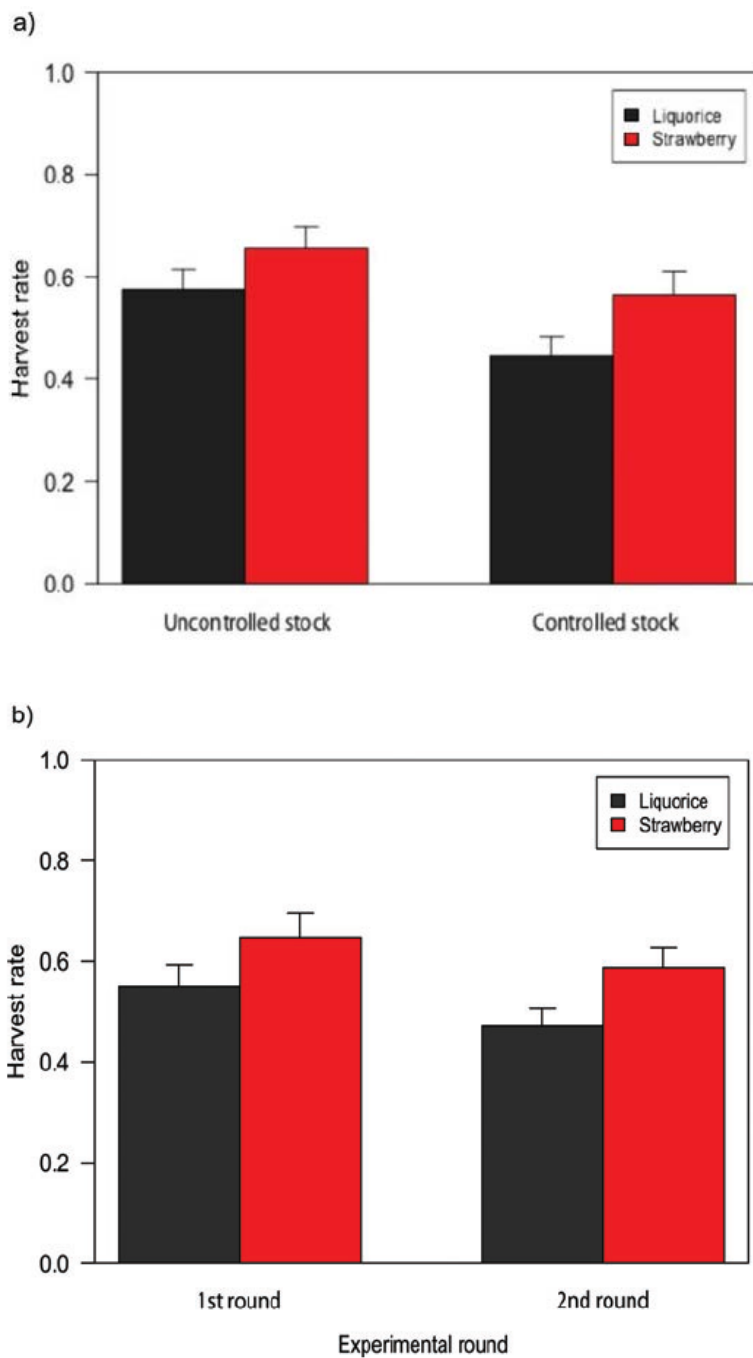


Figure 3a. Average harvest probability for strawberry and liquorice candy-fish without ( $N = 252$ ) and with a stock manager controlling exploitation ( $N = 144$ ). Mean + SE bars, total  $N = 396$ . Figure 3b. Average harvest probability for strawberry and liquorice candy fish during the first ( $N=198$ ) and second round ( $N=198$ ) of the experiment. Mean + SE bars, total  $N= 396$ .