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Asilvestramiento de los peces introducidos por la acuicultura y sus efectos ecológicos potenciales: el caso de la lubina, *Dicentrarchus labrax* (Linnaeus, 1758), escapada en las Islas Canarias

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A mis padres

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General Summary / Resumen General

Fish farming in floating cages is a constantly growing economic activity worldwide. The Canary Islands have not been outside this, and since the early 90's production has grown, becoming one of the most important regions of Spain in aquaculture production. This rapid expansion has been accompanied by increased environmental monitoring of pollutants. Nonetheless, escapees have been traditionally relegated to the background, receiving no consideration as a threat to the sustainability of aquaculture.

Escape events can release a large number of fish occasionally (massive escape) or few fish recurrently (chronic or leaking escape). The massive escapes occur mainly through technical failure or breakage of the materials the facilities are composed of, triggered by unfavourable conditions in the sea (sea storms). Moreover leaking escapes often occur due to the presence of holes in the nets as well as during harvesting. Taking into account potential negative effects caused by escapees, information concerning the ecological role of these species in shallow coastal habitats of the Canaries is scarce.

This thesis addresses the problem by focusing on the process of feralization of sea bass (*Dicentrarchus labrax* L.) once they escape from floating cages, since this species is considered

El cultivo de peces en jaulas flotantes es una actividad económica en constante crecimiento en todo el mundo. Las Islas Canarias no han sido ajenas a este fenómeno, y desde principios de los años 90 la producción acuícola ha crecido, situándose como una de las regiones más importantes de España. La rápida expansión de la acuicultura ha venido acompañada de una mayor vigilancia ambiental de sus efectos contaminantes, sin embargo, los escapes de peces desde las jaulas han quedado relegados a un segundo plano, y no se han considerado como una amenaza para la sostenibilidad de la actividad.

Los eventos de escape pueden liberar al mar una gran número de peces de forma puntual (escapes masivos) o bien un menor número de manera recurrente (escapes crónicos o por goteo). Los escapes masivos se producen principalmente por fallos técnicos o rotura de los materiales que forman la instalación, desencadenados por condiciones desfavorables en el mar (temporales). Por otro lado, los escapes por goteo suelen ocurrir por la presencia de agujeros en las redes o durante las tareas de despesque. Teniendo en cuenta los efectos potencialmente negativos de los escapes, la información acerca del papel ecológico que juegan estas especies en los hábitats costeros de las Islas Canarias es escasa.

Esta tesis aborda el problema de los escapes centrándose en el estudio del proceso de asilvestramiento que sufren las lubinas (*Dicentrarchus labrax* L.) una vez se escapan de non-native for the central and western islands of the Archipelago. The spatial distribution patterns of the bass and its relation to escape events are also explored. All the foreseeable ecological effects of escapees are discussed and measures for monitoring and mitigation are proposed.

After the introductory Chapter, which sets the study framework, Chapter 2 is a preliminary study on escaped fish off Tenerife. Therein, it is shown that abundance of escaped sea bass depends mainly on the distance from the aquaculture facility. Habitat features also affect their distribution. Preliminary data on the diet of fugitives is also provided, it is demonstrated that escapees actively predate in natural environments, and their diet is similar to that of wild sea bass in their natural range.

Farmed sea bass feralization is further analysed in Chapter 3. There the biological changes sea bass undergo once they have escaped are explored. For this the morphometric traits of escaped and farmed fish that have spent all their life-cycle in culture conditions are compared. Differences in growth profiles measured in scales and condition indexes are also studied. Results show that the escaped sea bass have a more streamlined body-shape than those in culture. The growth profiles show that sea bass

las jaulas de cultivo, ya que esta especie puede considerarse no nativa para las islas centrales y occidentales del Archipiélago. También se exploran los patrones espacio-temporales de distribución de las lubinas y su relación con los eventos de escape. Desde una perspectiva general, se analizan todos los efectos ecológicos potenciales de los escapes y se proponen medidas para su seguimiento y mitigación.

Tras un primer capítulo de introducción a la problemática, el capítulo dos supone un estudio preliminar de los escapes en la isla de Tenerife, definiendo un patrón espacial donde la abundancia de escapados disminuye con la distancia a las instalaciones acuícolas. Esta distribución se ve afectada también por la estructura del hábitat. Por otro lado, se aportan datos preliminares de la dieta que demuestran que las lubinas escapadas depredan activamente en el medio natural, y que su dieta es similar a la de los individuos salvajes en su rango de distribución natural.

Un análisis más profundo sobre el asilvestramiento de la lubina se lleva a cabo en el capítulo 3. En él se exploran los cambios biológicos que se producen en las lubinas una vez escapadas. Para ello se compara la morfometría de los ejemplares escapados con la de aquellos que han pasado todo su ciclo de vida en condiciones de cultivo. También se estudian los perfiles de crecimiento en escamas así como diferentes índices de condición. Los resultados revelan que las lubinas escapadas tienen una forma más hidrodinámica que

escapees' somatic growth rates are similar to those of farmed fish. Additionally, the general loss of fats causes a decrease in Fulton and hepatosomatic indices to levels similar to wild counterparts. This is the result of a combination of individual phenotypic plasticity and natural selection, the former allows individuals to adapt themselves in order to survive, and the latter makes the fittest individuals have higher survival rates in the wild. This suggests that those escapees that survive long enough show good performance in the wild.

Gonadal maturation and potential for reproduction of the sea bass escapees are analysed in Chapter 4. This paper contains the first record of male and female escapees' simultaneous maturation in the wild. The males' gonad parasite *Sphaerospora testicularis* is also cited for the first time in the Canaries. Possibly it was introduced together with fry brought from mainland. The implications of these results regarding the possibility of self-sustaining populations and the spreading of parasites by escaped fish are discussed.

Chapters 5 and 6 are dedicated to studying the mass escape that occurred off La Palma in early 2010. This is the largest sea bass escape event officially reported to date worldwide, during which around a million and a half individuals

las mantenidas en cultivo. Los perfiles de crecimiento demuestran que los individuos escapados tienen unas tasas de crecimiento somático similares a los de cultivo. Además, la pérdida general de grasa hace que el índice de condición y el hepatosomático disminuyan a niveles similares a los de las lubinas salvajes. Todo esto es resultado de una combinación de la plasticidad fenotípica individual y la selección natural, que hace que los individuos más aptos tengan tasas de supervivencia mayores en el medio natural, e indica que aquellos individuos que logran sobrevivir un tiempo suficiente lo hacen en buen estado fisiológico.

La maduración gonadal y el potencial reproductor de las lubinas escapadas se analiza en el capítulo 4. En este trabajo se detecta por primera vez la maduración simultánea de machos y hembras de lubinas escapadas en el medio natural. Además, se cita por primera vez para Canarias la presencia del parásito *Sphaerospora testicularis*, en las gónadas de los machos, posiblemente introducido a través de la importación de juveniles. Las implicaciones de estos resultados son discutidas ante la posibilidad de que las lubinas escapadas puedan dar lugar a poblaciones reproductoras y, además, dispersar parásitos a especies nativas.

Los capítulos 5 y 6 están dedicados a estudiar el escape masivo ocurrido en La Palma a principios de 2010. Este es el escape de lubinas más grande a nivel mundial del que se tiene constancia oficial; durante el cual se liberaron alrededor de un millón y medio de lubinas. En el capítulo 5 were released into the wild. Abundances of escaped fish at different spatiotemporal scales, before and after the escape event, are analysed in Chapter 5. It is also examined whether the La Palma Marine Reserve, near the escape point, has any influence on the number of escaped fish observed. 'First- sale' data of the two fishermen's associations on the Island are collated to detect changes in local artisanal fisheries. Escaped sea bass abundances in the wild suggest temporal patterns in which during the winter there is a higher number of escapes due to sea storms. Meanwhile, during summer, bass abundance is lower due to a lower escape rate and possibly increased fishing mortality. La Palma Marine Reserve showed no special patterns of escapee abundance, thus it was equally affected by the escape event. The Island's artisanal fisheries were clearly altered by the massive escape, and some months, escaped fish amounted up to 40% of bentho-demersal fish catches. A year after the escape event there were substantial sea bass captures off the west coast of the Island.

In Chapter 6 the changes in trophic structure of fish assemblages after the massive escape are explored. As the trophic level of escaped fish is medium-high (3.3-3.8), the mean trophic level of the fish assemblage would be expected to increase due to the presence of

se analizan las abundancias a diferentes escalas espacio-temporales, antes y después del escape masivo. Además se examina si la Reserva Marina de La Palma, cercana al punto de escape, tiene alguna capacidad de control sobre el número de peces escapados que llegan a la misma. Por otra parte, se analizan los datos de primera venta de las dos cofradías de pescadores de la Isla, en busca de alteraciones en las pesquerías artesanales locales. Los datos de abundancia en el medio natural permiten detectar patrones temporales, en los cuales durante el invierno existe una mayor tasa de escapes debido a rotura de materiales por una mayor frecuencia e intensidad de los temporales. Mientras tanto, en verano la abundancia de lubinas es menor debido a una menor tasa de escape y, posiblemente, una mayor mortalidad por pesca. La Reserva Marina de La Palma no mostró patrones diferenciados de presencia de lubinas, es decir, estuvo igualmente afectada por los escapes. Las pesquerías de la Isla se vieron claramente alteradas por el escape masivo, ya que, en algunos meses, los peces escapados llegaron a representar cerca del 40% de las capturas de especies bentodemersales. Un año después del escape las capturas de lubinas eran todavía importantes en la costa oeste de la Isla.

En el capítulo 6 se profundiza en los cambios en la estructura trófica de los poblamientos de peces tras el escape masivo. Debido a que las especies escapadas son de un nivel trófico medio-alto (3,3-3,8), es esperable que el nivel trófico medio de la comunidad de peces se incrementase por la presencia de escapes. Los escapees. The data support the latter, but the MPA showed some resilience to these changes due to a better structured fish community. This assemblage has a biomass of herbivores that prevents increments in mean trophic level such as those in unprotected areas. However, the presence of escapees did induce a significant increase in mean trophic level, even in the marine reserve. The consequences of these changes are highly unpredictable because of the complex interactions that occur in the marine environment. Furthermore the diet of individuals caught off La Palma MPA six months after the massive escape and that of single individuals fished at different sites off Tenerife and La Palma is compared. Stomach contents suggest that the resources exploited by escaped sea bass depend on the size of the latter, but also on how long ago they escaped. This is consistent with wild sea bass foraging behaviour, which is known to suffer ontogenetic changes throughout their life cycle, and confirms that feral sea bass diet is very similar to that of wild counterparts, crustaceans and fishes being the most important prey.

The results of this thesis show the potential impacts of escapees in the Canaries, which may generate undesirable consequences if escape events are not managed properly. These interactions range from food webs modification

datos así lo indicaron, aunque la Reserva Marina de La Palma mostró cierta resiliencia a estos cambios debido a una comunidad de peces mejor estructurada. Dicha comunidad cuenta con una biomasa de herbívoros que evita que el nivel trófico medio aumente tanto como en las áreas no protegidas. Sin embargo, el aumento de nivel trófico medio debido a la presencia de escapes resultó significativo incluso en la reserva marina. Las consecuencias de estos cambios son muy impredecibles, debido a las complejas interacciones que se dan en el medio marino. Por otro lado, se analizó la dieta de las lubinas escapadas comparando individuos capturados aisladamente en diferentes puntos de Tenerife y La Palma con otros pertenecientes al escape masivo, capturados en la Reserva Marina. El análisis de la dieta muestra que los animales escapados explotan recursos tróficos dependiendo de su talla, pero también del tiempo que llevan en el medio. Esto concuerda con lo registrado para las lubinas salvajes, en las cuales se observan cambios ontogénicos de la dieta a lo largo de su ciclo de vida, y se confirma que la dieta es muy similar a la de individuos salvajes, siendo peces y crustáceos las principales presas de las lubinas escapadas.

Los resultados de la presente tesis ponen de manifiesto el impacto potencial de los escapes en Canarias, que pueden generar consecuencias no deseadas si no se lleva a cabo una gestión adecuada de los mismos. Estas interacciones van desde aspectos ecológicos, como la modificación de redes tróficas, hasta aspectos de salud pública debido a la falta de trazabilidad to public health issues due to the lack of traceability of escapees, and include fisheries interactions. The effects of escaped fish are difficult to model in a complex ecosystem such as coastal waters and, in most cases, they have barely been identified. This generates a high degree of uncertainty, in an environment where restoring habitats after negative impacts is costly. All these features lead to the need to manage escapees within the paradigm of risk evaluation and management. Therefore mitigation, contingency and restoration plans, jointly with constant monitoring and research should be encouraged. These tools, and a precautionary approach would enable a sustainable and environmentally-compatible management of aquaculture in the Archipelago, and are clearly relevant to its future development on an international scale.

de los escapes, pasando por la interacción con las pesquerías. Los efectos producidos por los escapes son difícilmente predecibles en un ecosistema tan complejo como el marino y tan particular como el canario, además de que en la mayor parte de los casos apenas se han identificado. Esto hace que el grado de incertidumbre sea elevado en un medio donde revertir los posibles impactos negativos es altamente costoso. En definitiva, queda clara la necesidad de gestionar los escapes bajo el prisma de la evaluación de riesgos, con planes de mitigación, contingencia y restauración, de un seguimiento constante y del fomento de la investigación. Son estas herramientas, junto al principio de precaución, las que posibilitarán un desarrollo de la actividad acuícola sostenible y compatible con el medio ambiente en el Archipiélago Canario, y son claramente relevantes para su futuro a escala internacional.

CHAPTER 1

General Background

1.1 A brief history of fish domestication

Aquaculture, the farming of aquatic plants and animals, was introduced as a twin term to agriculture, the farming of terrestrial plants and animals (Shelton and Rothbard, 2006; Bilio, 2007). However, it was 8,500 years after the first clear evidence of agriculture, when the basis for domestication of aquatic species was established, although exact dates on the origin of agriculture and aquaculture are in constant appraisal (Mannion *et al.*, 1999). The first evidence of some kind of control over the reproduction of captive Nile tilapia (*Oreochromis niloticus*, Cichlidae) is found in paintings and bas-reliefs in Egyptian tombs from around 3,500 years BP (Rabanal, 1988; Harache, 2002). Further development of aquaculture is found in Asia about 2,500 years BP, due to the desire of an emperor to have a constant supply of his favourite fish. A treatise entitled 'Fan Li on Pisciculture' is most likely the earliest book on aquaculture in the world (Rabanal, 1988; Liao, 2000). At Europe, the Romans practised pond-rearing of many marine and fresh-water species, and later, in the Middle Ages, monks introduced the culture of brown trout (*Salmo trutta*, Salmonidae). By the 19th century, aquaculture was a common practise in most of the European countries (Rabanal, 1988; Teletchea and Fontaine, 2012). Nonetheless, it was not until the 60's of the past century that aquaculture began to grow exponentially (Fig. 1.1) both in production and diversity of cultured species (Duarte *et al.*, 2007; FAO, 2012). This growth has been accompanied by the stagnation of world fisheries, which reflects the over-exploitation suffered by a large proportion of the fish stocks (Jackson *et al.*, 2001; Worm *et al.*, 2006).

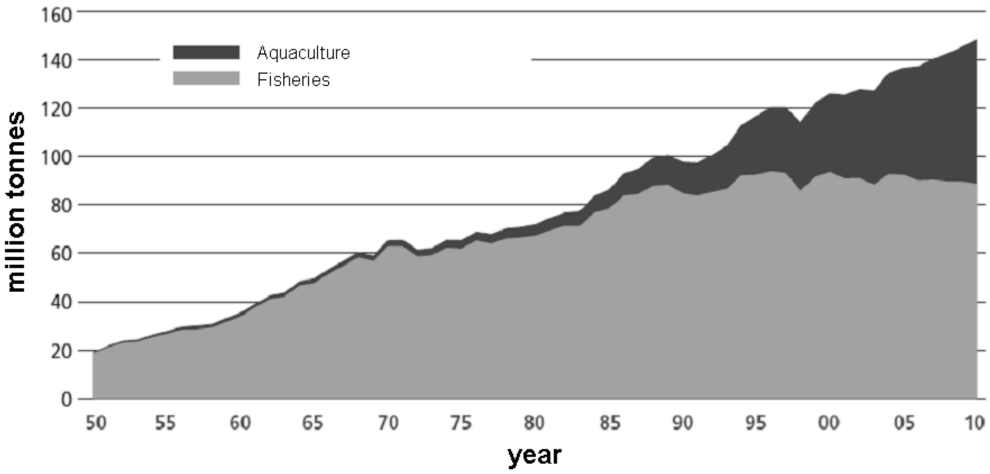

Figure 1.1. World fish production by aquaculture and extractive fisheries (FAO, 2012).

1.2 Domestication of European sea bass (*Dicentrarchus labrax)*

In his book 'On agriculture', Columella (circa 42) dedicated a whole chapter to explaining the art of rearing fish. Among the species he mentions as good for culturing is the '*lupus*' (wolf in Latin) referring to sea bass. He details that rocky or sandy fish-ponds near the coast are the best for maintaining this kind of fish, how to construct them and which elements to add for fish welfare. The diet for optimal growth of the fish is also described; such details show that pond-rearing was already a frequent practice on the coasts of the Roman Empire. This tradition was almost lost after its collapse (Rabanal, 1988; Pillay, 1990). Later, in the Middle Ages, sea bass aquaculture was further developed by modifying estuaries, marshes and coastal lagoons, in a manner known as extensive aquaculture that has reached our days (Girin, 1979; FAO, 2000). It has been, however, in the last decades of the 20th century when intensive culturing and breeding programs have been carried out to enhance sea bass production. The first attempts to intensively cultivate sea bass started in France during the 1970's (Barnabé and Tournamille, 1972; Bolineau, 1973). Experiments carried out from 1976 to 1978 solved problems dealing with the development of the swim-bladder and deformities (e.g. lordosis) (Barahona-Fernandes and Girin, 1977; Girin, 1978; Girin and Devauchelle, 1978). This led to a definition of environmental rearing conditions for sea bass (Coves *et al.*, 1991). Initially the culture of sea bass was carried out in land-based facilities, but the improvements in floating fish-cage engineering made it possible to situate aquaculture facilities off semi-exposed Mediterranean and Atlantic coasts (Beveridge, 1987). Nowadays, its production in Spain has largely surpassed the extractive catches (687 tonnes) and is nowadays over 14,000 tonnes (APROMAR, 2012).

1.3 Domestication versus feralization: two sides of the same coin

Animal domestication can be defined as "the process by which captive animals adapt to man and the environment he provides" (Price, 1999), and fish are no exception to this. Adaptation to the captive environment is achieved through genetic changes occurring over generations, and environmental conditions during an animal's lifetime. In this sense, domestication can be viewed as both an evolutionary (i.e. genetic) process and a developmental (i.e. phenotypic) phenomenon (Price, 1999). Genetic changes due to the domestication process can be classified as:

- 'Rearing traits': those related with survival in rearing conditions. This changes are not consciously selected by aqua-farmers; this would be the kind of 'natural selection' that we find in a controlled environment. However, rearing conditions exert such a weak selection that allows the survival of maladapted fish (e.g. deformed fish).

- 'Commodity traits' (*sensu* Lorenzen *et al.*, 2012): these are characteristics selected by aquaculturists, the more domesticated is the fish, the more commodity traits are promoted through selective breeding, genetic manipulation or targeted interventions in developmental processes. Advanced domestication can select traits that are commercially advantageous but non-adaptive even in a confined environment.

The mentioned genetic changes implicitly incorporate the idea of successive generations being selected to promote some traits. In contrast to that, there are evident individual-level changes that are manifested when an animal is collected from the wild and is reared in controlled conditions. Behavioural, physiological and even morphological changes have been observed in wild animals under captivity (Benhaïm *et al.*, 2012). The capacity of an individual to adapt to a different environment through the production of an alternative phenotype is known as phenotypic plasticity.

In the same way that a species' phenotypic plasticity aids it to succeed in the initial stages of domestication, it can also be crucial in the survival of escaped animals. The latter is known as feralization and when no self-sustainable populations of escaped animals are established in the wild, it consists of a series of behavioural, physiological and morphological changes in the individual during its lifetime. These changes help each fish to overcome drastic environmental stress once away from human control (Brown and Laland, 2001).

1.4 Systematic, Biology and Ecology of wild *Dicentrarchus labrax*

The European sea bass (*Dicentrarchus labrax*, L.) has always been a species coveted by fishermen, which probably explains the numerous studies dealing with the biology and ecology of this species (Arias, 1980; Kelley, 1979, 1987, 1988; Pawson *et al.*, 1987, 2000; Fritsch, 2005 and references therein). Consequently, without intending to be exhaustive, the aim of this overview is to outline the main biological and ecological characteristics of this species in areas where it is naturally found.

1.4.1 Systematic

Phylum:	Chordata
Subphylum:	Vertebrata
Superclass:	Gnathostomata
Class:	Actinopterygii
Order:	Perciformes
Family:	Moronidae
Genus:	*Dicentrarchus*
Species:	*Dicentrarchus labrax* (Linnaeus, 1758)

The specific name of the bass has changed considerably since the first descriptions known. Currently, it is commonly designated as *Dicentrarchus labrax* (Linnaeus, 1758). There is another species of the same genus, *Dicentrarchus punctatus* (Bloch, 1972), that has similar habits to *D. labrax* but is distributed farther south than sea bass (Bellemans *et al.*, 1988) but not north of UK waters (Froese and Pauly, 2012). The European genus *Dicentrarchus* occupies comparable latitudes and is taxonomically related to the American genus *Morone* (with four species) and both belong to the family Moronidae. Some authors long considered this family as a synonym of Serranidae. But today Moronidae is accepted as a valid family, based on genetic criteria (Eschmeyer and Fong, 2011; Williams *et al.*, 2012). Actually, the most recent molecular study situates Moronidae and Serranidae as families belonging to different orders (Betancur-R. *et al.*, 2013)

1.4.2 Morphology

As with all Perciformes, the body is symmetric. The pectoral fins are in a high position on the sides, pelvic fins in thoracic position and a spiny anal fin is present. In the genus *Dicentrarchus* the mouth is protrusible and the operculum spiny. The dorsal fin is twofold, counting nine spines in the first dorsal fin, followed by 10 to 14 soft rays in the second. The main criteria to distinguish between *D. labrax* (Fig. 1.2a) and *D. punctatus* (Fig. 1.2b) are:

- Permanent dark spots on the back and sides of *D. punctatus*, absent in adults of *D. labrax.*

- A vomer bone completely covered by teeth which form an arrow in *D. punctatus*, although they are smaller and 'V' shaped in *D. labrax*.

Sexual dimorphism has been suggested for *D. labrax*. Barnabé (1973) identified some criteria to discern visually the sex of sea bass, such as length of the head and pre-dorsal length, which are slightly larger in the female. However, the identification of the sex according to morphology is not a reliable method, because it results in a substantial percentage of error around 20% (Fritsch, 2005).

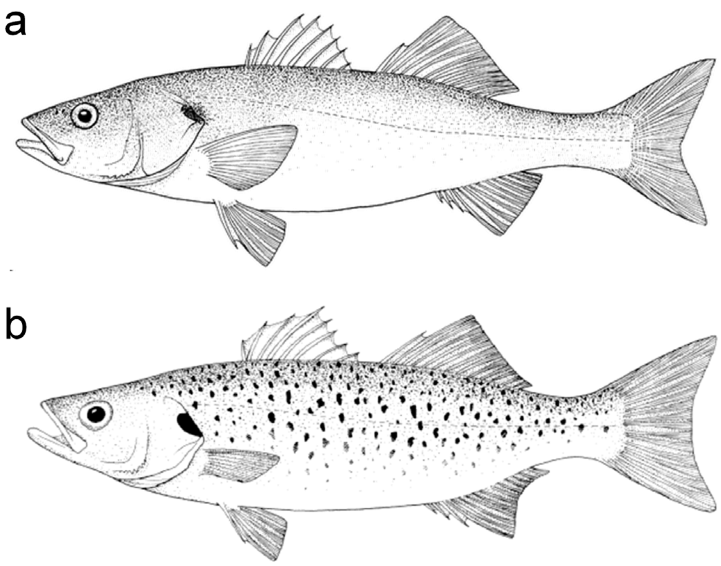

Figure 1.2.Morphological characteristics of (a) *Dicentrarchus labrax* and (b) *Dicentrarchus punctatus.* Illustrations from FAO factsheets available at www.fao.org.

1.4.3 Biogeography

The bulk of *D. labrax* populations are distributed in the North-East Atlantic from 30°N (coast of Morocco) to 60°N (southern Norway). It is present in the Irish Sea, North Sea and Baltic Sea, and the entire Mediterranean and the Black Sea (Fig. 1.3). It can be found down to 100 m deep, and up to about 80 km offshore in areas with a wide continental shelf (Froese and Pauly, 2012). Thanks to the upwelling system that provides cold waters off Saharan coast, sea bass has substantial populations in zones southward along the African coastline as far as Cape Juby (Gravier, 1961; Froese and Pauly, 2012), but it is absent southern Cape Blanc (Cadenat, 1937; Collignon and Aloncle, 1973; Maigret and Ly, 1986; Bellemans *et al.*, 1988; Toledo-Guedes *et al.*, 2009). In the Canary Islands its natural distribution includes only some

Figure 1.3. World biogeographical distribution of *D. labrax* and regional distribution of wild populations in the Canary Islands. Data from FAO factsheets available at www.fao.org and own data.

spots on the west coast of Fuerteventura and north of Lanzarote (Brito, 1991; Brito *et al.*, 2002; Fig.1.3). It is believed that this distribution is linked to cold coastal water associated with local upwelling systems present in both islands (Brito, 1991; Hernández-Guerra *et al.*, 1993; Pacheco and Hernández-Guerra, 1999; Brito *et al.*, 2002), but its populations probably depend on larval input from African coasts through upwelling filaments reaching eastern islands (Brochier *et al.*, 2011). This is supported by recent studies on ichthyoplankton across the Canaries that found only five *Dicentrarchus sp.* larvae in coastal zones off Fuerteventura and Lanzarote (Bachler, 2011). In any case, the wild populations are believed to be very scarce and overexploited as their catches are limited to sport fishers, with low frequency (González *et al.*, 2012). Additionally, no individuals were found in visual census surveys (Falcón *et al.*, 1996) or captured by artisanal fisheries (Franquet and Brito, 1995) in central and western islands before aquaculture activity became widespread in the Archipelago.

1.4.4 Growth

Sea bass is a slow-growing species with considerable longevity (up to 15-20 years). Females grow at higher rates than males in the same areas. But temperature is the most important factor influencing growth rates; sea bass show better growth rates in the Mediterranean than in the English Channel (Arias, 1980). As shown by scale growth profiles, in both areas there is an annual growth stop due to the low water temperature during winter. (Arias, 1980; Fritsch, 2005).

1.4.5 Reproduction and larval development

As with growth, reproduction is strongly influenced by temperature. In the Mediterranean, sizes at maturity are smaller than in the Atlantic. Low temperatures seem to trigger gonadal maturation. However, when minimum water temperatures of 10-12 °C are not reached (e.g. in Portugal), photoperiod is then the triggering signal for maturity (Vinagre *et al.*, 2009). This explains the existence of a temporal spawning gradient, for example, spawning is during May and June off UK coasts and progressively earlier as we move southward, taking place between January and March along the south coast of Spain (Arias, 1980).

Fertilized eggs have a diameter of 1.3 mm and are pelagic. Their neutral buoyancy makes them remain at shallow depths so they are never found at the surface (Kennedy and Fitzmaurice, 1972). It takes between two and five days to hatch after fertilization. Larvae at hatching are 4 mm in length. After 30 days (10 mm in length), larvae are prepared to enter estuaries, where they will stay at least three years (Kelley, 1988).

1.4.6 Habitat use and migrations

Some studies have pointed to the importance of estuaries for sea bass, especially as nursery areas (Kelley, 1988; Fritsch, 2005). There, 0-year groups inhabit shallow waters (no more than 5 m depth) with varying salinities as they are euryhalines. Muddy and mixed muddy/sandy bottoms are frequented by these individuals. Adult sea bass are also euryhaline and eurythermic, capable of supporting large differences in temperatures (2-32 °C) and wide variations in salinity (0.5-40). They are found in brackish waters in estuaries (even ascending rivers) and open sea in coastal areas. Adults are frequently found in wave-battered rocky coasts and in sandy/pebble beaches in the surf zone (ICES, 2006; Froese and Pauly, 2012).

Very little is known about sea bass larval distribution and movements. Their densities are low and it can only be said that they are found offshore preferentially at depths between 15 and 20 m. Movements of juveniles seem limited and probably related to water temperature (Kennedy and Fitzmaurice, 1972). In estuaries they are usually found in shallower waters during summer while moving to the mouth of rivers during winter as temperatures are milder in deeper waters (Kelley, 1979). Adult sea bass migration has been studied by tagging experiments (Kennedy and Fitzmaurice, 1972; Kelley, 1979), especially in the English Channel. In autumn (September-October) adult sea bass move southward to areas situated in the western Channel where water temperature is higher. Then during spring (April-May) individuals move northwards to coastal waters of the UK and France where short coastal foraging displacements are observed (Pawson *et al.*, 1987).

1.4.7 Diet

The diet of sea bass is highly diverse and is closely related to the size of the individual. A trophic shift has been described for this species between 200 and 400 mm of total length, when individuals start feeding on fish. Thus, there is a tendency for the trophic level of the fish to rise as it grows (Kelley, 1987; Rogdakis *et al.*, 2010).

Post-larvae and juveniles feed mainly on Mysidacea, Amphipoda (Gammaridae and Corophidae), Copepoda, and the larvae of Decapoda and Cirripedia. Occasionally juveniles can also predate on insects in nursery areas. Adults have a diet dominated by two groups of preys: decapods and fish. Sea bass is a voracious predator that can swallow prey of large sizes in comparison to its body size (Arias, 1980; Fritsch, 2005; Leitão *et al.*, 2008; Rogdakis *et al.*, 2010). Some individuals have been found with stomachs full of algae and seagrass suggesting sporadic herbivorous behaviour (Fritsch, 2005).

1.5 Aquaculture in the Canary Islands

Aquaculture is an activity with little tradition in the Canary Islands (Arnal, 1982). The first attempts, in the early 20th century, were the establishment of oyster racks off Playa de Las

Canteras (Gran Canaria) and Puerto Naos (Arrecife). However, they had a short duration and the results are almost unknown (PROAC, 2008). Other trials consisted of catching fish, keeping them alive in seawater tanks on the vessels and transferring them to cages moored in harbours. The fish were marketed in accordance with the demand and business strategies. This system remained until the thirties, when port areas began to be polluted with petroleum and its derivatives.

The Institute for the Conservation of the Nature (ICONA) launched in the seventies a pilot freshwater trout-farming project in Aguamansa, La Orotava (Tenerife) that is still working today. The following advances in aquaculture in the Canaries were made in the framework of research projects. Between 1975 and 1976 the Spanish Oceanography Institute (IEO) undertook two research actions aimed at the culture of mussels (*Perna perna*) on the west coast of Fuerteventura (Fig. 1.4). The exposed nature of this coast (with several sea storms during the year) prevented the success of these projects.

An important milestone for aquaculture in the Canaries was the organization of the First Conference on Marine Culture (CONCUMAR I) in Lanzarote (1980). This can be considered the starting point of modern aquaculture in Spain. In the middle 80’s a pilot project for land-based culture of prawns was carried out on Gran Canaria, but the need for large extensions adjacent to the coast drastically reduced the profitability of this enterprise. On the same Island during 1987 a land-based facility was installed for the fattening of sea bream (*Sparus aurata*). It is noteworthy that the technologies and materials for the construction of floating cages robust enough to support semi-exposed conditions were still in development (Beveridge, 1987). However, at the same time artisanal-constructed fish cages were placed off southwest Tenerife and began to culture sea bream and sea bass. Shortly after in 1990, one more land-based facility was built on the southeast coast of Fuerteventura, but two years later it was closed due to design problems.

The first specifically designed sea cages were placed off Arguineguín on the southeast coast of Gran Canaria. A land-based facility for the culture of turbot (*Scophthalmus maximus*) was also constructed there, but the need for water with lower temperature than that surrounding the Canaries stopped this attempt. Some of these pioneering enterprises still illustrate the lack of budget, technologies, and biological knowledge that characterized the aquaculture industry in the region at this initial stage of development. Actually, none of the

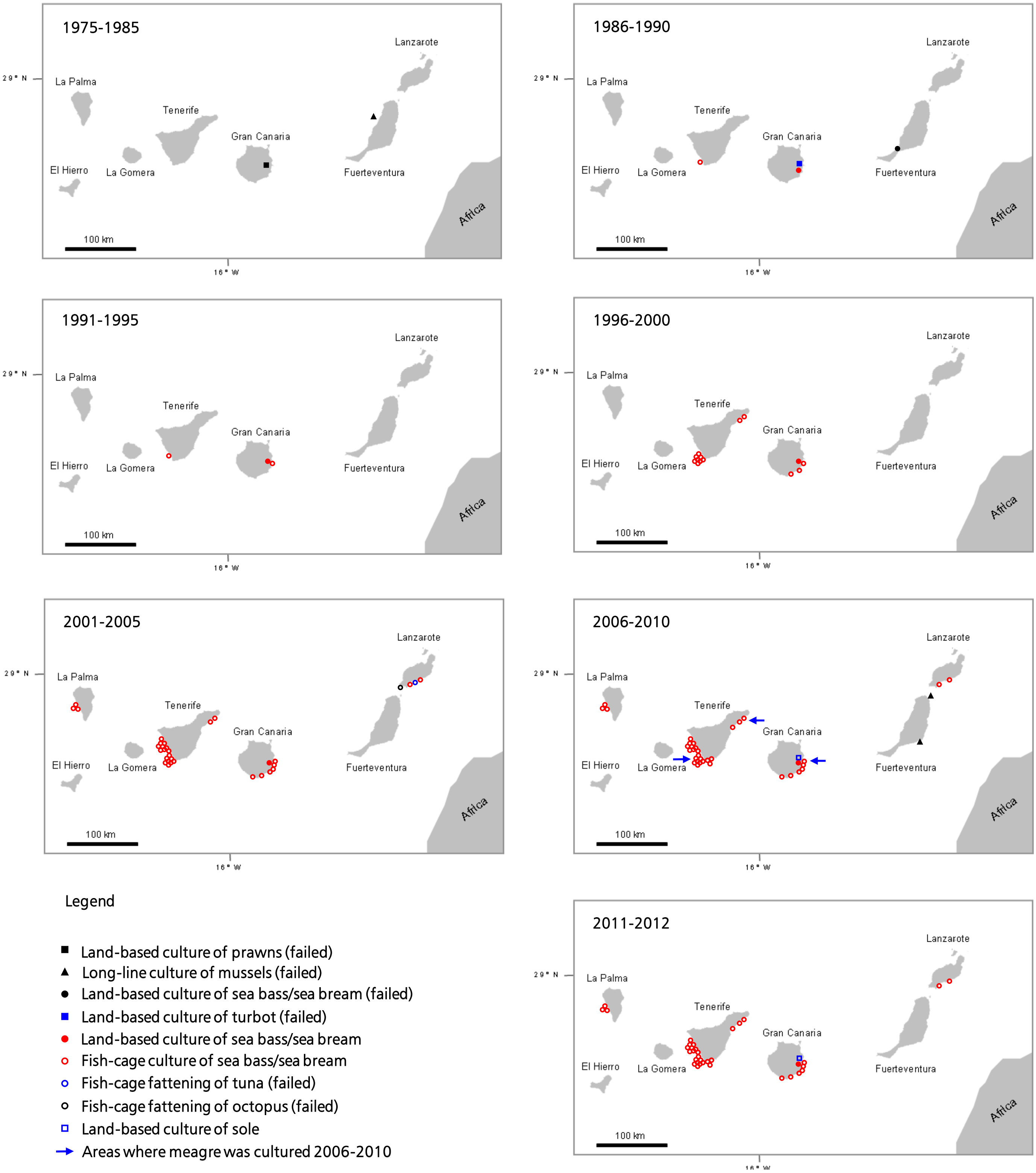

Figure 1.4. Aquaculture activities carried out in the Canary Islands in the period 1975-2012. Note that aquaculture facilities are not to scale and their location is only for guidance. Not all the farms were producing continuously and even some of them were never deployed despite the granting of a concession. Data from BOC (Official Bulletin of Canary Island Government) and PROAC, 2008.

aforementioned projects are still active today.

In the final 90's, interest was renewed after new authorizations for aquaculture facilities and the creation of several new companies (BOC, 1999, 2000). In 2007, the year with the maximum production of fish in the region (9,376 tonnes), a total of 28 companies were working across the Archipelago (APROMAR, 2012). The majority of them were centred on the on-growing of sea bream and sea bass in floating cages, these are, by far, the most cultured species in the region. It is noteworthy that in 2003 a new species was brought to the Canaries to diversify the production, meagre (*Argyrosomus regius*) was cultured several years in some facilities off Tenerife and Gran Canaria (Ortega *et al.*, 2011; Fig. 1.5). However, this species is not being cultured nowadays since no authorizations or permits have been granted for this purpose (APROMAR, 2012; Fig 1.5).

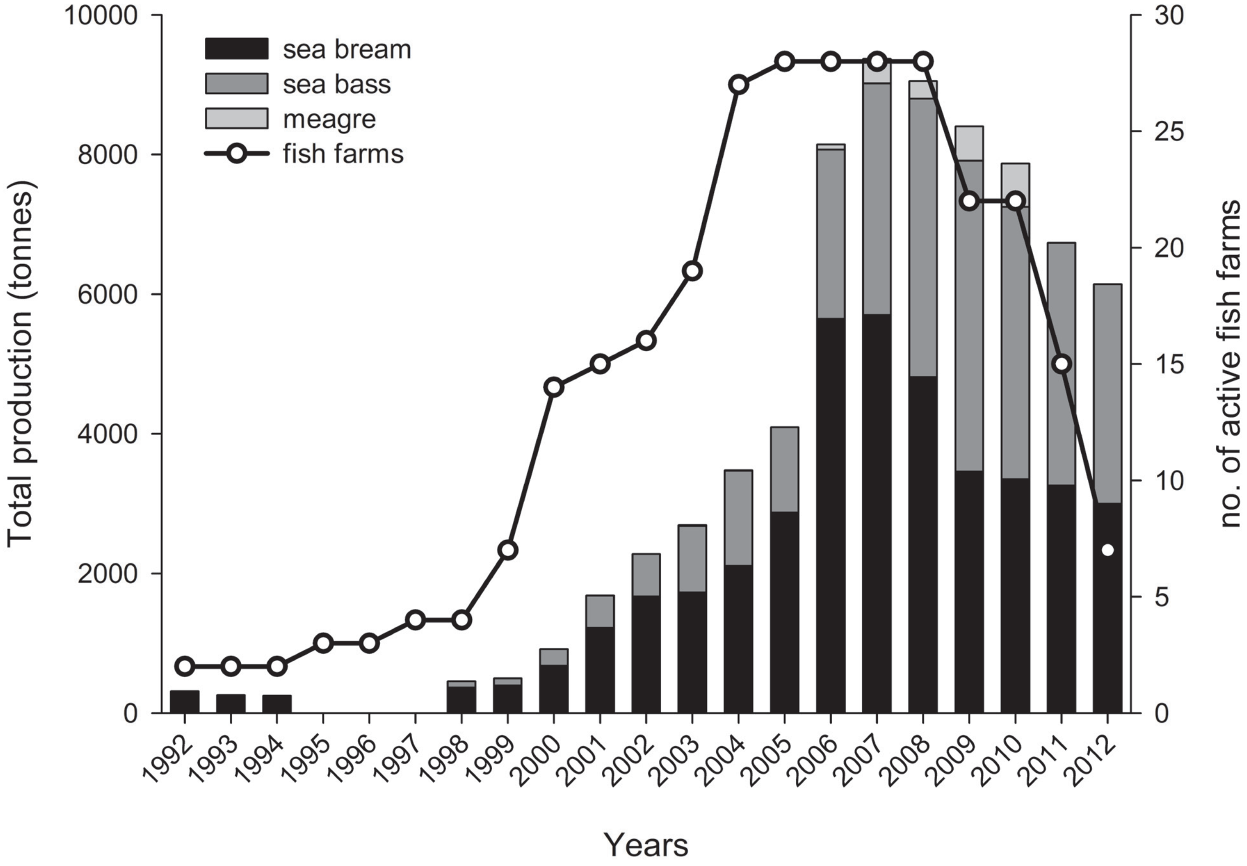

Figure 1.5. Fin fish production in the Canary Islands during the last twenty years and number of farms in production each year. Data between 1995 and 1997 were not available. Data from Franquet and Brito, 1995 and APROMAR reports from 2004 to 2012.

The global crisis, price collapse (Asche *et al.*, 2001) and the loss of competitiveness with countries such as Greece or Turkey have lead to a general contraction in the activity in Spain (APROMAR, 2012). Stakeholders point out that less restrictive legislation regarding environmental, sanitary, and employment conditions in those countries is disadvantageous for Spain. In the Canaries this situation is aggravated by the cuts in EU subsidies for aquaculture, delay owing to licensing procedures, decrease in fish consumption and the lack of a regulatory framework for optimal development of the activity. This latter is noted in the diminishing production and lower number of active aquaculture enterprises (APROMAR, 2012; Fig. 1.5). In fact, recent data reveals that in the Canaries less than ten companies are in production nowadays and total production has fallen to 6,144 tonnes during 2012 (Lozano-Soldevilla pers. comm.). Despite this, the Spanish Marine Aquaculture Producers Association (APROMAR) classed the region as one of the top fin-fish producers in Spain (APROMAR, 2012).

1.6 Escape events

An escape event is defined as the process by which one or several fish (in any point of their life-cycle) lose their confinement and reach the unenclosed marine environment (Dempster *et al.*, 2013). Fish escapes typically involve losing part of the biomass contained in the fish-cage, which is released into the wild. However, the recent definition of ‘escape through spawning’ (Jørstad *et al.*, 2008) has extended the concept to the release of fertilized eggs due to spawning in fish cages. Escape events are inherent to net-pen aquaculture in open sea and pose a great economic loss (Jackson *et al.*, 2013). Aside from escape through spawning, escape events can be classified depending on their frequency of occurrence and number of fish escaping:

- Leak escapes: high frequency and small number of escaped fish. This kind of escape event is often illustrated as a continuous leakage of one or several individuals. Fish usually escape through small holes in the net created by biting behaviour of both predators and cultured fish (Jackson *et al.*, 2013). Lack of maintenance can also favour the occurrence and enlargement of holes. Sometimes escapes occur during harvesting operations, especially when sea conditions hinder the manoeuvre. Unnoticed in many cases these recurrent escapes can lead to a significant loss of up to 1% of the biomass of the cage each month (Jackson *et al.*, 2013).

Table 1.1. Massive escape events recorded by reliable sources: technical reports (JACUMAR, 2007; Ramírez *et al.*, 2011), marine researchers and aquaculture companies staff. (*) Bankrupt companies.

Year	Month	Location	Cause	Cages affected	Species	Estimated Escaped Biomass	Estimated Loss in biomass	Estimated Loss in facilities
1998	January	S Gran Canaria	SSW sea storm (2-3 m waves height)	12	-	-	2,000,000 €	120,000 €
1998	January	E Gran Canaria	SSE sea storm (3 m waves height)	5	sea bass	200 tonnes	954,480 €	43,800 €
2001	November	E Gran Canaria	NE sea storm (wind 6-7 Bf and 2.5 m waves height)	4	-	-	435,880 €	29,000 €
2001	-	SW Tenerife	-	-	sea bream	-	-	-
2002	January	E Gran Canaria	ESE sea storm (wind 5-6 Bf and 2.5 m waves height)	3	-	-	254,648 €	21,600 €*
2002	December	S Gran Canaria	SW sea storm (wind 7 Bf and 2-3 m waves height)	-	sea bream and sea bass	220-500 tonnes	2,000,000 €	750,000 €*
2004	January	E Gran Canaria	NE sea storm (2 m waves height)	2	Sea bass (1 kg. weight)	90,000 individuals	490,000 €	7,000 €
2004	July	W Tenerife	Sabotage	3	sea bream and sea bass	130,000-390,000 individuals	-	-
2005	February	E Gran Canaria	NE sea storm (wind 5-6 Bf and 4 m waves height)	2	-	-	3,000 €	6,000 €
2005	December	E Gran Canaria	-	-	Meagre	15 tonnes	-	-
2005	November	W Tenerife	NW sea storm (wind 27 knots and >3 m waves height)	-	-	-	570,000 €	110,000 €
2005	November	W Tenerife	NW sea storm (wind 27 knots and >3 m waves height)	-	-	-	141,000 €	47,760 €
2005	November	SW Tenerife	NW sea storm (wind 27 knots and >3 m waves height)	6	-	-	160,525 €	41,100 €
2005	August	SW Tenerife	Boat crashed into a fish cage	1	-	-	60,000 €	24,000 €
2009	December	W La Palma	W sea storm (up to 6 m waves height)	12	sea bass (90%) and sea bream (10%)	400 tonnes (1.5 million fish)	-	-
2013	March	SE Gran Canaria	S sea storm (4-6 m waves height)	2-4	sea bass	250,000 ind. (1 kg) and 150,000 ind. (all sizes)	-	-

- Massive escapes: low frequency and large number of escaped fish, involving sudden loss of biomass of one or several fish cages. Infrequent cases of sabotage have also provoked this kind of escape events. However, the main causes are sea-storms, when materials undergo maximum mechanical stress combined with lack of continued maintenance due to reduced access during long stormy periods (Jensen, 2013).

1.7 Interactions of escaped fish

There are many studies dealing with the interactions of farm-origin fish around the world, especially in salmonids (McGinnity *et al.*, 2003; Lorenzen, 2008; Arismendi *et al.*, 2009; Van Poorten *et al.*, 2011), but also with strictly marine species (Friedlander *et al.*, 2002; Liao *et al.*, 2010). Except for genetic interaction (that involves the existence of a counterpart wild population), other interactions can potentially occur independently of the origin of escaped species. Populations of escaped fish can be maintained through new escapees as long as aquaculture activity continues. Thus, the interactions do not depend on the establishment of self-sustaining populations of farm-origin fish (*et al.*, 2005; Arismendi *et al.*, 2009).

Trophic interactions

They are the most evident consequence of escaped fish. As soon as they are able to survive in the wild, fugitives exploit natural resources (Arechavala-Lopez *et al.*, 2012c). To what extent their diet resembles that of their wild counterparts may depend on their degree of domestication, time since escape, and available prey in the wild. Direct predator-prey interactions, interspecific competition for resources (i.e. diet overlap) and even trophic cascade effects could be observed due to the input of farmed fish into natural environments (Soto *et al.*, 2006; Arismendi *et al.*, 2009; Edelist *et al.*, 2013). However these interactions are more easily studied in closed and semi-closed systems (i.e. lakes and rivers) where migration is limited and changes in fish communities can be measured easily. In contrast, consequences of this interactions are unlikely to be detected in open-complex ecosystems such as the marine coastal habitats (Edelist *et al.*, 2013).

Genetic interactions

When escaped fish share habitats with their wild counterparts with whom they can interbreed. Some studies have suggested that interbreeding with low genetic diversity stocks (i.e. farmed fish) can have negative consequences through genetic introgression (see Araki and Schmid, 2010). Lower genetic diversity means a more limited capacity to respond to changes in the environment at population level. Additionally, the loss of local adaptations of life-history traits in wild populations can promote a mismatch between those traits and the environment (i.e. maladaption; Youngson, 2001).

Pathogenic interactions

High density of individuals inside the cages facilitates the appearance and transmission of some diseases (Butler, 2002; Krkošek *et al.*, 2006; Pulkkinen *et al.*, 2010). It has been shown that the occurrence and prevalence of some parasites during culture is higher than in the wild, thus fish cages act as pathogen reservoirs (Sitjà-Bobadilla and Alvarez-Pellitero, 1990). However, other studies have found a similar parasite load in wild populations aggregated around fish farms in comparison to populations far from aquaculture facilities (Fernandez-Jover *et al.*, 2010). In any case, escaped fish bring with them their parasites and diseases and some authors point out the need to address and incorporate this problem into management plans (Arechavala-Lopez *et al.*, 2013b).

Fisheries interactions

Once in the wild, fugitive fish become potentially available for sport and professional fisheries. Thus, they could provide extra income for professional fishermen and enhance the recreational activity for anglers. This issue has been extensively studied for salmonids (Lund *et al.*, 1991; Walker *et al.*, 2006; Green *et al.*, 2012a and references therein), however much less is known for species produced in the Mediterranean (e.g. sea bass and sea bream; Dimitriou *et al.*, 2007; Arechavala-Lopez *et al.*, 2012c). These studies suggest that escaped fish are being caught by professional and sport fishermen, and the proportion on the whole may indeed be significant.

Secondary interactions

Fish escapes can also have a variety of other consequences worth commenting on, which must be addressed in order to achieve integrated management. For example, escape events can attract fishing pressure over certain areas (i.e. release point surroundings) promoting the over-exploitation of other (initially) non-targeted species and wild counterparts if present (Lorenzen *et al.*, 2012). Recapture efforts can also pose a problem in certain cases as by-catch may surpass recaptured fish (Serra-Llinares *et al.*, 2013). Market prices of farmed (and even wild) fish can collapse locally, due to the high availability of escaped fish, easily caught by non-professional fishermen (pers. obs). In areas where native species are farmed, escaped fish of these species are mislabelled and sold as wild fish with subsequent detriment to the consumer (Arechavala-Lopez *et al.*, 2012abc, 2013a). Another important aspect is food safety and traceability. Escaped fish reaching markets and labelled as wild could bear inappropriate concentrations of antibiotics and other chemicals if they were treated against any disease just before escape and were caught shortly after (Juan-García *et al.*, 2007).

1.8 Escape events in the Canary Islands

Since the establishment of the first fish cages twenty-five years ago, escape events have been continually occurring in the region. Nevertheless, aqua-farmers are not required to communicate escape events to authorities. Table 1.1 shows a non-exhaustive record of massive escape events that have occurred in the Canary Islands. Our data come from personal communications and public reports that are also supported by those provided by the aquaculture industry (JACUMAR, 2007; Ramírez *et al.*, 2011). Some of these accidents led to the bankruptcy of the companies involved.

1.9 Objectives

Taking into account all the elements described before we find that, after twenty-five years of aquaculture activities in the region, very little attention has been paid to fish escapes. This is not in concordance with growing social and scientific concern about potential problems posed by escaped fish (Dempster *et al.*, 2013), which need to be deeply studied in order to assure an environmentally sound aquaculture industry in the region. There is an evident lack of knowledge about performance, potential ecological impacts of escapees and massive escape events in the Archipelago. This science-based information is essential to reduce the uncertainty in risk assessments, management and monitoring schemes, and to develop better mitigation and contingency plans. This thesis is particularly timely as attempts to establish an integrated regulatory framework for the aquaculture industry have been made by the Canary Islands government (PROAC, 2008). Additionally, a draft of a contingency plan regarding large escape events has recently been sent to stakeholders for comments and recommendations. Therefore, this research sheds light on the problems posed by escaped fish in the Canaries.

Hence, the overall purposes of this thesis are to assess **escaped sea bass feralization** and their **ecological role** in shallow coastal waters of the Canary Islands. To evaluate the **largest sea bass escape** event recorded to date **worldwide** and to provide **management recommendations** to **minimize** the likelihood of **negative effects** caused by escaped fish. In order to **achieve** the aforementioned general goals a series of **objectives** were **accomplished**:

Chapter 2

2.a. To investigate the spatial distribution, abundance of escaped sea bass related to distance from fish farms.

2.b. To test the influence of environmental features on the abundance of escaped sea bass and their habitat use in shallow coastal waters.

2.c. To analyze stomach contents of escaped fish to check if they exploit natural resources after escaping from fish farms.

Chapter 3

3.a. To compare body morphometry of farmed and escaped sea bass to quantify phenotypic plasticity during the feralization process.

3.b. To contrast body condition indices between escapees and farmed fish.

3.c. To assess post-escape growth rates in the wild comparing growth profile in scales of farmed fish against escaped fish.

Chapter 4

4.a. To study the gonads of escaped sea bass and provide data on size and period of maturation in the wild for the region.

4.b. To check gonad functionality of male and female escapees through histology.

4.c. To analyze the prevalence of the gonad parasite *Sphaerospora testicularis* in males of escaped sea bass.

Chapter 5

5.a. To investigate spatiotemporal patterns of escapees' abundance in the wild before and after a massive escape event off La Palma.

5.b. To evaluate the influence of La Palma Marine Protected Area on escaped fish abundance.

5.c. To assess possible alterations in La Palma artisanal fishery catches induced by escaped fish.

Chapter 6

6.a. To examine the potential of escaped fish to alter the mean trophic level of fish assemblages off La Palma.

6.b. To test the resilience to changes in fish assemblages' mean trophic level within La Palma Marine Protected Area.

6.c. To compare abundances of escaped fish against other medium-top predators in shallow coastal waters off La Palma.

6.d. To provide data on the diet of escapees in relation to size and time at liberty.

Chapter 7:

7.a. To discuss degree of domestication, performance in the wild and ecological interactions of farmed sea bass in the Canaries.

7.b. To propose a risk evaluation framework to prevent escape events and minimize the potential negative interactions of escaped fish in shallow coastal ecosystems off the Canary Islands.

CHAPTER 2

Detecting the degree of establishment of a non-indigenous species in coastal ecosystems: sea bass *Dicentrarchus labrax* escapes from sea cages in Canary Islands (Northeastern Central Atlantic)

Toledo-Guedes K, Sanchez-Jerez P, González-Lorenzo G and Brito A (2009) Detecting the degree of establishment of a non-indigenous species in coastal ecosystems: sea bass *Dicentrarchus labrax* escapes from sea cages in Canary Islands (Northeastern Central Atlantic). *Hydrobiologia*. 623: 203-212.

SUMMARY

This chapter gives an insight into the degree of establishment and potential impact of escaped sea bass in shallow coastal habitats of Tenerife. We studied spatial distribution, abundance, size frequency and use of habitat by visual census. Stomach contents and gonadal maturity of escaped sea bass were analyzed. Results show that abundance of escaped sea bass is related to distance from to the nearest fish farm and to the habitat complexity. The most frequent size found in the wild corresponds to that of first marketing size. Stomach contents indicate that escaped sea bass were able to exploit natural resources, especially fish. The presence of a female with mature gonads indicates that conditions for successful maturation exist. However, further studies are needed to ensure whether or not escaped sea bass are able to establish self-reproducing populations. Thus, we can conclude that sea bass seem to be already established in shallow coastal habitats of Tenerife, but their populations may depend mainly on escapees. Due to being an opportunistic piscivore, sea bass could be predating on and competing with other native species that are economically important. These results are useful to develop a risk assessment based on quantitative data to predict negative effects. Moreover, management policies such as reporting of massive escapes or mitigation measures are needed to prevent future impact on the marine environment.

RESUMEN

Este capítulo da una visión del el grado de establecimiento y del impacto potencial de las lubinas escapadas en hábitats costeros someros de Tenerife. La distribución espacial, la frecuencia de tallas y el uso del hábitat fueron estudiados mediante censos visuales. También se analizaron los contenidos estomacales y la madurez gonadal. Los resultados muestran que la abundancia de las lubinas está relacionada con la distancia a la granja de cultivo más cercana y con la complejidad del hábitat. La talla más frecuentemente encontrada en hábitats naturales corresponde a la talla de primera comercialización. Los contenidos estomacales indican que las lubinas escapadas son capaces de explotar recursos naturales, especialmente peces. La presencia de una hembra con gónadas maduras indica que existen las condiciones para una maduración exitosa. Sin embargo, son necesarios más estudios para asegurar si las lubinas escapadas pueden establecer poblaciones reproductoras. Por tanto, podemos concluir que las lubinas parecen encontrarse establecidas en hábitats costeros someros de Tenerife, pero la población podría depender principalmente de nuevos escapes. Al ser un piscívoro oportunista, la lubina podría estar depredando y compitiendo con otras especies nativas que son económicamente importantes. Estos resultados son útiles para desarrollar un análisis de riesgo basado en datos cuantitativos para predecir los posibles efectos negativos. Además, son necesarias políticas de gestión tales como la comunicación de escapes masivos o medidas de mitigación para prevenir impactos futuros en el medio marino.

2.1 Introduction

Non-indigenous species are an increasing problem in aquatic systems (Ruiz, 1997; Ruiz *et al.*, 2000; Streftaris *et al.*, 2005; Casal, 2006) but the consequences for native and economically important species are poorly understood (Colautti *et al.*, 2006; Kalogirou, 2007). Extinction or drastic reduction of certain populations due to competition, loss of genetic diversity, predation or pathogen transfer processes have been documented (Fleming *et al.*, 2000; McGinnity *et al.*, 2003; Dextrase and Mandrak, 2006; CIESM, 2007). Aquaculture is one of the main ways non-native species are introduced into aquatic systems (Casal, 2006). A total of 1205 instances of fish introductions due to aquaculture have been reported in freshwater ecosystems (Casal, 2006). Marine aquaculture in net pens is also an important vector of release for both native and non-native species and escapes from fish cages are a common well-documented problem around the world (*et al.*, 2005). Two types of escapes can be distinguished; massive escapes which occur when a fish cage is broken by a storm or sabotage, and daily escapes due to small holes in fish-cage nets, maintenance and harvesting (CIESM, 2007).

Numerous studies into the impact of alien fish species on aquatic natural assemblages have been carried out although mainly for fresh-water fish or salmonids. Alien invasive species were a primary factor in four out of five extinctions of Canadian freshwater fish and a secondary threat factor for other species (Dextrase and Mandrak, 2006). Different studies show the impact of introduced salmonids on Australian and New Zealand native fauna (Cadwallader, 1996 and references therein; Townsend and Simon, 2006), and also in Chile (Buschmann, 2001).

Aquaculture has undergone rapid expansion throughout coasts all around the world during the last two decades (*et al.*, 2000). In Europe, production of marine fish had an annual growth rate of 14% over the last ten years, reaching nearly 160 thousand tonnes in 2006 (FAO, 2003). Marine fish production is mainly limited to two species: gilt-head sea bream (*Sparus aurata*) and European sea bass (*Dicentrarchus labrax*). This trend is similar in the Canary Islands, and the production of fin fish has increased from 1685 t in 2001 to 9600 t in 2007 (APROMAR, 2007), where sea bream and sea bass are legally cultured around different islands (La Palma, Tenerife, Gran Canaria and Lanzarote). Canary Islands have led the production of sea bass in Spain during 2007 with a total predicted production of 3500 tonnes (APROMAR, 2007).

Some evidence points to the fact that both sea bass and sea bream have been introduced to the central and western islands of the Archipelago through aquaculture. Firstly, these species were not captured around the central and western islands (e.g. Tenerife) (Brito, 1991; Brito *et al.*, 2002). Secondly, studies of coastal fish assemblages using visual census surveys did not record any individual in coastal areas of central islands between 1990 and 1991 (Falcón *et al.*, 1996); all three reports refer the situation before aquaculture development. However, small native populations are established on eastern islands (Lanzarote and Fuerteventura) (Brito *et al.*, 2002) which possibly depend on larval dispersion through upwelling filaments from African coastal populations (Rodríguez *et al.*, 1999; Becognée *et al.*, 2006).

Sea bass *D. labrax* is distributed in the North Atlantic from Norway and the British Isles southward to Morocco and the easternmost Canaries. Data from African coasts show it is common down to Cape Juby, Western Sahara (27° 56’ 52’’ N, 12° 55’ 24’’ W) and does not extend southward of Cape Blanc (20° 46’ 17’’ N, 17° 2’ 50’’ W), a natural faunistic barrier, in Mauritania (Falcón *et al.* 2002; Maigret and Ly, 1986; Collignon and Aloncle, 1973). It is also present in the Mediterranean and Black Sea. European sea bass exhibits demersal behaviour, inhabiting coastal waters down to about 100 m depth, but is more common in shallow waters, on various kinds of bottoms; often entering estuaries and even ascending rivers. It predates mainly on fish and benthic crustaceans, also feeding on molluscs and insects (Tortonese, 1986; Leitão *et al.*, 2008) and it is an important species for commercial fishing.

An unknown number of fish are escaping from cages in the Canary Islands, which could be affecting natural fish assemblages. There is some evidence on the persistence of sea bass escapees in natural habitats. To understand the impact of this species on the coastal systems, it is essential to know its role in shallow water fish assemblages after escaping. Only one previous study has been carried out in Tenerife, studying the diet of *Dicentrarchus labrax* (González-Lorenzo *et al.*, 2005). However, there is a lack of information about the spatial distribution and population abundance of this species in the Canaries.

Taking into account the information gaps in this field, the general aim of the present study was to evaluate the degree of establishment of *Dicentrarchus labrax* escapees in the wild habitats of Tenerife and the influence of fish farms on their distribution and abundance.

For this we investigated (1) the spatial distribution, abundance and size structure of the escaped population regarding distance from fish farms, (2) habitat preferences, (3) stomach contents, to check if they can exploit natural resources after escaping from fish farms and (4) gonad development, to explore their potential for reproduction.

2.2 Material and Methods

2.2.1 Study area

The Canary Islands are a subtropical archipelago situated in the North of the Eastern Central Atlantic. The study of *D. labrax* distribution and habitat use was carried out in Tenerife, one of the two central islands, during winter-spring (from January to May 2007). A total of eight localities were chosen for visual census, four of them were close to fish farms (between 0.3 and 6 km from fish cages): Igueste, Los Cristianos, La Caleta and Isorana, and four more distant from fish cages (between 23 and 53 km from the nearest farm), i.e. Guayonje, Garachico, Güímar and Abades (Fig. 2.1). Three sites were sampled at each locality and a total of six transects were made within each site.

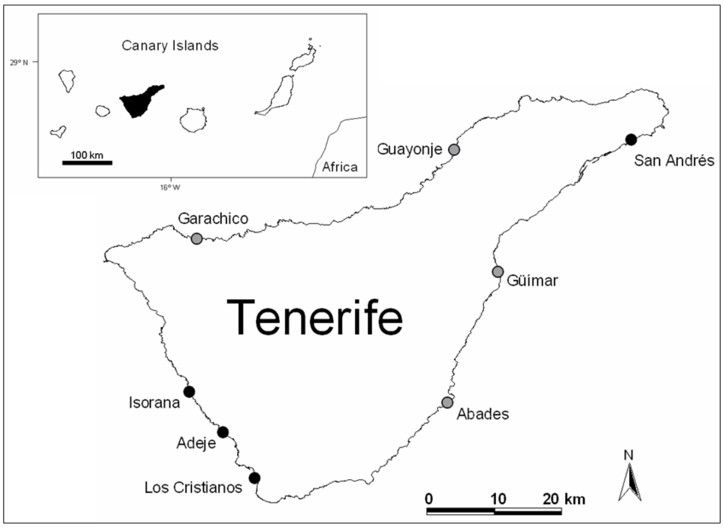

Figure 2.1. Study area. Black dots are localities within 6 km from fish farms, grey dots are localities at least 23 km away from fish farms.

2.2.2 Sampling method

Visual census

Previous studies have shown that *D. labrax* concentrates in very shallow waters between 0 and 5 m depth when they escape from fish farms (González-Lorenzo *et al.,* 2005). In order to avoid biases and due to the high mobility of this species, visual count transects 100 m in length following the shoreline were made by snorkelling. Transects were limited to 5 m width so total sampled area was 500 m^2 per transect. The first survey was used for counts of *D. labrax*. Total length of each individual was also estimated. A second survey of the same transects was made to establish habitat heterogeneity and complexity, measuring cover of different habitats and habitat features; sandy bottom, rocky platform, cliff, and boulders classified by the size of their maximum length (ML): small boulders-SB ($ML \leq 50$ cm), medium boulders-MB (50 $cm < ML \leq 1$ m), and large boulders-LB ($ML > 1$ m) (García-Charton *et al.*, 2004). Six replicates were made at each site so a total of 144 transects were surveyed. Visibility was always more than 5 m and surveys were done during the morning.

Stomach contents and gonad development.

Individuals of *D. labrax* were caught by spearfishing. All fish were measured (total length TL) to the nearest mm and weighed (accuracy of 0.01 g). The stomach-intestine was separated from the body, and its contents removed. Prey items were counted by number, fresh-weighed and identified to the lowest possible taxonomic level. Stomach Fullness (SF) was determined visually using the following scale: 0-empty; 1-very little content; 2-some content; 3-full, but not bloated; 4-bloated; 5-everted (Prokopchuk and Sentyabov, 2006). Thus, for each prey, percentage by number (N%) and weight (W%), frequency of occurrence (O%) and the alimentary coefficient ($Q = N\% \times W\%$) were calculated (Hureau, 1970). The importance of prey groups was assessed using the following categories (based on values of Q and O%; Rosecchi and Nouaze, 1987): main preferred prey ($Q>100$, $O\%>30\%$); main occasional prey ($Q>100$, $O\%<30\%$); secondary common prey ($10<Q<100$, $O\%>10\%$); secondary additional prey ($10<Q<100$, $O\%<10\%$); accidental prey ($Q<10$). The index of relative importance (IRI) (Pinkas *et al.*, 1971) was also estimated, $IRI = (N\% + W\%) \times O\%$. Finally, gonad development was visually estimated using a scale of eight states of maturity (FAO, 1974).

2.2.3 Statistical analysis

To test whether abundance of escaped sea bass was higher in the vicinity of fish farms, a three way ANOVA was carried out. The factor 'distance' with two treatments, close *vs.* distant from fish farm, was treated as a fixed effect. Three 'localities' were chosen for spatial replication at a scale of 10's of km and three 'sites' were also considered for spatial replication at a scale of km, both nested with 'distance' and random. As no transformation rendered variances homogeneous (Underwood, 1997), ANOVA was used as it is robust to heterogeneity of variances, particularly for large balanced experiments (Underwood, 1997). The significance level was thus lowered from 0.05 to 0.01 (Underwood, 1981). To ensure that close and distant localities were similar in relation to environmental variables, and differences in densities of escaped sea bass were not due to a biased choice of localities, a PERMANOVA (Anderson, 2001; McArdle and Anderson, 2001; Anderson, 2005) to test differences in environmental variables was performed. For this test, data were transformed with *arcsinx+1* prior to test because it was in percentages.

Multiple regression was performed to test which habitat variables (and their quadratic, cubic and logarithmic terms), including distance from the nearest fish farms, explained the abundance of *D. labrax* around the coast of Tenerife. In this case, stepwise forward selection of variables was run, with the aim of maximizing the deviance reduction, followed by a stepwise backward elimination to prevent loss of statistical significance in some variables due to the later incorporation of new variables into the model (García-Charton and Pérez-Ruzafa, 1998). Before accepting a model, an analysis of residuals was performed to detect outliers with high influence on the models (García-Charton and Pérez-Ruzafa, 1998). The leverage and the Cook statistic of each sampling unit were measured, so that any unit with high values of these was removed and the model refitted to ensure consistency (McCullagh and Nelder, 1989).

2.3 Results

A total of 94 *D. labrax* were censused. Mean densities of *D. labrax* varied from no individuals in Guayonje and Abades to a figure of 0.43 ± 0.21 per 100 m^2 in San Andrés. The density of escapees was always higher at localities near fish farms, (Fig. 2.2). Localities nested within

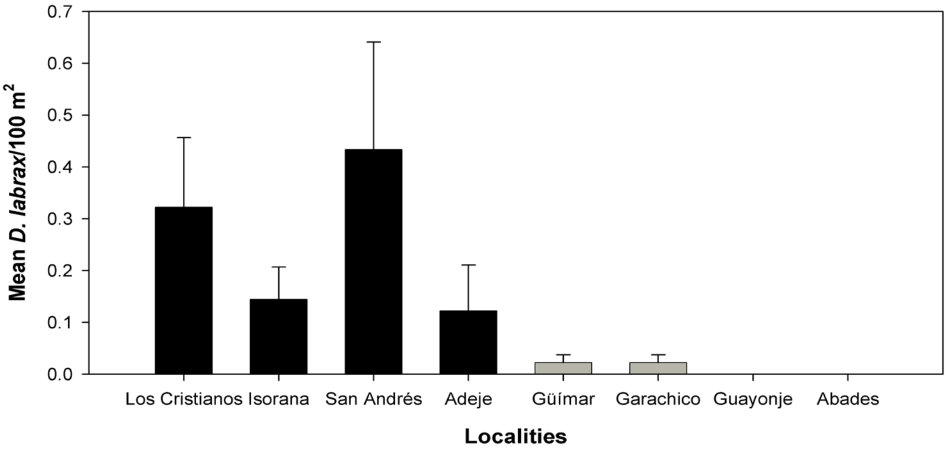

Figure 2.2. Mean densities (individuals/100 m^2) of escaped *Dicentrarchus labrax* in localities close to fish farms (black) and distant from fish farms (grey). Error bars represent standard error.

Table 2.1. Analysis of variance (ANOVA) of the abundance of escaped *Dicentrarchus labrax*. CD: Close/Distant; Lo: Locality; Si: Site.

Source	SS	DF	MS	F	P	F versus	P pooling
CD	2.1511	1	2.1511	10.76	0.0168	Lo(CD)	**0.0005**
Lo(CD)	1.2000	6	0.2000	2.36	0.0796	Si(Lo(CD))	
Si(Lo(CD))	1.3556	16	0.0847	0.48	0.9521	RES	
RES	21.1333	120	0.1761				
TOT	25.8400	143					

Distance showed differences and Sites within Localities showed no differences (Table 2.1), which means that the abundance varied mostly at a scale of 10's of km. Sizes of sea bass censused in the wild were between 15 and 55 cm TL. The most frequent size class was 26-30 cm TL (Fig. 2.3). The PERMANOVA test did not distinguish between the environmental variables that could explain differences in abundance between close and distant localities (Table 2.2).

Multiple regression (adjusted $R^2 = 0.293$) relates abundance positively to the quadratic term percentage of Small Boulders (%SB^2) and negatively to the logarithmic term of Distance log(distance) (Table 2.3). Figure 2.4 shows these relations in a 3D dispersion graphic to simplify visual interpretation.

Table 2.2. Results of PERMANOVA analysis of environmental variables (n.s.=not significant; *= p< 0.05; **=p<0.01; ***=p<0.001).

Source	df	SS	MS	F	P(perm)
CD	1	3963	3963	0.30	n.s.
Lo(CD)	6	78554	13092	1.84	*
Si(CDxLo)	16	113688	7105	2.80	***
Residual	120	304760	2539		
Total	143	500967			

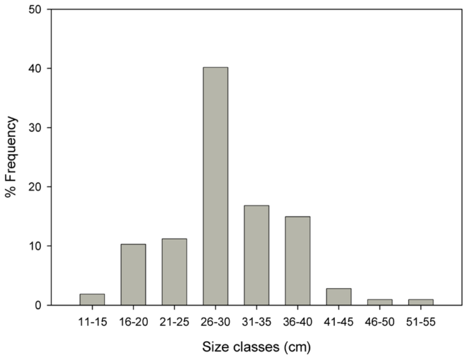

Figure 2.3. Size frequency of escaped *Dicentrarchus labrax* found in the wild.

Table 2.3. Multiple linear regression model explaining abundance of *Dicentrarchus labrax* in relation to environmental variables and distance from fish farms.

Variables	coefficient	SE	partial R^2	T
Constant	0.239	0.047		5,131
%SB^2	6.16x10^{-5}	0.000	0.424	5,970
log(distance)	-0.165	0.038	-0.308	-4,337

N = 143; adjusted R^2 = 0.293; F = 30,438; P < 0.001

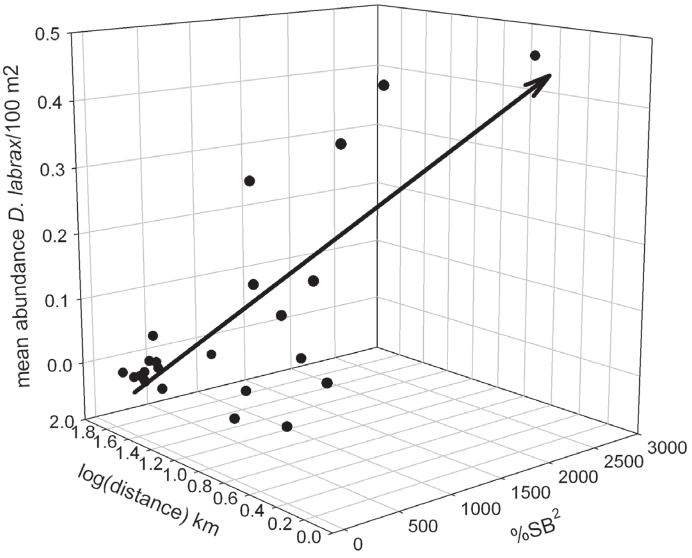

Figure 2.4. 3D dispersion graph showing relation between the dependent variable (mean abundance *D. labrax*) and independent variables introduced by the model: %SB^2 and log(distance).

An amount of 34 sea bass specimens were caught. Total lengths varied from 18.8 to 51 cm, with a mean value of 30.6 ± 8.5 cm. Diet indices are provided in Table 2.4. Mean Stomach Fullness was 1.13 and percentage of Vacuity was 50%. Alimentary coefficient (Q), frequency of occurrence and IRI identifies Osteichthyes as main preferred prey, Crustacea and seagrass *Cymodocea nodosa* as secondary common items and Insecta and Cephalopoda as accidental prey. The most important preys by number were insects of the order Hymenoptera, and those which contribute highly by weight to the sea bass diet were the Osteichthyes *Thalassoma pavo* and *Sparisoma cretense*. No food pellets were found in the stomach contents. Only one female of 51 cm TL had developed gonads (stage IV) at the time of capture. The remaining specimens could not be identified visually as males or females as they did not present developed gonads at all (stage I).

Table 2.4. Diet composition of escaped *Dicentrarchus labrax*. MSF mean stomach fullness, *N%* numeric percentage, *W%* weight percentage, *O%* frequency of occurrence, *Q* feeding coefficient, *IRI* index of relative importance.

Prey	***N%***	***W%***	***O%***	***Q***	***IRI***	**Prey Preferences**
Insecta						Accidental prey
Hymenoptera	14.9	0.06	23.5	0.89	351	
Coleoptera	3.7	0.02	5.9	0.07	21	
Unidentified	7.4	0.23	11.7	1.70	89	
Total	26	0.31	35.3	8.06	928	
Crustacea						Secondary Common prey
Plagusia depressa	3.7	0.2	5.9	0.74	23	
Pachygrapsus sp.	7.4	0.31	5.9	2.29	45	
Xantho sp.	3.7	0.31	5.9	1.15	23	
Unidentified	3.7	0.02	5.9	0.07	21	
Total	18.5	0.84	23.5	15.54	454	
Cephalopoda						Accidental prey
Unidentified	3.7	0.2	5.9	0.74	23	
Osteichthyes						Main Preferred prey
Atherina presbyter	3.7	0.02	5.9	0.07	21	
Sparisoma cretense	3.7	21.66	5.9	80.14	149	
Thalassoma pavo	11.1	35.17	11.7	390.39	541	
Scorpaena sp.	3.7	16.12	5.9	59.64	116	
Trachinus draco	3.7	19.2	5.9	71.04	135	
Unidentified	11.1	0.74	17.6	8.21	208	
Total	37	92.91	47	3437.67	6105	
Plants						Secondary Common prey
Cymodocea nodosa	7.4	3.85	11.7	28.49	131	
Human origin items	7.4	1.89	11.7	13.99	108	
MSF	1.13					
Vacuity	50 %					

2.4 Discussion

This study highlights that sea bass is commonly found in shallow coastal habitats, using natural trophic resources, but its abundance depends strongly on distance from fish farms. This spatial distribution could mean that escaped individuals show little mobility and site fidelity or mortality rates are high. In this second case, the population may strongly depend on escaped individuals. We also demonstrate that the escapees are able to exploit natural resources, feeding mainly on fish. In consequence, its diet overlaps with other top predators in the Canaries and once established in the western islands may become a new competitor for local species. While cultured sea bass is commercialized in a range of weights between 400 g (30 cm TL approx.) and 1,500 g (40 cm TL approx.), 26-30 cm was the most frequent size-class found in the wild. This size fits with those of the smallest marketed sizes and may indicate that a large number of escapes are occurring during harvesting. Despite this, mass escapes and/or high mortality of smaller sizes could mask and occasionally alter estimations of the most frequent escapee size.

The results confirm that the spatial distribution is closely related to fish farms. Escaped sea bass are more abundant at zones near fish farms. These results are similar to those found by Fiske *et al.* (2006) for escapees of *Salmo salar* on Norwegian coasts and Carr and Whoriskey (2006) for escaped juveniles from hatcheries of the same species in Canada. Abundance of sea bass was negatively related to the logarithm of distance. This means that the densities drop strongly as localities are further from fish cages, but our results predict that we could find escaped sea bass even at distant localities. This distribution could be due to two different processes: *D. labrax* shows a relative high degree of site fidelity and thus is more abundant near fish farms or, in contrast, present low site fidelity but high mortality rates; consequently, only few of them reach zones far away from fish farms. Recent studies on Atlantic cod (*Gadus morhua*) have demonstrated that farmed cod tends to disperse rapidly when it escapes (Uglem *et al.*, 2008). If sea bass showed similar behaviour, the hypothesis of high mortality rates would be a feasible explanation for its distribution pattern. Fishing pressure is probably a main cause of mortality among escaped sea bass; numerous spear-fishers and anglers fish in coastal zones near fish farms and frequent large captures have been confirmed (Toledo-Guedes *et al.*, in press b; Chapter 5). Despite this, sea bass can cover long distances, although this is likely to occur when there are massive escapes and thousands of individuals move together over a short period of time (González-Lorenzo *et al.*, 2005).

Habitat structure can also explain their spatial distribution on a local scale. The quadratic term of percentage of small boulders was positively related to its abundance. Successful feeding may be related to this fact. This kind of substratum in shallow waters (between 0 and 5 m depth) involves high mobility of these small boulders due to wave action. This causes turbidity and sea bass could take advantage of it to predate in this zone (Laffaille *et al.*, 2001) because in this less complex habitat potential prey are more exposed and vulnerable (ICES, 2006). There is evidence that sea bass also enters harbours, marinas and artificial beaches that are also characterized by turbidity due to sediment particles in suspension (pers. obs.) but additional studies are needed, to quantify the populations using these habitats.

Escaped sea bass is clearly able to exploit natural resources as we can see from stomach content data. Although this data is from a limited number of specimens, the results are in concordance with other studies on wild and escaped sea bass (Laffaille *et al.*, 2001, 2005; González-Lorenzo, 2005; Sá *et al.*, 2006: Leitão *et al.*, 2008). This confirms the hypothesis that the hunting behaviour of reared fish released into the wild is not degraded at present, as the majority of these fish belong to the first or second generation away from wild breeders (ICES, 2006). The high percentage of vacuity (50%), low mean stomach fullness (1.13) and the absence of food pellets in stomach contents could indicate that these individuals escaped some time ago, but need some time of adaptation to natural conditions. Moreover, the presence of *C. nodosa* in stomach content may be evidence of predation activity in zones where seagrass is present.

We can consider sea bass as an opportunistic high trophic level species with tendency to piscivory, so it could be competing with other piscivorous species such as juvenile serranids (*Mycteroperca fusca*, *Epinephelus marginatus* and *Serranus spp*.) and *Pomatomus saltatrix*, that frequent similar shallow habitats (Brito, 1991; Báez-Acosta *et al.*, 1998; Morato *et al.,* 2000; Brito *et al.*, 2002; Reñones *et al.*, 2002). Nonetheless, marine ecosystems are open, complex and influenced by multiple variables, make it difficult to correlate changes in ecosystems structure with the appearance of a particular species (Kalogirou *et al.*, 2007). However, the impact of escaped sea bass as a new piscivore in shallow waters of the central-western Canary Islands must be taken into account. Other studies point out the effects of non-indigenous piscivore species on natural freshwater assemblages, such as changes in prey and predation behaviour and local extinction of certain species (Townsend and Simon, 2006 and references therein). In addition, we found no male specimens with developed gonads and only one female of 51 cm TL had developed gonads at the time of capture. First maturity size in *D. labrax* is around 30-35 cm TL for males and 35-40 cm for females (Farrugio and Le Corre, 1986). So no evidence of reproduction of escaped *D. labrax* has been found. However, a larger sample of specimens is needed to ensure this, and the presence of an individual with well-developed gonads indicates that conditions for successful maturation exist. Thus, more data is necessary to know if they are able to establish self-reproductive populations. Both these aspects are very important to predict the potential risks. It has been suggested that the rate of escapes from the salmonid industry (0.1-0.3%) is similar to that from sea bass production (Fiske *et al.*, 2006; ICES, 2006). However, the rate of escapes in the Canary Islands should be higher as fish cages are situated in semi-exposed shores (affected by storms) while salmon farms are in more protected areas. Harvesting techniques are also different; crowding and net transfer to ice used in sea bass culture could be more subject to escapes that the pumping technique used in salmon farms. Estimations of population size, and in consequence future impact, become complex if we add reproduction as a factor maintaining or increasing numbers in the wild. Moreover, reproduction of an introduced species is a necessary step in any invasion process (Lockwood *et al.*, 2005).

Can we predict the degree of establishment of cultured *D. labrax* in the Canary Islands? A higher probability of this is often correlated with greater frequency of releases (propagule pressure) (Carlton, 1996; Grevstad, 1999; Fowler *et al.*, 2006). This, in part, is related to the concept of invasion windows (Johnstone, 1986), that is, in the broadest sense, any environmental change in the recipient region that alters its susceptibility to the establishment of a non-indigenous species. Thus, we can assume that a higher probability of good conditions for establishment will coincide with the release of individuals, taking into account these fish are escaping from sea cages possibly every day (pers. obs.). Data on propagule pressure (number of escapees per cage and year) are urgently required, to predict future impact of this species. From density data we can extrapolate that their present population in Tenerife is relatively small, so it is more vulnerable to stochastic or density dependent events (Lockwood *et al.*, 2005). Nonetheless, when a spatial element is added to this population model, two new scenarios appear: small populations can be maintained for a long time through immigration (Brown and Kodric-Brown, 1977), in this case new escapees, and there is a lower probability of population extinction if individuals are well spread out such that adverse conditions in one location will not also negatively affect individuals in another (Hanski, 1989). Large or continuous releases of individuals (both present in aquaculture activities) into one location should enable the incipient population to overcome problems associated with small population sizes (Lockwood *et al.*, 2005). On the other hand, fish farms are well distributed along Tenerife's coasts and, in consequence, so are these releases. All these processes could be beneficial for a successful establishment of sea bass here.

Risk assessments are useful tools to predict the consequences of introducing non-indigenous species. However, this kind of protocol is often based on hypotheses without experimental evidence. In this context, quantitative data on issues like behaviour, distribution, densities, trophic resources exploited and, in general, degree of establishment of introduced species are valuable. Some authors (Carlton, 1996; Casal, 2006) point out the lack of information and the need for experimental studies that will be essential to keep up with the present-day flow of establishments and invasions of introduced marine species, and their impact on marine ecosystems. The Canary aquaculture industry is at present expanding sea bass production, due to its economic success. Indeed, large numbers of new cages are to be installed across the Archipelago. The negative effects of escapes on natural populations have been demonstrated (Cadwallader, 1996 and references therein; *et al.*, 2005; Townsend and Simon, 2006), and this species seems to be well-established in this Island's shallow coastal habitats. Further research on its potential effects on coastal fish assemblages should be done, to aid in the development of preventive and mitigation measures in order to avoid future environmental damage.

CHAPTER 3

Phenotypic convergence in sea bass (*Dicentrarchus labrax*) escaping from fish farms: the onset of feralization?

Toledo-Guedes K, Brito A and García de Leaniz C (in press) Phenotypic convergence in sea bass (*Dicentrarchus labrax*) escaping from fish farms: the onset of feralization? *Aquaculture Environmental Interactions*.

SUMMARY

The impact of fish escaping from fish farms may depend on the extent to which escapees adapt to the natural environment, resemble wild conspecifics and become feral. Yet, little is known about the process of feralization in marine fish. We examined phenotypic changes in body shape, body condition and scale growth profiles of sea bass escaping from fish farms in the Canary Islands, and quantified the extent to which escapees had diverged from farmed conspecifics. Most feral sea bass had sizes that overlapped with those of farmed fish, indicating that they had escaped throughout the production cycle. However, 29% of escapees were larger than the maximum size at harvesting, indicating growth in the wild. Analysis of scale growth profiles showed that some escapees had grown in the wild as fast as did in cages, albeit at more variable growth rates. Feral sea bass tended to converge towards a similar body shape, having more streamlined bodies, lower body condition, and lower hepatosomatic indices than fish in cages. Although our study cannot discriminate between phenotypic plasticity and differential mortality of escapees, we interpret phenotypic convergence as the likely result of a period of initial starvation, phenotypic plasticity, and selection against maladapted phenotypes. Our results warn against the risks of rearing sea bass in open-net cages and suggest that sea bass escapees could pose a threat to shallow coastal assemblages, particularly in areas where the species is not naturally found.

RESUMEN

El impacto de los peces escapados podría depender de hasta qué punto éstos se adaptan al medio natural, asemejándose a sus congéneres salvajes y asilvestrándose. Sin embargo, poco se sabe del proceso de asilvestramiento en peces marinos. Se han examinado los cambios fenotípicos en la forma y condición corporales y los perfiles de crecimiento en escamas de lubinas escapadas en las Islas Canarias, cuantificando en qué grado los escapes han divergido de sus congéneres en cultivo. La mayor parte de las lubinas escapadas tenían tallas que se solapaban con las de los peces cultivados, mostrando que escapan a cualquier talla a lo largo del ciclo de producción. No obstante, el 29% de los escapes eran más grandes que la máxima talla de despesque, indicando que estos peces crecieron en el medio natural. Los análisis de los perfiles de crecimiento mostraron que algunos escapes habían crecido en el medio natural tan rápido como en las jaulas, aunque las tasas de crecimiento eran más variables. Las lubinas asilvestradas tendieron a converger hacia una misma forma corporal, con cuerpos más estilizados, e índices de condición y hepatosomáticos más bajos que los peces cultivados. A pesar de que nuestro estudio no puede discriminar entre plasticidad fenotípica y mortalidad diferencial, interpretamos la convergencia fenotípica como el resultado de un periodo inicial de inanición, plasticidad fenotípica y mortalidad de fenotipos mal adaptados. Los resultados advierten de los riesgos de tener lubinas en jaulas flotantes e indican que los escapes podrían suponer una amenaza a las comunidades de aguas costeras, particularmente en zonas donde esta especie no se encontraba de forma natural.

3.1 Introduction

Not all aquaculture escapees survive and reproduce in the wild, but some do, and minimizing their impact on wild fish has become an issue of global concern (Naylor *et al.,* 2005). Yet, what makes some aquaculture escapees survive and others die has been little studied, which is surprising since the impact of escapees will likely depend on the extent to which they can survive and adapt to natural conditions, i.e. become feral.

Predicting establishment success of fish escaping from fish farms is not without difficulties (Bekkevold *et al.,* 2006; DeVaney *et al.,* 2009; Consuegra *et al.,* 2011), but it has been suggested that phenotypic plasticity - i.e. the production of alternative phenotypes in response to environmental change (West-Eberhard, 1989), is a trait that may facilitate feralization (Valiente *et al.,* 2010) because plastic individuals should have more opportunities to adapt to changing conditions and survive (Smith, 2009). Plasticity in fish can be substantial (Smith and Skúlason, 1996; Garcia de Leaniz *et al.,* 2007), though the underlying mechanisms are not well understood. Most studies of plasticity in fish have addressed changes caused by artificial rearing during the process of domestication. Domestication tends to result in large phenotypic variation because, as Darwin (1875) first noted, artificial selection tends to produce extreme phenotypes that can persist under favourable (relaxed natural selection) conditions in captivity (Trut *et al.,* 2009). Indeed, one of the defining traits of domesticated organisms is that they tend to exhibit morphological and physiological variations never seen in the wild (Balon, 2004; Teletchea and Fontaine, 2012). For example, European sea bass (*Dicentrarchus labrax*) undergo significant changes during domestication, including changes in body shape (Corti *et al.,* 1996; Loy *et al.,* 2000; Costa *et al.,* 2010), swimming performance (Claireaux *et al.,* 2006; Koumoundouros *et al.,* 2009), muscle growth dynamics (Ayala *et al.,* 2003), salinity tolerance (Varsamos *et al.,* 2002) and sex ratio (Navarro-Martín *et al.,* 2009). In contrast, very little is known about how domesticated fish adapt to the wild and become feral.

Fish escaping from aquaculture facilities can be expected to undergo changes in phenotypic traits during feralization (the process of domestication in reverse; Price, 1999; Zeder, 2012) and these can provide cues about the differential response of fish to artificial and natural selection. Such information will be useful for mitigating the impacts of aquaculture escapes because improvements in the adaptation of fish to captivity (domestication) should also translate into loss of fitness in the wild. In general, domestication is expected to increase phenotypic diversity by allowing the survival of extreme phenotypes that would not normally survive in the wild, while feralization is expected to result in phenotypic convergence by selecting some optima on behaviours and body plan (Trut *et al.,* 2009; Zeder, 2012).

Few studies have addressed feralization in fish, and those which done so have tended to concentrate on salmonids (Valiente *et al.,* 2010; Consuegra *et al.,* 2011) or have simply compared wild with cultured fish (reviewed in Lorenzen *et al.,* 2012). Although wild vs. hatchery fish comparisons are useful because they allow the detection of escapees (e.g. Schröder and Garcia de Leaniz 2011; Arechavala-Lopez *et al.,* 2012ab), they do not shed much light on feralization *per se* because they are comparing what are essentially different fish. A better approach would be to compare farmed fish *before* and *after* they escape. We capitalized on the accidental escape of sea bass in the coastal waters off the islands of Tenerife and La Palma (Canary Islands, Spain), where the species is not naturally found (Brito *et al.,* 2002), but where sea bass escape regularly (González-Lorenzo *et al.,* 2005; Toledo-Guedes et al., 2009). Some of these escapees are able to survive and feed on local trophic resources and this has resulted in a population of feral *D. labrax* in coastal waters off the islands of La Palma and Tenerife that is maintained through the regular influx of new escapees (Toledo-Guedes *et al.,* 2009, 2012). Here, recent and old escapees cohabit in the wild and this allowed us to make comparisons among individuals from a common farm origin that had spent different times at liberty. Thus, we examined the process of feralization by quantifying the phenotypic changes that are displayed by sea bass when they escape into the wild.

3.2 Material and Methods

3.2.1 Study site and sampling method

The study was carried out in the Canary Islands (Fig. 3.1), the region with the largest production of sea bass in Spain (3,800 tonnes in 2010; APROMAR, 2011). Fish were sampled in two of the islands where sea bass regularly escape from open-net fish cages: Tenerife and La Palma (Toledo-Guedes *et al.,* 2009). We spear-caught or hand-netted 73 feral sea bass in the vicinity of two fish farms during 2009 (11 in La Palma and 66 in Tenerife). For

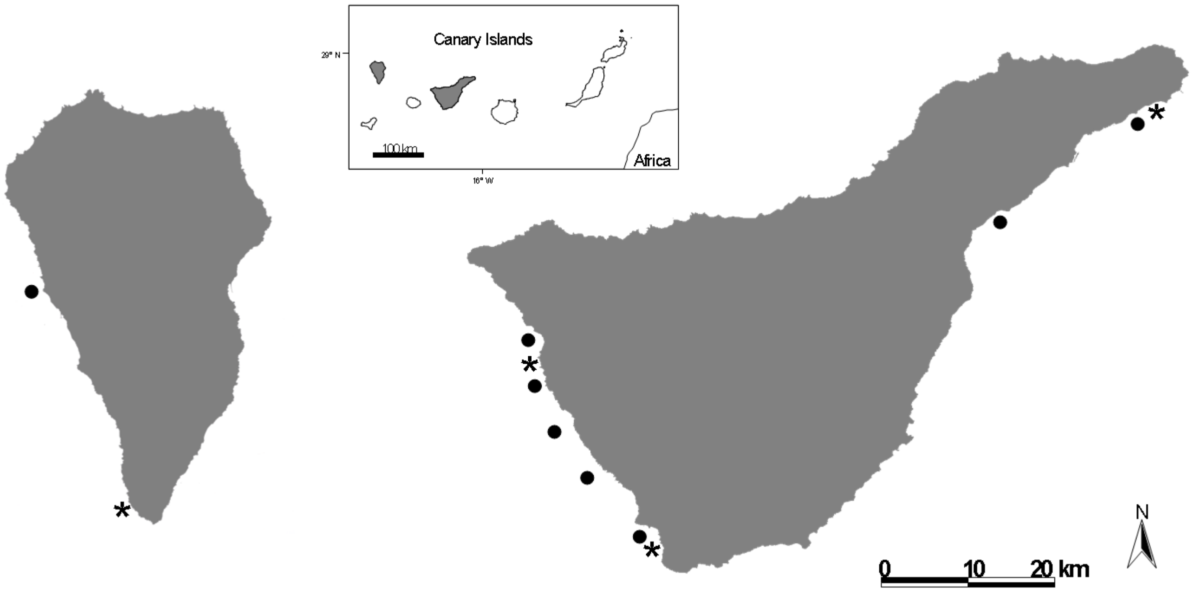

Figure 3.1. Location of sea bass farms (●) and sampling sites (*) in the coastal waters of the islands of La Palma and Tenerife (Canary Islands, Spain).

comparisons, 20 cultured sea bass were also sampled at the same time (10 in each island). Farmed fish are selected for fast growth and generally fed in excess in captivity. We therefore examined three phenotypic traits directly affected by growth and which are likely to change during the transition from captive to natural environments: growth rate – based in the analysis of growth rings (circuli) found on fish scales, body condition – inferred from the hepatosomatic index and the condition factor, and body shape – derived from measurements of multiple morphological traits obtained through digital photography.

3.2.2 Scale growth analysis

We examined the pattern of ring deposition (circuli) in the scales of cultured fish (n: 20) and escapees (n: 52) to derive comparative measures of growth. For each individual, five to ten scales were collected from a standardised region below the dorsal fin and above the lateral line. Three of the best scales, having clear, non-regenerated nuclei, were chosen for analysis. To avoid artefacts caused by excessive early scale erosion, we excluded scales with distances from the focus to the first circulus larger than 500 μm. Impressions were made on cellulose acetate slides using a pressure roller and then scanned with a Minolta MS 6000 microfiche reader at 23-50 magnifications and saved as a high resolution TIFF files, as in Kuparinen *et al.,* (2009). Starting from the scale focus, the position of each growth circuli was digitized using ImageJ (Abràmoff *et al.,* 2004) in order to estimate inter-circuli spacing and scale growth increments (Marco-Rius *et al.,* 2013). As scales in sea bass are ctenoid and do not have a single longest axis, we used scale dimensions, rather than estimates of back-calculated body size, to compare growth among individuals. Using scale dimensions for comparing growth assumes that body size is proportional to scale size (Francis 1990), but avoids introducing additional errors resulting from measurements of body size taken in the field (Marco-Rius *et al.,* 2012, 2013).

The Pearson correlation coefficient was used to estimate the strength of association between scale radius and body size, and a paired t-test was used to compare the original scales and their acetate impressions in order to quantify potential bias resulting from pressure from the hand roller. To ascertain precision in scale analysis, we measured the scale radii of 29 individuals twice in a double blind fashion and calculated the intra-class correlation coefficient (a-Cronbach) as a measure of repeatability (Kuparinen *et al.,* 2009).

Previous studies on other species have shown that farmed and feral fish may differ on the spacing between growth rings, as well as on the size of the scale nucleus (focus), and the variation in inter-circuli spacing within individuals (Stokesbury *et al.,* 2001). We therefore examined the following scale metrics in sea bass: radius from the scale focus to the first readable circulus (R), as well as the means (M) and standard deviations (SD) of the distance between consecutive growth circuli (inter-circuli spacing) for the whole scale (M_{tot}), the first twenty circuli (M_{20ini}), and the last twenty circuli (M_{20last}). Growth profiles were obtained by plotting circuli number against cumulative scale size and ordinary least regression was then used to determine growth slopes (B) for each specimen (Schröder and Garcia de Leaniz, 2011; Marco-Rius *et al.,* 2012).

3.2.3 Body condition indices

We examined two integrative indicators of body condition that may be expected to change when farmed fish escape into the wild (Mayer *et al.,* 1992): the hepatosomatic index [HSI = liver weight / total weight] and Fulton´s condition factor [K = 100 x total weight / (total length)^3].

3.2.4 Variation in body morphology

To examine the extent of body shape divergence associated with feralization in sea bass we took standardized photographs of 39 escapees and 20 cultured fish from each island with a Nikon Coolpix 5400 digital camera. The positions (x,y co-ordinates) of 25 landmarks were digitized using ImageJ and fifteen distances between selected landmarks were then calculated (Fig. 3.2) using the programme PAST v. 2.16. (Hammer *et al.,* 2001).

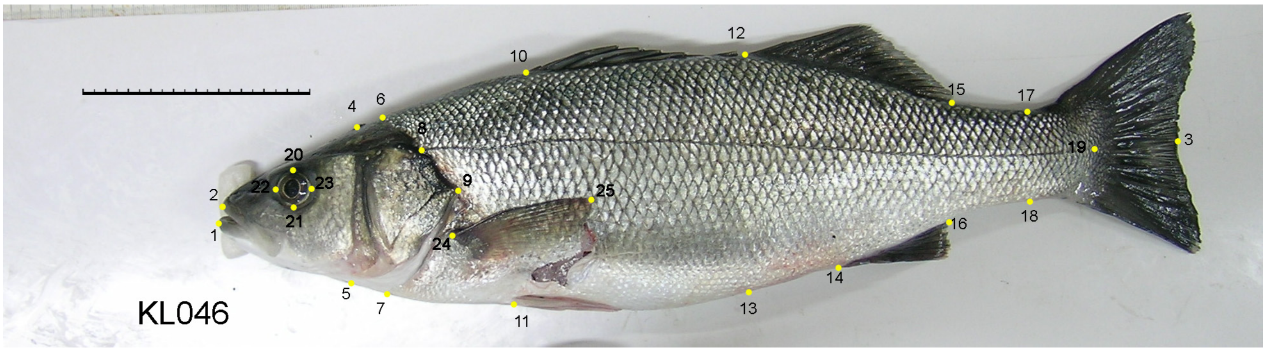

Figure 3.2. Landmarks used in the morphometric analysis of sea bass: Fork Length (1-3), Standard Length (1-19), Head Length (1-9), Lateral Line Length (8-19), First Head Depth (4-5), Second Head Depth (6-7), First Body Depth (10-11), Second Body Depth (12-13), Third Body Depth (15-16), Peduncle Depth (17-18), Second Dorsal Length (12-15), Anal Fin Length (14-16), Orbital Depth (20-21), Orbital Length (22-23), Pectoral Length (24-25).

3.2.5 Statistical analysis

Prior to analysis, all morphometric measurements were size-adjusted using the ‘allometric vs. standard’ method proposed by Elliott *et al.,* (1995) and implemented in PAST 2.15 (Hammer *et al.,* 2001). We employed a permutational multivariate analysis of variance (PERMANOVA, McArdle and Anderson, 2001) with fish origin (escape vs. farmed) as a fixed factor and location (Tenerife vs. La Palma) as a random factor nested within origin to examine variation in scale growth profiles and body shape between cultured fish and escapees based on Euclidean distances and 10,000 permutations. Pairwise differences in traits between groups were tested for significance by Bonferroni-corrected probabilities. Although morphometric traits were size-adjusted, body size can still account for a significant amount of morphometric variation (Loy *et al.,* 2000), and large fish are also more likely to show some scale regeneration than smaller ones (Fritsch, 2005). Hence, we included fork length (FL) as a covariate in our analysis to account for differences in body size between farmed fish and escapees. Principal component analyses (PCA) with varimax rotation were performed on morphometric and scale traits and all PCAs with eigenvalues >1.00 were considered to be influential (Chatfield and Collins, 1983). A discriminant function analysis (DFA) was undertaken using the 'leave-one-out classification' to assess the success of size-adjusted morphometric measurements and scale growth profiles in discriminating between cultured fish and escapees from the two islands. Differences in body condition and hepatosomatic index between feral and farmed fish were tested by paired *t*-tests at both islands. We used PRIMER 6+ , PAST 2.15 and SPSS 17.0 for statistical analyses.

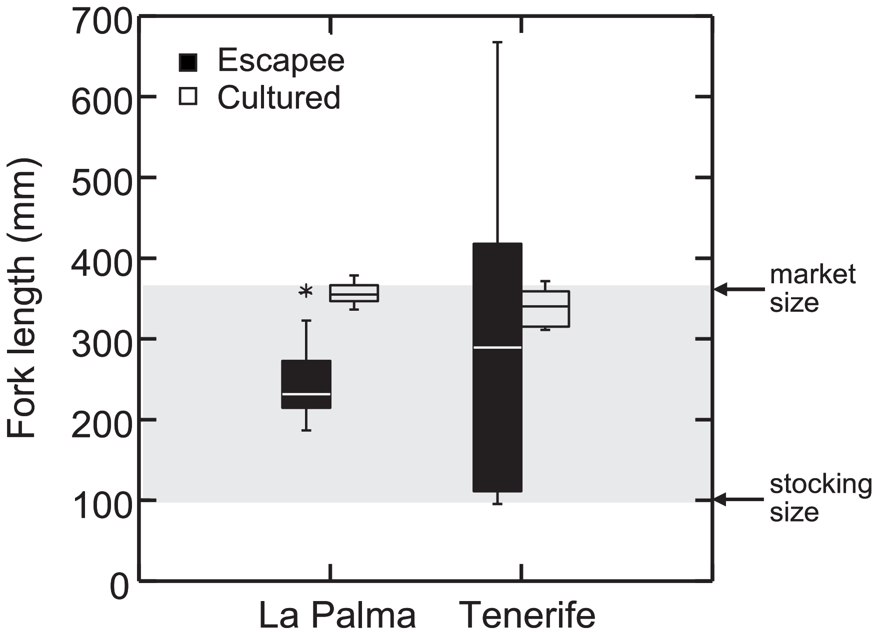

Figure 3.3. Size distribution of cultured and feral sea bass in each island. Grey area shows the typical size interval of sea bass during culture in sea cages, determined by the typical size at stocking (c. 100 mm) and the market size (c. 400 mm).

3.3 Results

3.3.1 Size distribution of escapees

Escapees had body sizes that covered the full size range found in culture (Fig. 3.3), ranging from the size at which fish were typically stocked in sea cages (c. 100 mm) to the size at which they were normally harvested (c. 400 mm). This suggests that escape events can occur at any time during the production cycle. We also found 21 escapees (representing 29% of escaped fish, and all restricted to Tenerife) that had body sizes outside the upper 95% confidence interval of fish found at cages (i.e. > 410 mm), and which are indicative of somatic growth in the wild. In one extreme case, an escapee had a size of 667 mm and an estimated age of 7.5 years, and given that farmed sea bass are typically marketed after 15 months, this would indicate that this fish had been growing in the wild for at least 6.3 years.

3.3.2 Scale growth profiles of farmed fish and escapees

There was a small but significant shrinkage of scale radius due to the acetate impression (matched $t_{28} = -2.46$, $P = 0.021$) but this amounted to only 1.24% of the scale size and was unlikely to bias the results, as impressions were made of all scales. More importantly, repeatability in measuring scale radius was very high (a-Cronbach = 1.00), and fork length was strongly correlated to both scale radius ($r = 0.90$, $P < 0.001$) and number of growth circuli ($r = 0.98$, $P < 0.001$) suggesting that scale measurements can be used to reconstruct changes in body size in sea bass.

Matched comparisons of scale growth increments between circuli numbers 20-40 (corresponding to a body size of < 90 mm, before fish were stocked in the cages) and circuli numbers 100-120 (corresponding to a body size of 171-199 mm, after c. 1 year of growth) revealed very different patterns of growth between farmed fish and escapees (Fig. 3.4). Thus, farmed fish (mean scale increment = 0.05 mm, SD = 0.03) grew on average more than twice as fast than escapees (mean scale increment = 0.02 mm, SD = 0.04) during this period ($t_{66} = -2.46$, $P = 0.016$), though some escapees showed evidence of compensatory growth (as revealed by the frequency of fish moving up the size rank, Marco-Rius *et al.,* 2012) and ended up growing as fast as farmed fish did.

Principal component analysis showed that three components explained 74% of the total variability in scale growth patterns and served to discriminate between farmed fish and escapees (Table 3.1). Results of univariate PERMANOVA indicated that four variables were significantly higher in escapees than in farmed fish at a = 0.05: the mean inter-circuli spacing for the first twenty ciculi of the scale (M_{20ini}), the radius from the scale focus (nucleus) to the

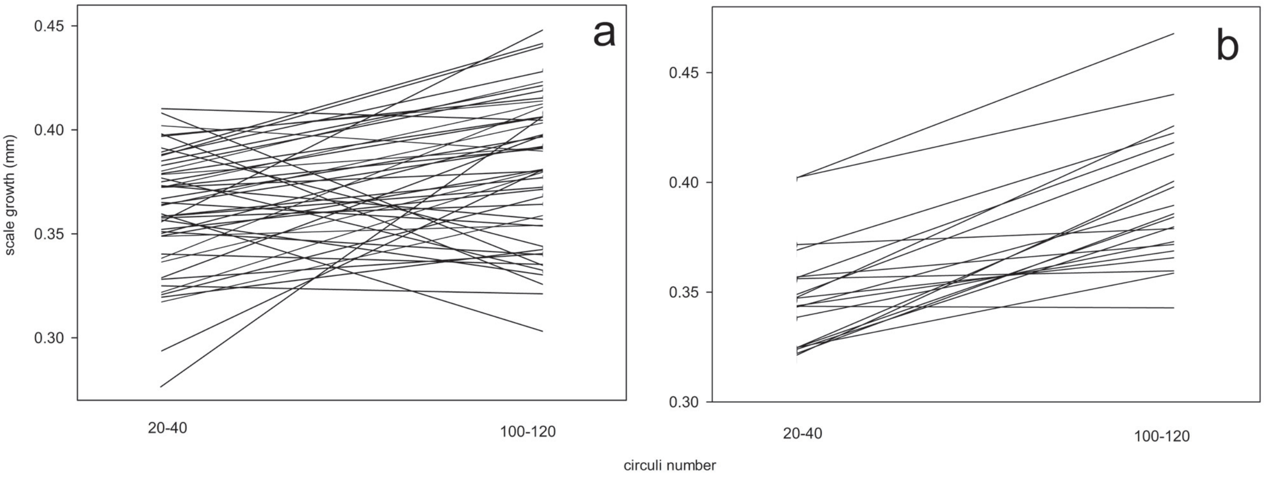

Figure 3.4. Matched individual comparisons of scale growth increments attained by feral (a) and cultured (b) sea bass before they were stocked into the cages (< 100 mm fork length , circuli number 20-40) and c. one year later (171-199 mm fork length, circuli number 100-120).

Table 3.1. Principal component analysis of scale growth profiles and their mean values (x10^2) for cultured and feral (escapee) sea bass. Morphometric traits showing significant ($P < 0.05$) differences between farmed and feral fish according to PERMANOVA are shown in bold.

	PC1	PC2	PC3	Cultured	Feral
B	.89			1.89 ± 0.14	1.91 ± 0.14
M_{tot}	.88			1.86 ± 0.13	1.90 ± 0.13
M_{20ini}	**.76**			1.65 ± 0.15	1.74 ± 0.14
SD_{20last}		.87		0.33 ± 0.09	0.39 ± 0.12
SD_{tot}		**.84**		0.30 ± 0.04	0.35 ± 0.06
M_{20last}		.75		1.85 ± 0.23	1.98 ± 0.27
R			**.79**	11.68 ± 6.91	17.42 ± 10.35
SD_{20ini}			**.54**	0.27 ± 0.05	0.33 ± 0.06
% V.	30.04	29.70	14.55		
Eigenvalue	2.40	2.38	1.16		

first readable circulus (R), and the variability in inter-circuli spacing for the first twenty ciculi (SD_{20ini}) and the whole scale (SD_{tot}). Discriminant function analysis indicated that 60% of farmed fish in Tenerife and 70% of farmed fish in La Palma were correctly classified to their location of origin based on scale growth patterns. However, escapees were more similar in scale growth profiles than cultured fish and could not be assigned to location of capture with any confidence: only 59% of escapees from Tenerife and 36% of escapees from la Palma were assigned to the correct island, suggesting that there was phenotypic convergence in the wild .

3.3.3 Condition factor and hepatosomatic index

Sea bass had significantly lower hepatosomatic indices (HSI) in the wild than in the cages at both locations (Tenerife $t_{34.030} = -4.80$, $P < 0.001$; La Palma $t_{19} = -6.76$, $P < 0.001$). Body condition factor was also significantly lower amongst escapees than among farmed fish in one of the islands (Tenerife $t_{37.718} = -9.28$, $P < 0.001$) but not in the other (La Palma $t_{19} = 0.40$, $P = 0.692$).

3.3.4 Morphometric analysis

Farmed and feral sea bass were significantly different in morphological traits (MANOVA Wilks´ l = 0.05, $F_{45,122.6} = 4.64$, $P < 0.001$). Discriminant plots reveal a greater separation in body shape between cultured stocks than between escapees, which tended to converge on a similar morphotype at the two locations (Fig. 3.5). Such convergence in body shape of escapees is reflected in the different classification accuracies of the discriminant function. Thus, while farmed fish were correctly assigned to their island of origin in 100% (Tenerife) and 80% of cases (La Palma), correct classification of escapees decreases to 68% (Tenerife) and 55% (La Palma). Overall, the accuracy of the morphometric analysis in discriminating between farmed fish and escapees was 81.4% with the leave-one-out procedure.

Pairwise PERMANOVA comparisons revealed significant differences in morphometric traits between the groups recognized in the discriminant plots (Table 3.2). Thus, while there were highly significant differences in the body shape of cultured fish between farms ($P < 0.001$), no differences were detected in the body shape of escapees between locations ($P > 0.05$). Additionally, there were significant differences between cultured fish and escapees in Tenerife ($P < 0.01$) and nearly so in La Palma after applying a conservative Bonferroni-correction ($P = 0.079$). A combination of four principal components explained 79.5% of the total variation of size-adjusted morphological variables. The first extracted component accounted for variables related to body depth and head length and showed that escapees were generally more streamlined (lower body depth) and had longer heads than farmed fish (Table 3.3). The second principal component was formed mainly by variables related to body size and orbital depth, which were both higher among escapees than among farmed fish.

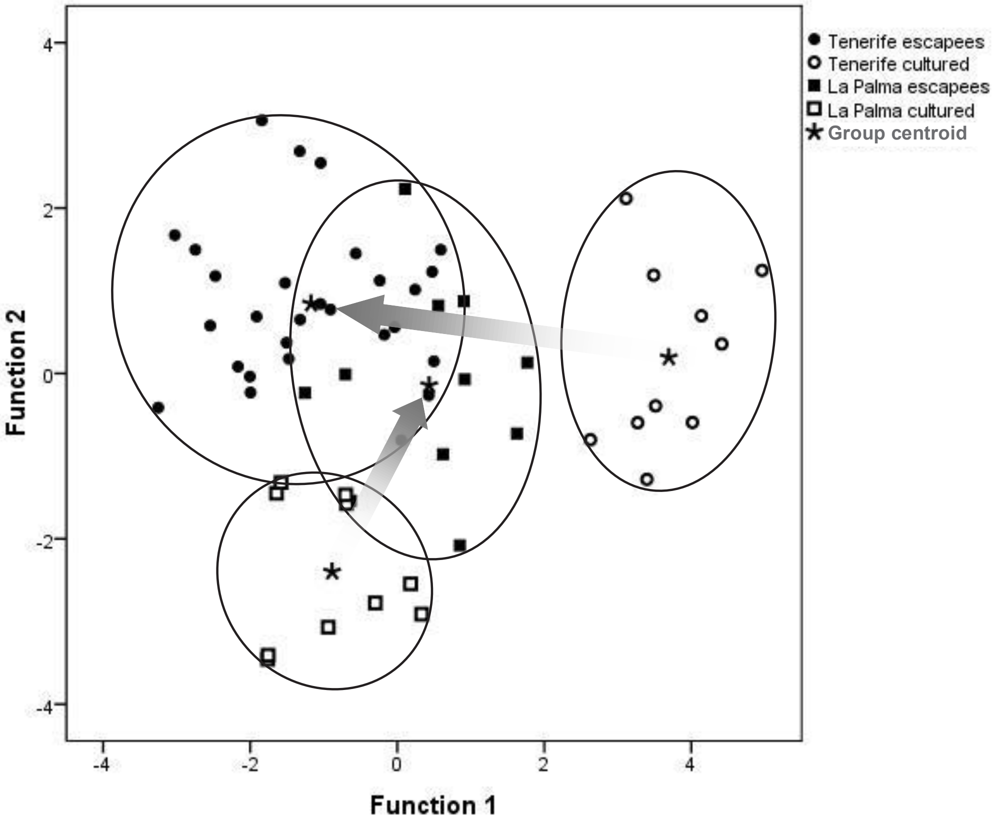

Figure 3.5. Discriminant plots based on size-adjusted morphometric measurements of cultured and feral sea bass (escapees). Group centroids are indicated by asterisks and inferred phenotypic shifts during feralization are indicated by arrows extending from farms to feral centroids in each island.

Table 3.2. Matrix of pairwise PERMANOVA comparisons of body shape between cultured and feral sea bass at the two study locations (Tenerife – TF; La Palma – LP). Shown are Bonferroni-corrected pairwise probabilities (significant values in bold) derived from 10,000 permutations ($F = 4.11$, $P < 0.001$).

Group	Feral – TF	Feral– LP	Cultured – LP
Feral – LP	1.000	-	-
Cultured– LP	**0.019**	0.079	-
Cultured– TF	**0.002**	**0.001**	**0.001**

The third component accounted for variation in head depths, and showed that farmed fish have deeper heads than escapees. Finally, the fourth component captured variability in the length of the anal and dorsal fins, which were larger in farmed fish.

Table 3.3. Principal component analysis for size-adjusted morphometric traits and their mean values (x10^3), for cultured and feral (escapee) sea bass. Numbers in bold indicate significant ($P < 0.05$) morphometric differences according to PERMANOVA.

Morphometric trait	PC1	PC2	PC3	PC4	Cultured	Feral
2nd Body Depth	**.92**				4.98 ± 0.06	4.91 ± 0.08
1st Body Depth	.80				4.98 ± 0.05	4.97 ± 0.06
Peduncle Depth	**.77**				3.93 ± 0.04	3.92 ± 0.08
3rd Body Depth	**.72**				4.21 ± 0.07	4.16 ± 0.12
Head Length	**-.77**				5.05 ± 0.06	5.13 ± 0.08
Orbital Length	-.60				2.95 ± 0.11	2.98 ± 0.10
Standard Length		**.84**			6.49 ± 0.03	6.51 ± 0.12
Lateral Line Length		.84			6.18 ± 0.04	6.18 ± 0.09
Fork Length		**.82**			6.62 ± 0.03	6.63 ± 0.14
Orbital Depth		**-.78**			2.88 ± 0.12	2.97 ± 0.12
Pectoral Length		-.61			4.46 ± 0.06	4.50 ± 0.08
1st Head Depth			.91		4.60 ± 0.07	4.62 ± 0.05
2nd Head Depth			**.82**		4.71 ± 0.04	4.69 ± 0.05
Anal Fin Length				**-.86**	4.52 ± 0.05	4.45 ± 0.11
2nd Dorsal Length				**-.70**	4.86 ± 0.08	4.80 ± 0.08
% Variance	27.86	25.51	14.27	11.90		
Eigenvalue	4.18	3.83	2.14	1.78		

3.4 Discussion

Our study reveals that sea bass escaping from fish farms undergo significant phenotypic changes in the wild and tend to converge towards a more similar phenotype compared to farmed conspecifics. We found clear differences in body shape between cultured and escaped sea bass, with escapees having smaller body depths, and more streamlined bodies compared to the fatter, more rounded body shape of farmed fish. Significant differences were also found on the relative sizes of the anal and dorsal fins, which were smaller and less variable in feral fish. Similar changes has been reported for a range of other species and serve to highlight the nature of feralization in fish, which is thought to be guided by a shift in food regime, non-random survival of maladapted phenotypes, and morphological changes (Lorenzen *et al.*, 2012).

The fact that the body shape of feral sea bass differed greatly from that of farmed fish may be indicative of high plasticity, as body shape is very dependent on local rearing conditions on this species. For example, sea bass can show marked differences in body shape among sea cages, even when fish originate from the same breeders (Costa *et al.,* 2010), apparently due to variation in temperature and rearing densities which affect body shape indirectly through their effects on growth and swimming activity. Studies on other species have also documented the strong effects that food regime and swimming activity can have on body shape (Pakkasmaa and Piironen, 2001; Marcil *et al.,* 2006).

Morphometric traits in fish are greatly affected by rearing conditions, environmental complexity and food source (Wimberger, 1992; Loy *et al.,* 2000; Hegrenes, 2001; Costa *et al.,* 2010) and these can differ markedly between fish cages and the natural environment. An unpredictable food supply, presence of predators, and a reduction in densities of conspecifics are amongst the main changes faced by farmed fish when they escape into the wild. In this sense, the more streamlined body shape of feral fish should reduce swimming costs and improve swimming performance in the wild (Enders *et al.,* 2004), while the larger anal and dorsal fins of cultured fish may have resulted from departures from isometric growth under crowded conditions in captivity.

We found a significant decrease in the hepatosomatic index – and in many cases also in the condition factor, of escapees, which may reflect a response to food deprivation and trophic adjustment following the escape. A period of slow growth in the first part of the scale followed by a period of faster growth is also evident in the scales of some escapees, which may be indicative of compensatory growth (i.e. fast growth following a period of growth depression) typically caused by food deprivation (Ali *et al.,* 2003; Marco-Rius *et al.,* 2012). Compensatory growth has been reported in sea bass before (Sahin *et al.*, 2000; Dosdat *et al.,* 2003; Rubio *et al.,* 2010; Chatzifotis *et al.,* 2011), although the underlying mechanisms remain poorly understood. It is likely that in this case compensatory growth may have been the result of trophic adjustment following escape into the wild, as suggested also by changes in condition indices.

Trophic adjustment appears in any case to have been short-lived, at least for those escapees that survived in the wild, because feral sea bass showed similar values of total inter-circuli spacing and scale growth slopes than farmed fish. Under the assumption that scale size is positively related to somatic growth – an assumption generally upheld in a number of fishes (e.g. Cheung *et al.,* 2007; Marco-Rius *et al.,* 2012) and which appears to be the case also in our study, this would suggest that escapees can grow in the natural environment as fast as farmed fish do in fish cages. Yet, growth of feral sea bass tended to be more variable than in sea cages (as evidenced by the larger standard deviation in inter-circuli spacing), which likely reflects the greater unpredictability of trophic resources in the wild, as well as a period of foraging adjustment to natural prey, which has a strong learning component (Brown and Laland, 2003; Olsen and Skilbrei, 2010).

Feralization in sea bass appears to involve a sudden and dramatic shift in food regime and a variable period of starvation, as reported also for sea bream (Arechavala-Lopez *et al.,* 2012c). Food deprivation would result in the mobilization of lipids and subsequent loss of weight, especially hepatic weight (Pérez-Jiménez *et al.,* 2007), as observed in our study. In this sense, the presence of recent escapees is suggested by the existence of several individuals with very high condition factors and high hepatosomatic indices, more similar to those found amongst cultured fish. Indeed, discriminant function analysis on body shape classified 15% of feral fish as farmed fish, suggesting that these may have been recent escapees.

We found that feral sea bass had body sizes that extended over the full size continuum, between the size at which they were stocked in the cages and the size at which they are typically harvested, indicating that sea bass in this region are escaping at all stages during the production cycle, as found for other fish farmed in open net cages (Dempster *et al.,* 2007; Consuegra *et al.,* 2011). A relatively large proportion of escapees (29%) had body sizes larger than the maximum size at harvesting, which supports the contention that these were fish had been at liberty for some time and grown in the wild, in some cases for several years. It is possible that such large escapees have had more time to adapt to natural conditions, and had therefore diverged more from the farm body template. This would explain why feral sea bass were morphologically more different from farmed fish in Tenerife (where all the large escapees were found) than in La Palma, where all the escapees were below harvest size and thus likely more recent escapees.

We did not conduct a mark and recapture study of individual fish, and cannot therefore discriminate between phenotypic plasticity and selection, although our results are consistent with both. Thus, the observed phenotypic convergence in the wild may be indicative of differential mortality of extreme phenotypes and stabilizing natural selection (Manly, 1985), while the changes observed in the body shape of escapees, most notably a more streamlined body and longer heads may be indicative of phenotypic plasticity (Rogdakis *et al.,* 2011). Intense selection in the wild would explain why we failed to find escapees with marked deformities in the wild (Toledo-Guedes *et al.,* 2009), features that are common among fish in cages, suggesting that deformed sea bass may have sustained elevated mortalities following their escape into shallow coastal waters. Thus, the combination of phenotypic plasticity, intense selection against maladapted phenotypes, and a period of initial starvation give a plausible explanation for the observed results. It must be noted, however, that phenotypic convergence does not necessarily imply adaptive change (Garcia de Leaniz *et al.,* 2007) and that variation among families in their propensity to the escape might have also affected our results.

Sea bass is a particularly plastic species (Corti *et al.,* 1996; Loy *et al.,* 2000; Costa *et al.,* 2010) with environmentally induced sex determination (Vandeputte *et al.,* 2012) and our results suggest that such plasticity may have aided in the feralization process by allowing escapees to adapt quickly to natural conditions. In areas where farmed and wild sea bass coexist (e.g. the Mediterranean), it would be interesting to determine how long it takes for escapees to resemble the wild counterparts (Arechavala-Lopez *et al.*, 2013c). This is something that was outside the scope of our study but that would help to gain valuable insights into the scope for introgression. Although it is not yet known if sea bass escapees have developed self-sustainable populations in the study area (Toledo-Guedes *et al.,* 2012), multiple escapes, high propagule pressure and high plasticity would make this species a likely invader of the coastal waters of the Canary Islands. Such concerns stress the need for monitoring plans of open-net cages in aquaculture, particularly when the species being farmed are not naturally found in the region.

CHAPTER 4

Escaped introduced sea bass (*Dicentrarchus labrax*), infected by *Sphaerospora testicularis* (Myxozoa), reach maturity in coastal habitats off Canary Islands

Toledo-Guedes, K., Sanchez-Jerez, P., Mora-Vidal, J., Girard, D. and Brito, A (2012). Escaped introduced sea bass (*Dicentrarchus labrax*) infected by *Sphaerospora testicularis* (Myxozoa) reach maturity in coastal habitats off Canary Islands. *Marine Ecology*, 33: 26-31.

SUMMARY

Aquaculture activities have introduced European sea bass (*Dicentrarchus labrax*) on the coasts of some of the Canary Islands. We present the first record of simultaneous male and female gonad maturation of escaped sea bass in the wild, indicating that this species is finding its Essential Fish Habitat (EFH). Individuals with ripe gonads were only caught during January and February 2009, although the maturation and spawning season may last from November to February in the studied area. Bass infected by *Sphaerospora testicularis* were found and the incidence of the parasite was checked. This represents the southernmost record of the parasite, probably introduced together with sea bass stock. These results are discussed from the point of view of risk assessment and the ecology of invasions being valuable for aquaculture management in Central North Atlantic and Mediterranean area.

RESUMEN

La actividad acuícola ha introducido la lubina (*Dicentrarchus labrax*) en las costas de algunas de las Islas Canarias. Se cita por primera vez la maduración gonadal simultánea de machos y hembras de lubinas escapadas en la naturaleza, indicando que están encontrando su Hábitat Esencial (HE). Los individuos con gónadas maduras fueron capturados únicamente durante enero y febrero de 2009, pero el período de maduración y puesta podría abarcar de noviembre a febrero en el área estudiada. Se encontraron lubinas infectadas por *Sphaerospora testicularis* y se estudió la incidencia del mismo. Este es el registro más meridional del parásito, posiblemente introducido junto al stock de lubina cultivada. Se discuten los resultados desde el punto de vista del análisis de riesgo y la ecología de las invasiones, siendo valiosos para la gestión de la acuicultura en el Atlántico Oriental y el Mediterráneo.

4.1 Introduction

To understand ecological processes such as the establishment of non-native species in new habitats it is crucial to find the minimum ecological requirements for them to complete their life-cycle (Elton, 1958; Carlton, 1996). In this context, 'Essential Fish Habitat' (EFH) is defined as "those waters and substrates necessary to fish for spawning, feeding or growth to maturity" (Benaka, 1999). 'Waters' are taken to include the associated physical, chemical, and biological properties used by fish, the 'substrates' (i.e. sediment), hard bottom and other structures underlying the waters, and also any associated biological communities (NOAA, 2004). EFHs can provide information in two different ways: (1) if we know the EFH for a given species we can predict the likelihood of the species to complete its life cycle in an area and, alternatively, (2) if the species is known to complete its life cycle, it can be stated that an EFH for the species exists in the area. The first is a complex matter since EFHs involve many biotic and non-biotic variables (Valavanis *et al.*, 2004). However the second is important when monitoring if a non-native fish is finding suitable conditions to establish self-reproducing populations, once introduced.

There are some studies pointing out the potential impacts of introduced marine fish: *Cephalopholis argus* and *Lutjanus kasmira* in Hawaii (Randall, 1987; Friedlander *et al.,* 2002; Dierking, 2007), *Fistularia comersoni* in Mediterranean (Kalogirou *et al.,* 2007) or the red lionfish (*Pterois volitans* and *Pterois miles*) in Western North Atlantic (Whitfield *et al.,* 2002; Schofield, 2009). Some of the studies on these and other introduced species show potential or demonstrated effects such as predation, competition and spread of pathogens (Ruiz-Carus *et al.,* 2006; Dierking, 2007; Albins and Hixon, 2008; Balart *et al.,* 2009). What the above introductions have in common is that the fish have established self-reproducing populations, through finding EFHs in which to complete their life-cycle.

Aquaculture has become the main vector of introduction of fish species into fresh-water ecosystems (Casal, 2006), while marine aquaculture has undergone rapid growth on coasts worldwide (FAO, 2009). The Canary Islands have followed the same trend during the last two decades, to become the leading Spanish region in European sea bass (*Dicentrarchus labrax*) aquaculture with an expected production of 4,330 tonnes in 2009 (APROMAR, 2009). Fish are maintained in sea cages until they reach harvesting weight/size (400-1500g/30-50cm approx.). However, they can escape massively due to sea storms or punctually through holes in the nets of the sea cages and during harvesting labours. Sea bass is considered a non-native species for the central and western islands of this Archipelago and escapees have been shown to exploit natural resources and survive in natural conditions, but there are scarce data on reproductive success (Brito *et al.,* 2002; Toledo-Guedes *et al.,* 2009).

One of the potential risks of introduced species is the spread of parasites and diseases along with them (Baltz, 1991; Ruiz-Carus, *et al.* 2006). There are some studies involving the parasite assemblages of marine-cultured fish and their possible transmission to wild fish (Mladineo, 2006; Mladineo *et al.,* 2009; Fernandez-Jover *et al.,* 2010). Nonetheless, these studies are centred on macro-parasites located in and affecting stomach and gills, but very little is known about gonad-specific parasites. This is the case of the Myxosporean parasite *Sphaerospora testicularis,* which is specific to testicular tissue and has been studied in cultured and wild sea bass (Sitjà-Bobadilla, 2009). The pathology of *S. testicularis* includes the destruction of both testicular germinal cells and Sertoli cells, potentially leading to parasitic castration (depending on exact location and intensity of infection), since these cells are crucial for spermatogenesis (Alvarez-Pellitero and Sitjà-Bobadilla, 1993; Nóbrega *et al.,* 2009; Sitjà-Bobadilla, 2009).

In this study we present two important findings: the first record of simultaneous male and female gonad maturation in escaped sea bass and the first and southernmost record of the Myxosporean parasite *Sphaerospora testicularis*. Data are given on gonadal histology and on maturation period in the Canaries. The results are discussed from the point of view of non-indigenous species ecology, and are relevant for risk-assessment studies in the North-East Atlantic and Mediterranean, where this species is cultured.

4.2 Material and Methods

4.2.1 Study Area

Tenerife is one of the central islands of the Canarian Archipelago, situated in the North sector of the Eastern Central Atlantic. The study was carried out at different localities around the Island in shallow waters between 0 and 5 m depth (Fig. 4.1).

4.2.2 Sampling method

Escaped sea bass were caught by spearfishing, from September 2008 to July 2009, no individuals were caught during November and December. Spawning was checked *in situ*, gently pressing the abdominal zone of the fish. In the laboratory, each fish was measured to the nearest mm (total length TL) and weighed (fish weight FW, ±0.01 g), gonads were removed and weighed (gonad weight GW, ±0.01 g). Sex and maturity was visually determined using a five-point scale (FAO, 1974). The gonadosomatic index (GW/FWx100) was calculated for each individual.

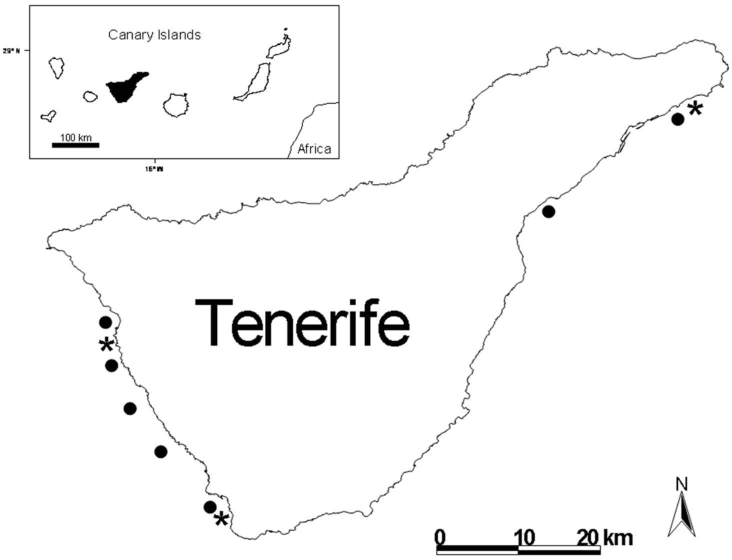

Figure 4.1. Study area. Asterisks indicate sites where escaped sea bass were captured by spearfishing. Black points are areas with aquaculture facilities.

4.2.3 Histological analysis

Histological analyses were performed on ripe gonads (stage III-IV). The posterior part of each gonad was fixed in 4% formalin, dehydrated and embedded in paraffin. Sliced 5 μm sections were stained with haematoxylin and erythrosine and checked for tissue abnormalities and presence of *S. testicularis*. Infection prevalence was calculated (number of individuals infected/ number of total individuals examined) and infection intensity rated on a semi-quantitative six points scale (Sitjà-Bobadilla and Álvarez-Pellitero, 1993).

4.3 Results

A total of 56 sea bass were caught during the study. TL varied between 110 and 658 mm, twelve individuals were found with developed gonads (10 males and 2 females) during January and February of 2009. Escapees with ripe gonads were found in stage III or IV of maturity; moreover, three of the males caught in January released sperm under slight pressure on the abdomen. Developed gonads were only found in males larger than 450 mm and females over 550 mm TL (Fig. 4.2).

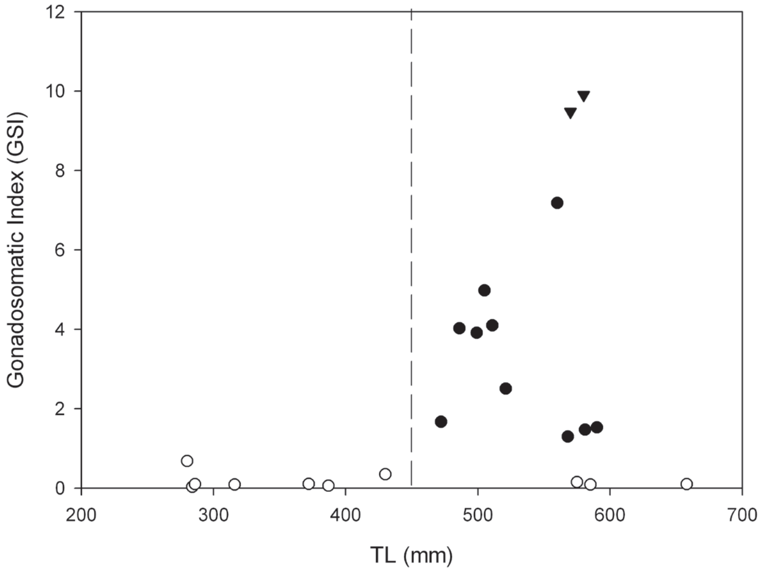

Figure 4.2. Scatter plot of gonadosomatic index (GSI) and total length (TL) of escaped sea bass captured during January and February. Dash line shows the TL beyond which ripe sea bass are found. White dots: immature sea bass; black dots: mature males; black triangles: mature females.

The gonadal histology of ripe individuals shows that both male and female gonads were morphologically functional at tissue level (Fig. 4.3 c and d), no alteration or abnormality of tissue structures were found. However, *S. testicularis* trophozoites and spores were found (Fig. 4.3 a and b) in two out of ten of the examined males, a 20% prevalence of infection. The mean intensity of infection was 4.5, which is considered as medium-high.

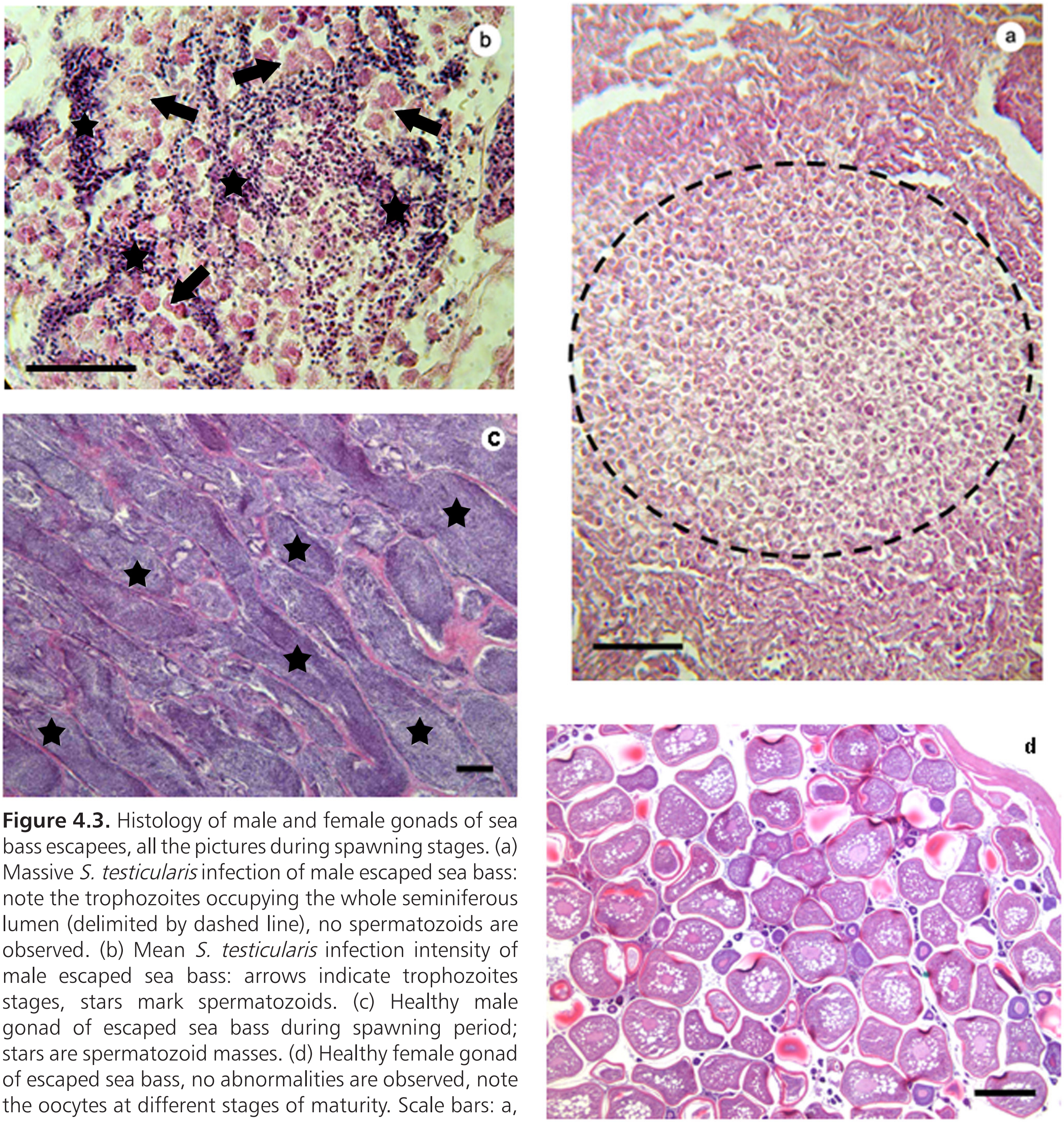

Figure 4.3. Histology of male and female gonads of sea bass escapees, all the pictures during spawning stages. (a) Massive *S. testicularis* infection of male escaped sea bass: note the trophozoites occupying the whole seminiferous lumen (delimited by dashed line), no spermatozoids are observed. (b) Mean *S. testicularis* infection intensity of male escaped sea bass: arrows indicate trophozoites stages, stars mark spermatozoids. (c) Healthy male gonad of escaped sea bass during spawning period; stars are spermatozoid masses. (d) Healthy female gonad of escaped sea bass, no abnormalities are observed, note the oocytes at different stages of maturity. Scale bars: a, b, c: 100 µm; d: 500 µm.

4.4 Discussion

Our study has shown male and female gonadal maturation of escaped *D. labrax* occurs in the wild. Therefore, this species appears to find its EFH in coastal habitats off the Canary Islands so as to complete its life-cycle, finding suitable conditions in terms of availability of trophic resources, temperature and photoperiod, to favour gonadal maturation. Moreover, histological analysis shows that their gonads are functional. However, further data are necessary to know the viability of sperm and ova, fertilization success, larval survivorship and if recruitment in the wild takes place. All these steps are required to maintain self-reproducing populations and have not been ascertained in the present study. The presence of *S. testicularis* alerts us of the possible spread and transmission of the parasite to native fish species, which would threaten normal spermatogenesis, and thus, reproduction of other species.

Non-biotic requirements, such as temperature, are of key importance for gonadal maturation and spawning onset of marine fish (Vinagre *et al.,* 2009). Various studies confirm that sea bass spawning season lasts from two to four months, during winter and spring. Depending on latitude, spawning can start in December e.g. in the Mediterranean (Barnabé, 1973) or not until April in Ireland (Kennedy and Fitzmaurice, 1972), revealing a gradient where it is delayed as one moves northward. Maturation of gonads and onset of spawning is strongly controlled by temperature (Vinagre *et al.,* 2009). However, in lower latitudes (e.g. the Canaries), temperature plays a secondary role, as water temperature is always above 10-12ºC, the minimum spawning trigger temperature found by other authors (Kennedy and Fitzmaurice, 1972; Pawson *et al.,* 2000), and photoperiod then becomes the powerful trigger. Although the first part of the supposed spawning period (November and December) was not sampled, it is feasible that the maturity/spawning period of sea bass in the Canary Islands spans four months; from November to February, in concordance with the supposed step forward of the spawning period (January-March) in southern Spain (Arias, 1980).

Only individuals above 450 mm TL were found with developed gonads. According to our results, size at maturity seems to be larger in escaped bass in the Canaries than for natural wild individuals in the Mediterranean (males 230 mm and females 340 mm) and North-Eastern Atlantic (males 320 mm, females 420 mm) (Pawson *et al.,* 2000 and references therein). Given the above data and maximum size at harvest (500 mm) the possibility of maturation and spawning before sea bass are harvested exists. Although sea bass could maturate before escaping, most of the mature sea bass captured for this study were well above 500 mm TL, thus growth and maturation have taken place into the wild. Nevertheless, intensive sampling throughout the year covering a wide range of sizes is required for accurate estimation of the size at maturation and spawning period of these escapees.

The combination of suitable biotic and non-biotic conditions, high frequency of escape events (Toledo-Guedes *et al.,* 2009), and low degree of conservation of fish assemblages in the coastal ecosystems (Tuya *et al.,* 2006; Clemente *et al.,* 2010) surrounding the Canary Islands could facilitate the establishment of self-reproducing sea bass populations around those islands where it has been introduced. Thus, it is important to monitor if sea bass are successful in completing its life-cycle in the wild (Elton, 1958; Carlton, 1996) and the possible invasion processes that could intensify the impact of this predator on wild fish. However, the present population in the central and westernmost islands still seems to depend on new escapees, and fishing mortality may be a major force in population control (Toledo-Guedes *et al.,* 2009).

The presence of *S. testicularis* has been recorded in reared and wild sea bass in the Mediterranean (Sitjà-Bobadilla and Álvarez-Pellitero, 1993) but never in escapees. Although we cannot be sure they were not infected after their escape, the most feasible explanation is that the parasite arrived with infected juveniles from mainland hatcheries. This is supported by our results showing a 20% prevalence of infection, in accordance with the 6-25% found in reared bass and in contrast to the 2.5% in wild populations in their natural distribution range (Sitjà-Bobadilla and Álvarez-Pellitero, 1993). Since the intensity of infection was medium-high and in some cases the seminiferous tubuli were completely occupied by different stages of the parasite, *S. testicularis* is probably being released to the environment during spawning. Despite its complete life-cycle remains unclear, direct fish to fish transmission is suggested as a viable transmission route, however this has not been demonstrated experimentally (Sitjà-Bobadilla, 2009). To our knowledge this is also the first time this parasite is recorded in the Canary Islands waters, and the most southern record. The risk of spread of Myxosporean parasites with the present flow of introductions for aquaculture or re-stocking of wild populations has been pointed out (Sitjà-Bobadilla, 2009), and in this case, its capacity to cause parasitic castration in native wild populations highlights the need to monitor its incidence in them.

Our findings have a wide range of implications for risk assessment and management plans of aquaculture activities. The evidence that escaped sea bass can reach maturity must be closely monitored and the authorities alerted about the establishment of self-reproducing populations, which could end in permanent deleterious effects on coastal fish assemblages. Moreover, our data are of special relevance to other regions like the Mediterranean, where sea bass is intensively cultured. The fact that escapees can reach maturity in the wild, together with their higher prevalence of *S. testicularis* parasitosis, could locally alter the reproduction dynamics of natural populations after massive escape events. This has been predicted for salmon in Norway (Hindar *et al.,* 2006) and is a feasible scenario in Mediterranean waters.

Risk assessment studies on the introduction of new aquaculture species and plans to monitor already introduced species should consider empirical data on the plasticity of fish species in finding their Essential Fish Habitat and completing their life-cycle in conditions unlike their natural distribution range. Furthermore, detailed studies should be carried out on the parasites and diseases that may be introduced along with aquaculture species, to prevent potential future damage.

CHAPTER 5

Follow-up of a massive aquaculture escape event and its influence on artisanal fisheries

Toledo-Guedes, K., Sanchez-Jerez, P. and Brito, A (in press). Follow-up of a massive aquaculture escape event and its influence on artisanal fisheries *Fisheries Management and Ecology*.

SUMMARY

In this chapter spatiotemporal patterns of distribution of escaped fish (sea bass and sea bream) and their influence on artisanal fisheries are explored before and after an escape event that released 1.5 million fish into the wild off La Palma (Canary Islands). Data were collected by *in situ* visual census and 'first-sales' data as a proxy of artisanal fisheries landings. Abundances of escaped fish in shallow coastal habitats were analysed by permutational ANOVA under multi-scale hierarchical models that included temporal and spatial factors. Consistent spatial patterns linked densities of these fish to distance from escape point, while temporal patterns were related to a higher biomass released during winter. A nearby marine protected area did not show different densities of escaped fish. Local artisanal fleet catches accurately reflected the massive escape event and offer the main contingency force to mitigate the potential negative effects of massive escape events over shallow coastal habitats

RESUMEN

En este capítulo se exploran los patrones de distribución espacio-temporales de los peces escapados (lubina y dorada) después de un escape que liberó 1,5 millones de peces al medio natural en La Palma (Islas Canarias). Los datos se tomaron a través de censos visuales *in situ* y de registros de 'primera venta' como proxy de las descargas de las pesquerías artesanales. Las abundancias de peces escapados en hábitats costeros se analizaron con ANOVA por permutaciones bajo modelos jerárquicos a múltiples escalas que incluyeron factores espaciales y temporales. Los patrones espaciales fueron consistentes y relacionaron las densidades de los escapes con la distancia desde el punto de escape, mientras que los patrones temporales estuvieron relacionados con una mayor tasa de escapes durante el invierno. La reserva marina cercana no mostró diferencias en las densidades de peces escapados. Las capturas de la flota artesanal de la zona reflejaron exactamente el escape masivo, suponiendo la principal fuerza de contingencia para mitigar los efectos negativos potenciales de los escapes en hábitats costeros.

5.1 Introduction

Fish release through escapes is one of the main problems that the aquaculture industry must face (Firestone and Barber, 2003; Naylor *et al.*, 2005; Jensen *et al.*, 2010). It leads to obvious economic loss and could be the source of new environmental stressors in areas already under human pressure, such as coastal waters. This problem can be intensified when the released fish are exotic or locally absent species (Naylor *et al.*, 2001; Liao *et al.*, 2010). Processes such as disease and parasite spread, competition, predation or inter-breeding have already been pointed out regarding escapees (Naylor *et al.*, 2001).

Farmed fish reach natural habitats from fish cages by recurrent-leak or sporadic-massive escape events; usually due to a combination of deficient harvesting operations, poor maintenance and bad weather conditions (Jensen *et al.*, 2010). Post-escape natural mortality is believed to be high (Arechavala-Lopez *et al.*, 2011), but an unknown proportion of fugitives are able to survive in the wild and disperse rapidly from aquaculture facilities (Uglem *et al.*, 2008; Arechavala-Lopez *et al.*, 2011, 2012c), becoming locally available for fisheries (Dimitriou *et al.*, 2007).

Previous studies have addressed the importance of farm-origin fish in both recreational and commercial fisheries of salmonids in the Pacific and the Atlantic (Soto *et al.*, 2001; Green *et al.*, 2012a) and sea bream in the Mediterranean (Arechavala-Lopez *et al.*, 2012c). However, these examples rely on the ability to distinguish between wild and farmed fish (apart from tagging experiments), as escapees share habitats with their wild counterparts. The latter adds some degree of uncertainty, as phenotypic plasticity could drive escaped fish to resemble their wild conspecifics (Arechavala-Lopez *et al.*, 2012ab, 2013c; Toledo-Guedes *et al.*, in press a). The situation is different (and fugitives are clearly identified) when the cultured species are known to be introduced or locally absent and there are no self-sustaining populations in the wild. This is the case for sea bass (*Dicentrarchus labrax*) and sea bream (*Sparus aurata*) around some of the western Canary Islands (Toledo-Guedes *et al.*, 2009).

A massive escape occurred off the island of La Palma between December 2009 and January 2010. In that period, 400 tonnes, equivalent to 1.5 million fish, were released (90% sea bass and 10% sea bream approx.; Ramírez *et al.*, 2011), due to repeated sea storms that generated waves up to 6 m high. This was, as far as we know, the largest accidental sea bass release ever recorded to date. Thus the objectives of our study were to investigate (1) spatiotemporal patterns of escapee abundance in the wild, (2) the influence of a nearby marine protected area (MPA) on escaped fish abundance, and (3) the influence of escaped fish on local artisanal fisheries. For this, we used *in situ* visual census and data from artisanal fisheries sales before and after the massive escape. The suitability of these data to detect and assess escape events is discussed, and management recommendations are provided to prevent potential damage caused by escaped fish.

5.2 Material and Methods

Our study was carried out on La Palma, one of the westernmost islands of the Canary Archipelago, situated in the northeastern part of the Central Atlantic. Aquaculture facilities are at a single location on the western coast of the Island. A marine protected area (MPA) is situated approximately 15 km to the south of the fish farms. Two professional fishermen's associations carry out their activity not far from their respective home-ports on opposite sides of the Island (Fig. 5.1).

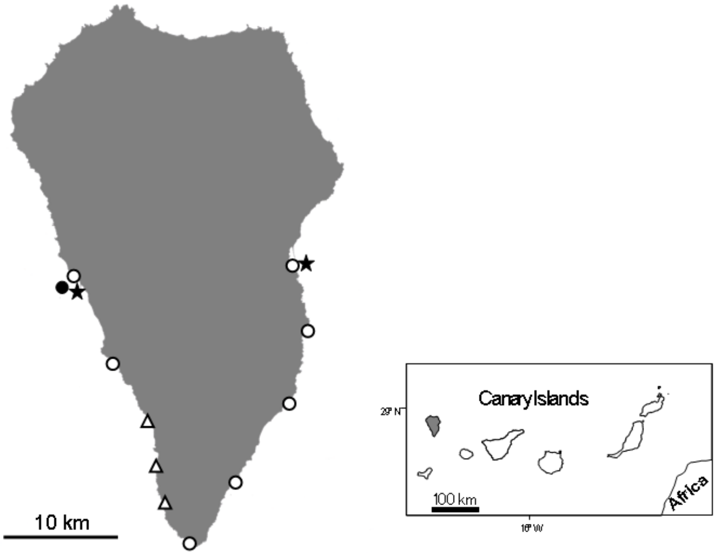

Figure 5.1. Study area. Black circle: aquaculture facilities / release point. Stars: professional fishing guilds. White circles: localities sampled outside La Palma MPA. White triangles: localities sampled in outer reserve. White square: locality sampled in no-take zone.

The first step was to evaluate the presence of escaped sea bass in coastal habitats through visual census. Owing to the high mobility and shallow habitat of escaped fish reported by various studies (González-Lorenzo *et al.*, 2005; Toledo-Guedes *et al.*, 2009; Arechavala-Lopez *et al.*, 2011, 2012c), escapees were counted while snorkelling through transects of 100x5 m, at between 1 and 5 m in depth. A second survey of the same transects was later made to establish habitat heterogeneity and complexity, measuring the cover % of different habitats and habitat features: sandy bottom, rocky platform, cliff, and boulders classified by the size of their major length (ML): small boulders and pebbles-SB (ML≤50 cm), medium boulders-MB (50 cm<ML≤1 m), and large boulders-LB (ML>1 m) (García-Charton *et al.*, 2004; Toledo-Guedes *et al.*, 2009).

A total of 720 visual censuses were carried out throughout the study, distributed over 10 localities (Fig. 1) with three sites each and six replicates at each site. All localities were sampled in a total of four time periods (March and October of 2009 and 2010). The localities were randomly chosen at different distances from the escape point (from 0.6 to 60 km) to establish a spatial generalization of the possible temporal patterns observed. Moreover, three of them were situated in La Palma MPA to ascertain if fishing pressure could influence or alter abundances of escaped fish in the wild.

Distance from release point has been demonstrated to be one of the most important variables explaining distribution patterns of escapees in the wild (Toledo-Guedes *et al.*, 2009). Thus, at site level, exponential decay regressions were fitted to each sampled period in order to identify alterations in the gradient of escaped sea bass and sea bream abundances.

The initial intention of sampling design was to test the hypothesis that at the end of winter the number of escaped fish in the wild was higher than at the end of summer. Our hypothesis was supported by the evidence that a significant percentage of escape events occurs due to bad weather conditions (i.e. sea storms; Jensen *et al.*, 2010). Therefore, two sampling months were established: at the end of the winter season (March) and at the end of the summer season (October), and replicated in two years (2009 and 2010). However, the sudden massive escape at the end of 2009 (Ramírez *et al.*, 2011) changed the scenario, and the opportunity for testing the effects of a massive escape on local fisheries appeared. Therefore the design was improved with the fixed factor of temporal replication 'Year' to test the hypothesis of a greater abundance of escapees in the wild after the massive escape event.

Owing to the scarcity of escaped sea bream records during the visual census, the following analyses were carried out only for sea bass escapees. Abundance of escaped fish in the wild was tested spatiotemporally using permutational ANOVA (Anderson, 2001). These analyses were performed over a Euclidean distance matrix of log-transformed abundances of escaped sea bass. Firstly, a five-way model was conducted with the following design:

Year – Ye – Fixed, two levels (2009, 2010). Test the influence of the massive escape event on escapees' abundance in the wild.

Season – Se – Fixed, two levels (March, October). Test possible seasonal changes due to a higher farmed fish winter release.

Protection – Pr – Fixed, two levels (marine protected area –MPA–, highly fished area –HFA–). Test the influence of fishing pressure on bass densities.

Locality – Lo – Random, nested in Protection (three levels).

Site – Si – Random, nested in Locality (three levels).

Additionally, distance from release point (in km) and *arcsinx +1* transformed environmental variables were added as covariates. In this way, any bias in sites selection is corrected to assure that spatiotemporal differences are due to the tested factors.

A second five-way model was applied, but in this case the factor Protection was substituted by Coast with two levels (West, East). Additionally, the factor Locality had four levels (i.e. four localities). As no significant differences were found between MPA and HFA localities on the west coast (see results), for this model the fourth locality was randomly selected from the three available within the MPA. This test assessed differences in escapees' density and consistency of temporal patterns between both coasts. Thus, only environmental variables were added as covariates in this model. For the interpretation of the ANOVA's, when random interaction terms were significant, we still considered the main effects. This is because the higher level fixed factor effect remains relevant regardless of the outcome of the interaction with a random factor (Quinn and Keough, 2002). For the analyses SigmaPlot 10.0 and PRIMER6 & PERMANOVA+ were used.

Fisheries data were collected from the two professional fishermen's associations on the Island, locally known as 'Nuestra Señora del Carmen' (27 boats) whose home-port is on the west coast, 2 km away from the release point, and 'Nuestra Señora de Las Nieves' (20 boats) based on the east coast, 60 km away from aquaculture facilities (Fig 5.1). There are no reliable data on landings of artisanal fleets in the Canaries. However, a system implemented by the Canary Islands Government records data of 'first-sale' (i.e. the financial transaction between the fisherman and the fish purchaser). It is compulsory for professional fishermen to declare the invoices with the total amount of fish sold per species. These data are the best proxy of the total landings and were used to detect the influence of aquaculture escaped fish in artisanal fisheries. The annual 'first-sales' data of the association situated near the aquaculture facilities were gathered annually from 2006 to 2010, while during 2009 and 2010 they were collected monthly at both fishermen's associations. Since our aim was to detect the importance of escaped fish in the total catch of shallow bentho-demersal fish, the data on molluscs, crustaceans and strictly pelagic fish (i.e. tunids) were removed. This is because the escaped fish do not inhabit the same area and/or depth, nor is the same fishing gear used to catch these groups (Franquet and Brito, 1995; Froese and Pauly, 2012).

5.3 Results

Visual censuses show that densities of escaped sea bass on the coast facing the release point were raised as much as three orders of magnitude after the massive escape event (Fig. 5.2). Exponential decay regressions (Fig 5.3 a and b) showed a significant relation between bass densities and distance from release point. However, the relationships were stronger (i.e. higher R^2 and lower p-values) for March (i.e. after winter) than October (i.e. after summer) in both years. The density of escaped sea bream showed a weak but significant ($R^2=0.145$) relation to distance from release point, but only immediately after the massive escape event (March 2010).

Spatiotemporal patterns in densities of escaped sea bass were detected by the permutational ANOVA test (Table 5.1 and Table 5.2). Despite the high variability detected on the scale of 100's of m, and the multiple interactions with random factors, the test showed a significant temporal pattern where bass densities were higher after the escape event ($p<0.01$; Table 5.1, Fig. 5.4). And for each year, the presence of escapees is significantly higher ($p<0.05$) after

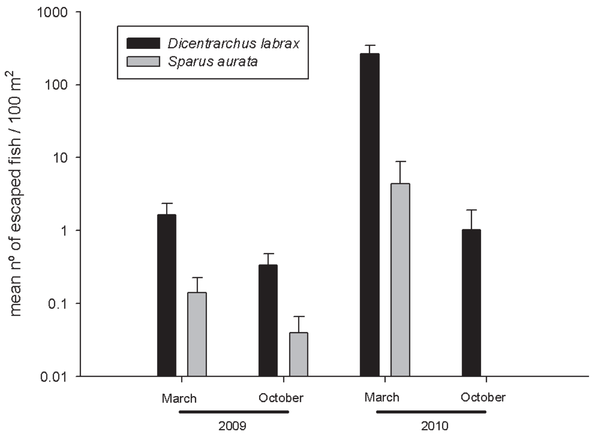

Figure 5.2. Escaped fish densities (± SE) at the release point for each sampling period. Note the logarithmic scale in 'y' axis.

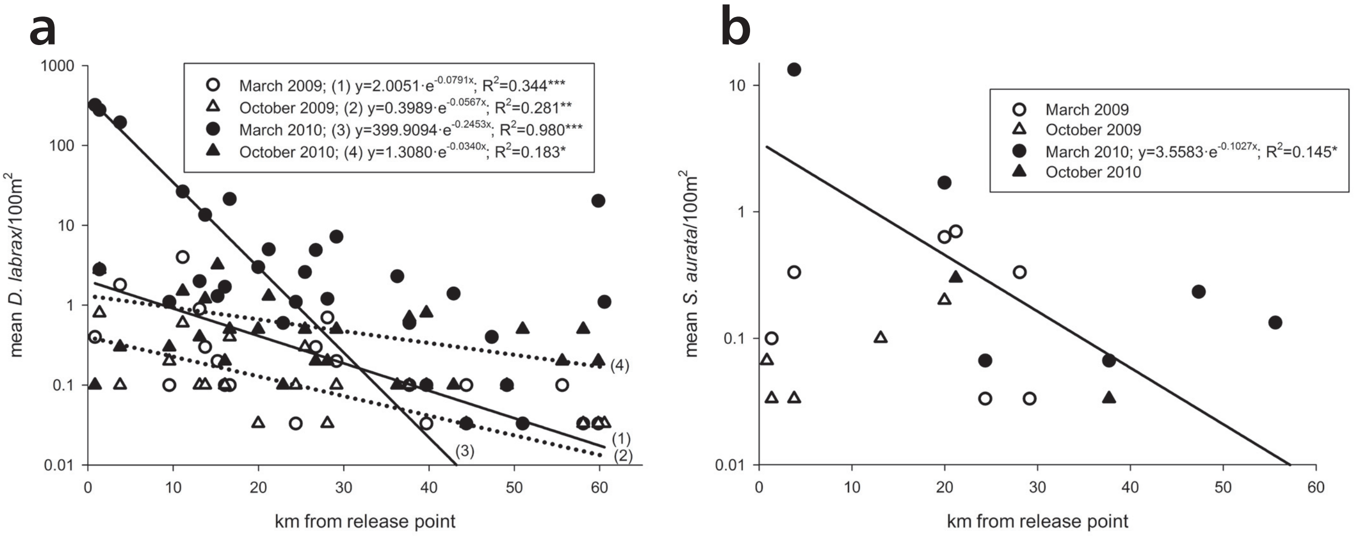

Figure 5.3. Linearized exponential decay regressions of site-level densities of (a) escaped sea bass and (b) escaped sea bream. Only significant regressions are showed. *: $p<0.05$, **: $p<0.01$, ***: $p<0.001$.

winter (March) than after summer (October). Regarding the influence of fishing pressure on densities of escaped fish, no difference was found between localities situated in the MPA and those in HFA. Several environmental variables including distance from release point were found to be significant ($p<0.05$), influencing density of sea bass in the wild (Table 5.1). The same temporal patterns were also found in the second model, and were consistent on both sides of the Island. However, the escapees densities were significantly lower on the east coast ($p<0.05$; Table 5.2; Fig. 5.5).

Regarding local fisheries, 'first-sale' data from 2006 to 2010 (Fig. 5.6) reflect the incidence of

Table 5.1. Univariate permutational ANOVA (covariates above the dashed line) of log transformed abundances of escaped sea bass. Ye: Year, Pe: Period, Pr: Protection, Lo: Locality, Si: Site. In bold: relevant factors and interactions with p-values <0.05.

Source	df	SS	MS	Pseudo-F	P(perm)	Unique perms
Distance	1	83.648	83.648	15.383	**0.0132**	4987
Cliff	1	9.4461	9.4461	4.8881	**0.0332**	4975
Rock	1	26.905	26.905	14.559	**0.0002**	4951
Sand	1	20.823	20.823	13.585	**0.0006**	4959
Small Boulders	1	0.16659	0.16659	8.587E-2	0.7662	4963
Medium Boulders	1	0.12284	0.12284	8.1735E-2	0.7772	4950
Large Boulders	1	1.5884	1.5884	1.0334	0.3014	4958
Year	1	185.39	185.39	16.47	**0.0136**	4955
Period	1	136.38	136.38	10.152	**0.035**	4945
Protection	1	4.0385	4.0385	1.0624	0.4086	4988
Locality(Pr)	4	14.68	3.6701	1.1615	0.384	4992
YexPe	1	80.716	80.716	4.8183	0.086	4958
YexPr	1	9.034	9.034	0.78763	0.435	4959
PexPr	1	37.168	37.168	2.7087	0.1592	4966
Site(Lo(Pr))	11	35.39	3.2173	3.1698	0.0002	4990
YexLo(Pr)	4	45.526	11.381	9.572	0.002	4989
PexLo(Pr)	4	54.346	13.586	5.986	0.0106	4993
YexPexPr	1	8.691	8.691	0.5203	0.5026	4952
YexSi(Lo(Pr))	12	14.236	1.1863	1.1688	0.3026	4979
PexSi(Lo(Pr))	12	27.148	2.2623	2.2289	0.0084	4988
YexPexLo(Pr)	4	67.046	16.761	6.7901	0.0058	4987
YexPexSi(Lo(Pr))	12	29.284	2.4403	2.4043	0.0058	4983
Res	354	359.3	1.015			
Total	431	1251.1				

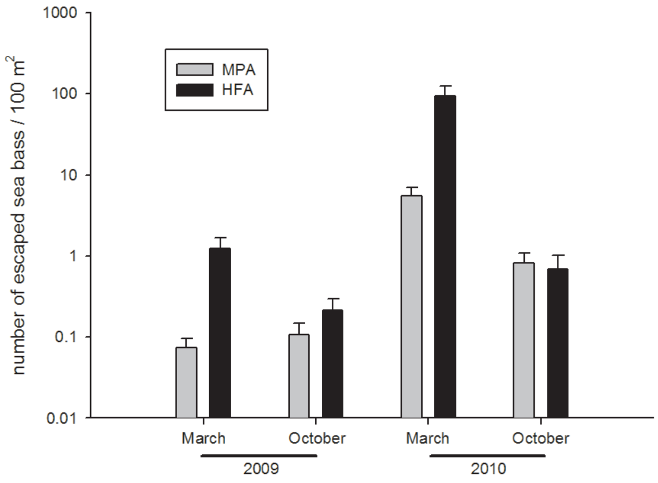

Figure 5.4. Mean values (± SE) of densities of escaped sea bass for each period in localities inside the MPA (grey bars) and in HFA (black bars). Note the logarithmic scale in 'y' axis.

Table 5.2. Univariate permutational ANOVA (covariates above the dashed line) of log transformed abundances of escaped sea bass. Ye: Year, Pe: Period, Co: Coast, Lo: Locality, Si: Site. In bold: relevant factors and interactions with p-values <0.05.

Source	df	SS	MS	Pseudo-F	P(perm)	Unique perms
Cliff	1	19.501	19.501	6.9374	**0.0124**	4957
Rock	1	6.4623	6.4623	2.7361	0.1022	4955
Sand	1	1.2135	1.2135	0.61	0.4448	4964
Small Boulders	1	3.7548	3.7548	1.131	0.296	4949
Medium Boulders	1	20.516	20.516	9.8789	**0.002**	4957
Large Boulders	1	5.6028E-3	5.6028E-3	3.4671E-3	0.954	4946
Year	1	131.8	131.8	16.654	**0.0072**	4960
Period	1	80.748	80.748	6.7716	**0.0416**	4960
Coast	1	122.38	122.38	13.358	**0.011**	4983
Locality(Co)	6	50.829	8.4716	3.0555	0.0352	4990
YexPe	1	39.757	39.757	3.3924	0.1024	4945
YexCo	1	33.281	33.281	4.2308	0.0846	4958
PexCo	1	67.694	67.694	5.7105	0.0586	4953
Site(Lo(Co))	16	45.977	2.8736	3.4916	0.0002	4983
YexLo(Co)	6	47.667	7.9445	6.9761	0.001	4989
PexLo(Co)	6	71.877	11.98	6.6656	0.0014	4987
YexPexCo	1	21.958	21.958	1.7866	0.2272	4965
YexSi(Lo(Co))	16	18.164	1.1352	1.3794	0.1446	4976
PexSi(Lo(Co))	16	28.654	1.7909	2.1761	0.004	4982
YexPexLo(Co)	6	72.932	12.155	6.912	0.001	4987
YexPexSi(Lo(Co))	16	28.203	1.7627	2.1418	0.0066	4978
Res	474	390.1	0.82299			
Total	575	1303.5				

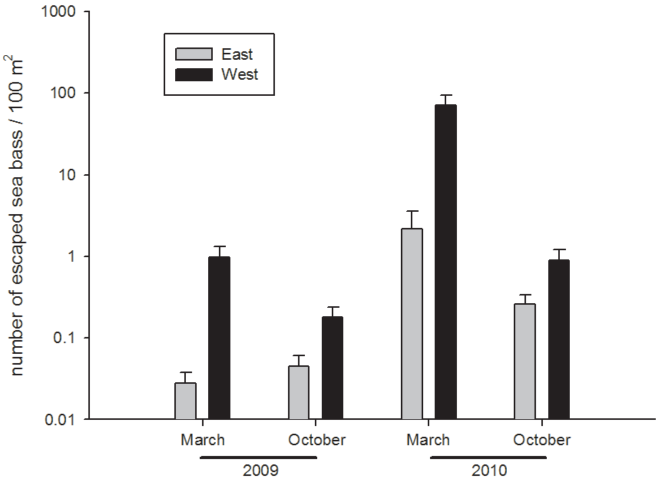

Figure 5.5. Mean values (± SE) of densities of escaped sea bass for each period in localities in the west (black bars) and east coast (grey bars). Note the logarithmic scale in 'y' axis.

escaped fish in local fisheries near the escape point. Only the captures of sea bream during 2006 (4,118 kg) were comparable to those found in 2010, the year of the massive escape (5,177 kg). Monthly data showed an increment in aquaculture-origin captures following the massive escape event (Fig. 5.7). The rise in captures is strongly reflected in the sales figures of the fishermen's association situated near the release point (Fig. 5.7a). Aquaculture-origin captures reached 37% of the total bentho-demersal fish catch in this area during February 2010. However, the largest catch, 3,554.9 kg of sea bass, was recorded in June 2010. Captures of both bass and bream occurred until May 2010 on the west coast, the rest of the year the aquaculture-origin captures are mainly sea bass. The captures on the east coast showed a lower incidence of aquaculture-origin fish, predominantly bream, until April 2010. A total of 19,975 kg of sea bass and 6,021 kg of sea bream were sold by the fishermen's associations during 2010.

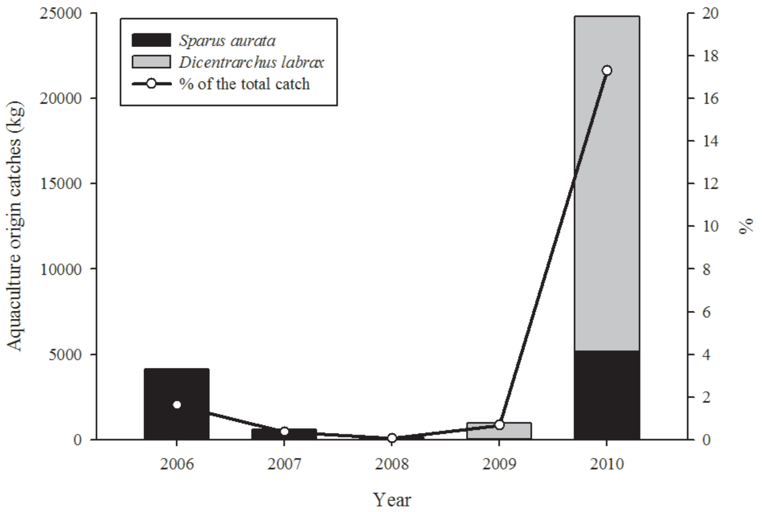

Figure 5.6. Annual catches (kg) of escaped sea bass and sea bream and their importance in total catch (%) for the fishermen's association on the west coast.

5.4 Discussion

Clear spatial patterns of escaped fish in the wild, related to distance from release point, are found in this study. Temporal patterns are linked to periods of intensive release in winter versus periods of decreased release intensity and a presumably higher fishing pressure during summer. This pattern was consistent even at long distances. The MPA had no detectable

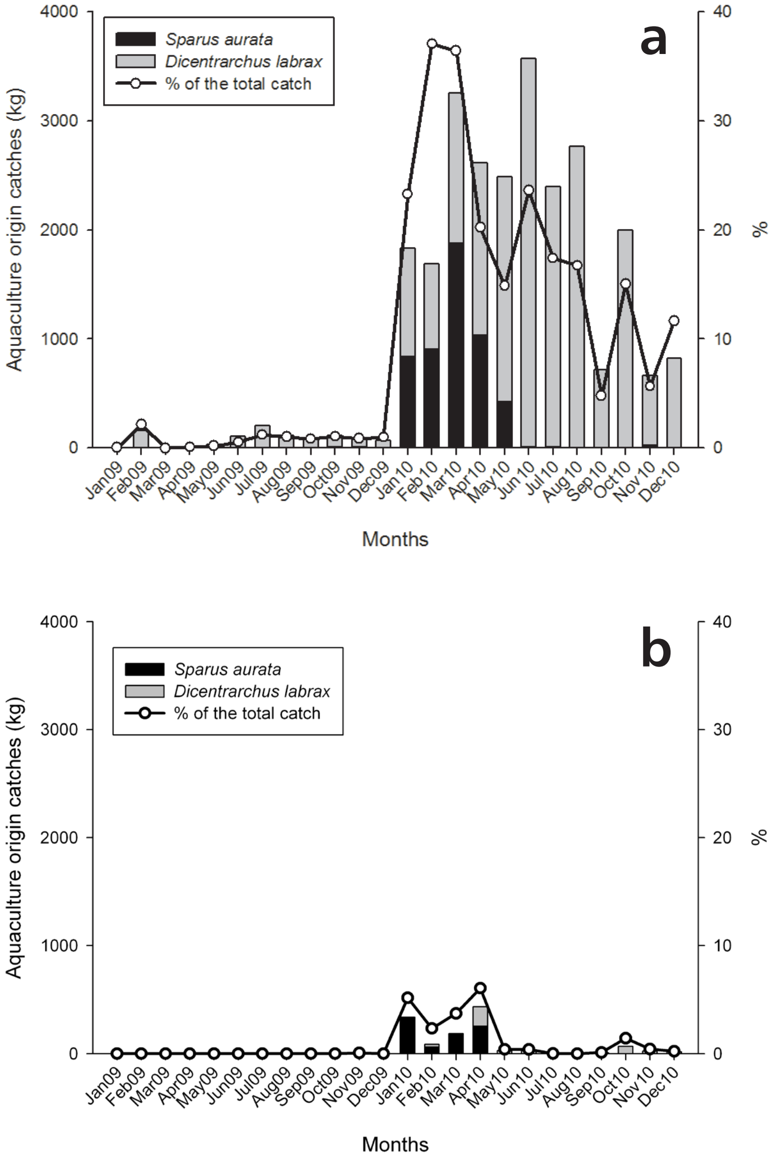

Figure 5.7. 2009-2010 monthly catches (kg) of escaped sea bass and sea bream and their importance in total catch (%) for fishermen's associations on La Palma: (a) west coast and (b) east coast.

effects on abundance of escaped fish within its limits. The massive escape showed an obvious effect on local fisheries, which seem to mitigate the escape event by reducing the survival of escapees in natural habitats. 'First-sales' data accurately reflected the massive escape event and suggest a higher catchability rate for sea bream. Thus, both visual census and fisheries data are useful in monitoring escape events and developing contingency plans.

Densities of escaped fish, especially sea bass, rose dramatically (i.e. up to three orders of magnitude) in shallow coastal waters after the massive escape event. A spatial pattern is observed; their density falls off exponentially as we move away from escape point. This is supported by exponential decay regressions and the statistical significance of the variable 'distance from the escape point' when it is used as covariate. The influence shown by several environmental variables also supports their use as covariates. Previous studies show that distance from escape point influences escapee densities at the scale of km, while environmental features do so at a scale of 100's of m (Toledo-Guedes *et al.*, 2009). Escapees are capable of moving around the sland and reaching distant zones (up to 60 km away). This is in concordance with other survey studies (Toledo-Guedes *et al.*, 2009) and tagging experiments (Arechavala-Lopez *et al.*, 2011).

Two opposing hypotheses were proposed regarding the influence of La Palma MPA. It might prevent the entrance of escaped fish due to a higher abundance of predators as part of a well-structured fish assemblage. Alternatively, the lower fishing pressure in the MPA could favour the presence of escaped fish in the area (Jouvenel and Pollard, 2001; Burfeind *et al.*, 2013). However, our results (Table 5.1) give no support either of these mechanisms. When the effect of distance from release point and environmental variables is removed, localities inside the MPA behave just like those in HFA. Thus, no impeding nor enhancing effect is observed on escaped fish due to the presence of an MPA. The extraordinary size of the escape, and their high mobility, could be masking the effect of this small MPA. This is because the effectiveness of MPAs is strongly related to their size and age (Claudet *et al.*, 2008), specially for highly mobile species. Thus, in such cases, long term studies are needed to detect the above responses.

Concerning temporal patterns, a series of processes that could broadly explain the results are identified. A higher number of sea bass at the end of winter is related to a combination of factors, mostly linked to seasonal bad sea conditions (Jensen *et al.*, 2010). Firstly, we have those promoting a higher release frequency at the facility: greater structural stress, and difficulty to carry out maintenance and harvesting. Secondly, certain factors affect removal of the fish from the wild: neither recreational nor professional fishers can carry out their activities at the same intensity during winter, as pointed out for the Canaries (Díaz de la Paz, 1993; Franquet and Brito, 1995). Finally, the picture is completed by the dispersal rate and natural mortality of escaped fish, which are both high (Toledo-Guedes *et al.*, 2009; Arechavala-

Lopez *et al.*, 2011). Thus, following a period of high release frequency (i.e. winter) there is a period (i.e. summer) of mortality/removal/dispersal. The latter, together with a lower number of escape events during summer, would promote a homogenization of densities around the coast of La Palma. This would explain why linearized exponential decay regressions showed weaker gradients in the October surveys (i.e. after summer) than in March (i.e. after winter; Fig. 5.3a). In this way, this escape event would be an extreme example of the habitual winter fish escape rates from aquaculture facilities. The above patterns are observed even at distant localities on the east coast, as reflected in Table 5.2, which highlights the plausibility of this explanation. For the bream these patterns are less clear, due to a lower number of escapees found in the wild, since they only represented 10% of the total massive escape.

In a long-term context, the annual sales data (Fig. 5.6) show the amount of aquaculture-origin captures during years with no recorded massive escape events. However, in 2006, a sea bream massive escape could have occurred, as captures are similar to those found in 2010. These figures may also reflect separate escape events during 2006. Since aquaculture activities in La Palma started in 2005, their influence has been and will be reflected (to a larger or lesser extent) in artisanal fisheries records as long as aquaculture continues.

Local fisheries were extensively influenced by the massive escape event (Fig. 5.7a and b). Soon after, professional fishermen began to capture both species, especially the association situated near aquaculture facilities. Large catches of sea bass were still obtained at the end of 2010. To our knowledge, such a clear effect has never been documented. In the case of La Palma, the fact that both are introduced species facilitates the identification of escapees. In other areas, where escaped cultured and wild counterparts coexist, the labelling method at harbours does not differentiate between them (Arechavala-Lopez *et al.*, 2013a). For salmonids, visual identification of escaped individuals is quite straightforward (Lund *et al.*, 1989). In contrast, for sea bream and sea bass, in areas such as the Mediterranean, tools for identification of escaped fish are still in the initial stage of development and have not been applied in fisheries management (Arechavala-Lopez *et al.*, 2013a). Therefore, there could be an underestimation of the importance of aquaculture-origin fin fish in the landings of professional fisheries in the light of our results. In addition to potential problems due to hybridization (Youngson *et al.*, 2001; Coscia and Mariani, 2011), this could be a major problem when evaluating the 'wild' stocks of these species.

Our results suggest a higher catchability (i.e. the relationship between resource abundance and efficiency of the fishing gear; Arreguín-Sánchez, 1996) for escaped sea bream in comparison to sea bass. Firstly, on the west coast from January to March 2010, its proportion in the captures in relation to sea bass was 1:1 approx. while it was expected to be 9:1 according to official data on the massive escape event (Ramírez *et al.*, 2011). Furthermore, sea bream virtually disappeared from catches after May 2010 on this coast. Secondly, a prevalence of sea bream captures on the east coast is observed which suggests that it is more easily captured. The bass was observed on that coast in larger numbers than sea bream during the visual censuses after the massive escape event (this study), but this is not reflected in fisheries data.

'First-sale' data showed that professional fishermen sold roughly 20 tonnes of sea bass and 6 tonnes of sea bream during 2010. Official reports reveal that aqua-farmers and local authorities promoted other post-escape recapture efforts (Ramírez *et al.*, 2011), that do not appear in our data. In the first months after the escape event and during July 2010, 51.2 and 11.7 tonnes of the escaped fish were recaptured respectively. This gives a total of 88.9 tonnes documented as being removed from the wild. This represents 22.2% of the total stock accidentally released. To these figures an unknown quantity could be added, as recreational fishermen intensively fished the coasts near aquaculture facilities after the escape event (pers. obs.). Rate of recapture in the Canaries is higher than that found for juvenile cod in Norway (<5%; Serra-Llinares *et al.*, 2013) and sea bream (9%) in the Mediterranean (Arechavala-Lopez *et al.*, 2012c). However, those studies released a limited number of fish in comparison to the massive escape. Therefore, post-escape mortality (i.e. predation) may prevent further recapture.

5.4.1 Management recommendations

The immediate impact of the massive escape event on fisheries data highlights the suitability of artisanal fishermen for mobilizing a rapid response to such incidents, especially in those cases where aquaculture managers do not communicate the problem in time. The fast response has been shown to be important, as the possibility of recapture is clearly diminished as time passes after the escape event (Uglem *et al.*, 2008). Thus, if a systematic recapture effort had been carried out just after the accidental release, it would had been more successful. This task should be carried out in the framework of contingency plans, in which professional

fishermen will play a key role. A rapid recapture of escapees would prevent potential trophic interactions and parasite spreading, as suggested for sea bass in the Canaries (Toledo-Guedes *et al.*, 2009, 2012).

Risk assessment tools have already been developed (Verbrugge *et al.*, 2010; Britton *et al.*, 2011). It is now time to apply them, particularly for introduction of non-indigenous or locally absent species. There is a need for independent organisms to audit the maintenance of aquaculture facilities and harvesting operations, to avoid bad practices. Capital importance should be given to maintenance operations just before winter, when facilities will be under high mechanical stress due to storms. Each aquaculture facility should provide comprehensive contingency plans. Collaboration and agreement with professional fishermen, as experts, is crucial to prepare this kind of protocol. In addition, frequent analysis of landing data could reveal abnormalities in captures, and alert authorities about non-communicated escape events. All these measures will contribute to prevent and diminish undesirable effects on marine ecosystem health and services due to escaped fish.

CHAPTER 6

Farming-up coastal fish assemblages: MPA resilience to changes in Mean Trophic Level due to a massive escape of non-indigenous cultured fish

Toledo-Guedes, K., Sanchez-Jerez, P., Benjumea, M. E. and Brito, A (submitted). Farming-up coastal fish assemblages: MPA resilience to changes in Mean Trophic Level due to a massive escape of non-indigenous cultured fish. *Oecologia*.

SUMMARY

In this chapter we investigate the changes on the mean trophic level of fish assemblages after a massive escape event occurred at La Palma (Canary Islands), which resulted in the release of 1.5 million fish into the wild, across different spatiotemporal scales. The presence of escaped fish altered significantly the mean trophic level of fish assemblages in shallow coastal waters. This alteration was exacerbated by the massive escape that also changed the size frequency distribution of escaped individuals in the wild. La Palma MPA was also affected, but showed certain resilience to changes in mean trophic level. In any case, the MPA exhibited the same temporal patterns as highly fished areas. Moreover, escaped fish exploited natural resources according to their total length and time at liberty. New concerns arise as a 'farming-up' process is detected in shallow coastal fish assemblages where marine aquaculture is established. This may lead to alterations in marine ecosystems through trophic cascade effects.

RESUMEN

En este capítulo se investigan los cambios en el nivel trófico medio de la comunidad de peces después de un escape masivo ocurrido en La Palma (Islas Canarias), que supuso la liberación de 1,5 millones de peces al medio natural, a través de diferentes escalas espacio-temporales. La presencia de los peces escapados alteró significativamente el nivel trófico medio de la comunidad de peces de aguas costeras someras. Esta alteración se vio exacerbada por el escape masivo, que también cambió la frecuencia de distribución de tallas de los peces escapados en el medio natural. La reserva marina de La Palma fue afectada igualmente, sin embargo, mostró cierta resiliencia a estos cambios en el nivel trófico medio. En cualquier caso, los patrones temporales fueron iguales a los de zonas con alta presión pesquera. Además, los peces escapados explotaron recursos tróficos en función de su longitud total y tiempo en libertad. Nuevas preocupaciones pueden surgir debido a la detección de un proceso de 'farming-up' en las comunidades de peces costeros en aquellos lugares donde la acuicultura marina se lleva a cabo. Esto podría desencadenar alteraciones en el ecosistema marino a través de cascadas tróficas.

6.1 Introduction

Aquaculture of high-trophic-level (HTL) fish species is growing, especially in developed countries, as a result of a rising demand on marine products of certain quality and the highest profit obtained from carnivorous species (Stergiou *et al.*, 2008). This process has been named 'farming-up' (Stergiou *et al.*, 2008), and one of its major concerns is the exploitation of wild fish stocks to fed very high trophic level species, called 'tigers of the sea' by Naylor and Burke (2005). In addition, culturing non-native or locally absent species is already a frequent practice (Casal, 2006; Arismendi *et al.*, 2009; Liao *et al.*, 2010) that is predicted to grow in the next years (Shelton and Rothbard, 2006). Thus, as a result of both mentioned trends, in some areas, HTL species that were absent or with low abundances in natural habitats are being released into the wild through escape events. Technical failures and sea storms generate both recurrent-small or punctual-massive escapes across the coasts where open-net cage aquaculture is established (Jensen *et al.*, 2010). This could be comparable to continuous restocking action with non-indigenous or locally absent species (Lorenzen *et al.*, 2012), which has been defended by some authors (Briggs, 2008; Schlaepfer *et al.*, 2011) but is, in general, not recommended due to the unpredictable effects it could have (Courtenay *et al.*, 2009; Ricciardi and Simberloff, 2009). Here we use the term farming-up as a process by which wild fish assemblages raise their mean trophic level (mTrL) due to the input of cultured fish through escape events.

Many studies have pointed out potential and detected negative consequences due to the release of fish (exotic or not): genetic hybridization (McGinnity *et al.*, 2003); predation on native species (Albins, 2013; Green *et al.*, 2012b); competition for trophic resources (Declerck *et al.*, 2002); introduction of parasites and diseases (Toledo-Guedes *et al.*, 2012); changes in fisheries dynamics (Dimitriou *et al.*, 2007), among others. Recently, it has been demonstrated that marine ecosystems are much more susceptible to large-scale invasion pressures than previously thought (Edelist *et al.*, 2013). Even if escaped fish do not establish self-sustainable populations, they may produce persistent impacts due to the repeated supply of propagules by aquaculture (Arismendi *et al.*, 2009; Jensen *et al.*, 2010).

In the Canaries, where finfish production in open-net cages during 2009 was 7,910 tons (APROMAR, 2012), European sea bass (*Dicentrarchus labrax*) and gilthead sea bream (*Sparus aurata*) have been introduced in some of the islands where no natural populations of these species were known (Brito *et al.*, 2002; Toledo-Guedes *et al.*, 2009). This is the case of La Palma island, where a massive escape evens occurred between December 2009 and January 2010. Repeated northwest sea storms generating waves up to 6 meters height resulted in both lack of maintenance operations and increased mechanical stress for aquaculture facilities (Ramírez *et al.*, 2011; Puertos del Estado, 2012). As a result, around 1.5 million fish, 90% of which were sea bass and 10% sea bream, were released into the wild during that period (Ramírez *et al.*, 2011). Only some massive escapes of salmonids seems to surpass these figures; the largest occurred in Chile, with an estimation of more than 5 million Atlantic salmon (*Salmo salar*) individuals released, due to a tsunami in 2007 (Thorstad *et al.*, 2008). In the Mediterranean Sea, of the 6.85 million sea bream reported to have escaped, two incidents accounted for 1.9 and 3.8 million fish respectively (Jackson *et al.*, 2013). As far as we know, this is the largest sea bass massive escape event documented to date worldwide.

We capitalize on this catastrophic event to examine the escapees' potentiality to altering the mean trophic level (mTrL) of fish assemblages in shallow coastal waters, and discuss the potential consequences of these changes. We hypothesized that (1) fish assemblages mTrL should be affected by the massive escape of HTL fish, (2) this effects should be related to distance to release point and (3) that marine protected area could show some kind of resilience to changes in mTrL. For this, the spatiotemporal variation of mTrL before and after the massive escape event is analyzed. Additionally, we studied the escaped bass trophic role, in relation to size and time at liberty, through stomach content analysis.

6.2 Material and Methods

6.2.1 Study site and sampling effort

Our study was carried out in La Palma (Fig. 6.1), one of the westernmost islands of the Canaries, situated in the north-eastern part of the Central Atlantic. Aquaculture facilities are at a single location off the western coast of the Island. A marine protected area (MPA) is situated 15 kilometres to the south from fish farms.

A total of 6 localities (Fig. 6.1), and three sites (n=6) in each locality, were sampled on the west coast of the Island, at different distances from release point (0.8 to 30 km). Three of the localities were situated in La Palma MPA, and other three localities were in highly fished areas (HFA). The localities were sampled four times: March 2009, October 2009, March 2010 and October 2010. A total of 432 visual censuses were carried out through the study.

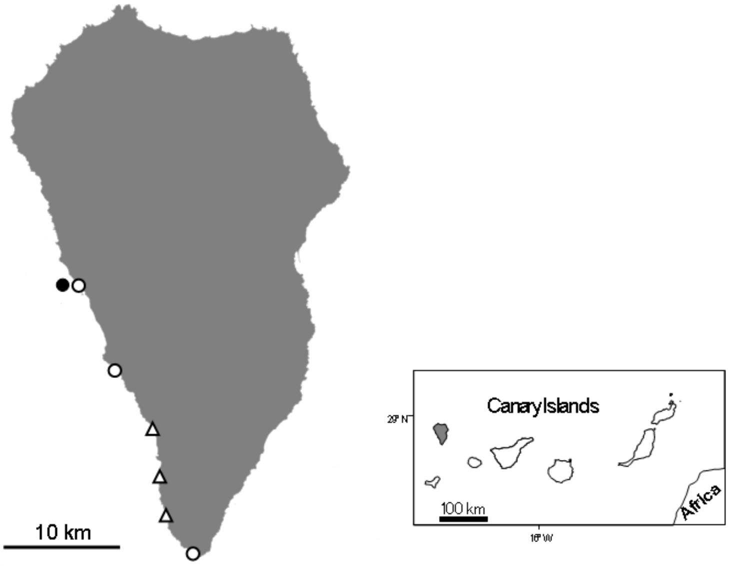

Figure 6.1. Study area. Black circle: aquaculture facilities / release point. White circles: localities sampled outside La Palma MPA. White triangles: localities sampled at MPA.

6.2.2 Visual censuses

Following previous methodology (Toledo-Guedes *et al.*, 2009), and due to the high mobility, and shallow distribution of escaped fish (González-Lorenzo *et al.*, 2005; Arechavala-Lopez *et al.*, 2011, 2012c), snorkelling visual censuses were carried out in transects of 100x5 m, between 1 and 5 m depth. In the initial 25 m, all the fish species abundances and sizes were recorded, while across the rest of the survey only escaped fish were counted. A second pass of the same transects was made to establish habitat heterogeneity and complexity, measuring the cover % of different habitats and habitat features; sandy bottom, rocky platform, cliff and boulders classified by the size of their major length (ML): small boulders-SB (ML≤50 cm), medium boulders-MB (50 cm<ML≤1 m), and large boulders-LB (ML>1 m) (García-Charton *et al.*, 2004).

6.2.3 Mean trophic level calculation

Fish length estimates were converted to weight by using the allometric length–weight conversion:

$$W = aTL^{b},$$

where W is weight in grams (i.e. biomass), parameters *a* and *b* are constants obtained from the literature (Froese and Pauly, 2012), and TL is total length in cm. When values for *a* and *b* were unavailable, the parameters from a congeneric species with similar shape and maximum total length were used.

Mean trophic level of the fish assemblage in each transect ($mTrL_t$) was then calculated as follows (CIESM, 2000):

$$mTrL_t = \sum_t (TrL_{i-n} \cdot W_{i-n}) / \sum_t W_{i-n},$$

where the summation of trophic level of each species (TrL_{i-n}) recorded in the transect, multiplied by their weight (W_{i-n}), is divided by the total weight amounted in the same transect. The TrL for each species was recorded from FishBase (Froese and Pauly, 2012).

We also calculated the mean trophic level of each transect removing escaped fish from the data ($mTrL_0$), with the aim of capturing the situation with no escaped fish in the wild. Moreover, to assess the magnitude of the changes in mTrL caused by escaped fish, we calculated ΔTroph as the difference between mTrL and $mTrL_0$.

6.2.4 Sampling design and analysis

Overall analysis

Possible relations (i.e. direct trophic interactions) between the presence of escaped fish and the abundance of other species were explored through Spearman’s correlation index.

To ascertain whether the mTrL of shallow coastal fish assemblages is altered by the presence of escaped fish, we compared untransformed mTrL of transects with no presence of escaped fish against those transects with presence of escapees across the study. Due to the unbalanced nature of the analysis, a permutational ANOVA (Anderson, 2001) test was carried out over Euclidean distance matrix and 4999 permutations, using distance to fish farm and *arcsinx+1* transformed environmental variables as covariates. The latter allowed detecting differences in mTrL irrespective of its influence on fish assemblages (García-Charton *et al.*, 2004).

Kolmogorov-Smirnov test was used to compare size frequency of sea bass and sea bream before and after the massive escape. Sizes structure have been previously hypothesized to change in case of massive escapes of certain sizes (Toledo-Guedes *et al.*, 2009).

Spatiotemporal design and analysis

In order to detect spatiotemporal patterns in mean trophic level of fish assemblages, permutational ANOVAs (Anderson, 2001) were performed over untransformed $mTrL_0$, ΔTroph and mTrL. Euclidean distances matrix and 4999 permutations were used. A five-factor design was tested as follows:

Year – Ye – Fixed, two levels (2009, 2010). Test de influence of the massive escape event over the variables.

Season – Se – Fixed, two levels (March, October). Test possible cold versus warm seasonal changes due to a higher winter release of farmed fish (Toledo-Guedes *et al.* in press).

Protection – Pr – Fixed, two levels (marine protected area –MPA–, highly fished area –HFA–). Test the resilience of the MPA to changes of mTrL due to escaped fish.

Locality – Lo – Random, nested in *Protection* (three levels).

Site – Si – Random, nested in *Locality* (three levels).

Environmental variables (*arcsinx+1* transformed) and distance from escape point in km were added as covariates to remove their possible effect over the tested variables. For the interpretation of the results, significant interaction terms with random factors involved were not taken into consideration, as the higher level fixed factor effect remains relevant regardless of the outcome of the interaction with a random factor (Quinn and Keough, 2002). When interactions between fixed factors resulted significant a pair-wise comparison was performed in order to interpret the interaction.

Escapees vs. wild assemblages

To assess the importance of escaped fish in the study area, their biomass (g $100m^{-2}$) was compared with that of other species of similar trophic level, which belong to the same functional group and have analogous role in shallow coastal ecosystems. Biomass of escaped sea bass (trophic level 3.8 ± 0.6; Froese and Pauly, 2012) was compared with the biomass of species whose trophic level is higher than 3.5 (i.e. medium-top predators). This group of species was composed of potential sea bass predators and competitors: *Seriola spp.*, *Pomatomus saltatrix*, *Mycteroperca fusca*, *Sphyraena viridensis*, *Aulostomus strigosus*, *Scorpaena maderensis*, *Belone belone*, *Pseudocaranx dentex*, *Mustelus mustelus*, *Pomadasys incisus*, *Epinephelus marginatus* and *Trachinotus ovatus*. This was also done for sea bream (trophic level 3.3±0.5; Froese and Pauly, 2012); in this case, we compared against species whose trophic level is between 3 and 3.5. This group was composed of sparids: *Diplodus cervinus*, *Diplodus sargus*, *Oblada melanura* and *Lythognathus mormyrus* and other species whose diet is composed mainly of small crustaceans: *Thalassoma pavo*, *Canthigaster capistrata*, *Sphoeroides marmoratus* and *Symphodus trutta*. Pair-wise comparisons were made for each area (MPA and HFA) and time period; U-Mann Whitney test assessed the differences in the mean biomass of the groups as normality was not met.

6.2.5 Stomach content analysis

Individuals of *D. labrax* (n=144) were caught by spearfishing. A total of 112 escaped fish were captured during surveys in Tenerife and La Palma in 2008 and 2009. These were not associated to any known massive escape event; therefore, this group of fish was assigned to recurrent leaking escapees (leak group). On the other hand, 32 fish were caught in June 2010 in La Palma Marine Protected Area and, thus, due to the recent massive escape and their schooling behaviour, were assigned to that event (massive group).

All fish were measured (total length TL) to the nearest mm and weighted (accuracy of 0.01 g). The stomach intestine was separated from the body and its contents removed. Prey items were counted by number, fresh weighted and identified to the lowest possible taxonomical level. Thus, for each prey, percentage by number (N%) and weight (W%), frequency of occurrence (O%) and the alimentary coefficient (Q = N% x W%) were calculated (Hureau, 1970). The importance of prey groups was assessed using the following categories (based on values of Q and O%; Rosecchi and Nouaze, 1987): main preferred prey ($Q>100$, $O\%>30\%$); main occasional prey ($Q>100$, $O\%<30\%$); secondary common prey ($10<Q<100$, $O\%>10\%$); secondary additional prey ($10<Q<100$, $O\%<10\%$); accidental prey ($Q<10$). The index of relative importance (IRI) (Pinkas *et al.*, 1971) was also estimated, IRI = (N% + W%) x O%.

The Bray Curtis similarity matrix of the weights of the three main prey groups (insects, crustaceans and fish) was analyzed through non-metric Multidimensional Scaling (MDS), to detect possible differences in the diet of recent escapees. In addition, permutational ANOVA was carried out comparing the diet of the two groups using total length (TL) as a covariate, given the knowledge that the diet of sea bass changes during its life cycle in the wild (Kelley, 1987; Rogdakis *et al.*, 2010). For all the statistical analyses, SPSS 15.0 and PRIMER6 & PERMANOVA+ were used.

6.3 Results

6.3.1 Overall results

None of the pair-wise Spearman's correlations resulted significant. Mean trophic level of fish assemblage was significantly increased ($p<0.001$) from 2.78±0.41 in surveys with no escapees, to 3.16±0.55 where their presence was recorded (Table 6.1 and Fig. 6.2).

Significant differences were found for sea bass ($Z=15.110$; $p<0.001$) and sea bream ($Z=6.948$; $p<0.001$) size frequency distribution before and after the massive escape event. Mean TL of escaped sea bass (28.01±5.51 cm) and sea bream (28.39±8.08 cm) were clearly increased after the massive escape: sea bass and sea bream mean TL was 40.35±9.3 cm and 43.73±3.52 cm, respectively (Fig 6.3a and b).

Table 6.1. Univariate permutational ANOVA, comparing mean trophic level of fish assemblages with presence of escaped fish versus those with no escaped fish. Dashed line separates covariates from main factor. In bold those p-values<0.05.

Source	df	SS	MS	Pseudo-F	P(perm)	Unique perms
Distance	1	0.55073	0.55073	2.4434	0.1126	4956
Cliff	1	0.27806	0.27806	1.2336	0.2728	4944
Rocky platform	1	3.1525	3.1525	13.986	**0.0004**	4954
Sand	1	5.5289	5.5289	24.53	**0.0002**	4944
Small Boulders	1	3.9254	3.9254	17.416	**0.0002**	4953
Medium Boulders	1	2.8459E-2	2.8459E-2	0.12626	0.7236	4940
Big Boulders	1	4.472E-3	4.472E-3	1.9841E-2	0.8894	4952
Presence vs. Absence	1	8.8648	8.8648	39.33	**0.0002**	4958
Res	423	95.343	0.2254			
Total	431	117.68				

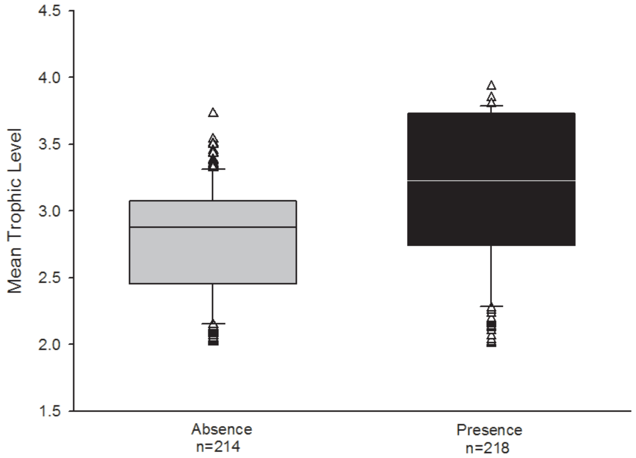

Figure 6.2. Box plot comparing mean trophic level of visual censuses with absence (grey) and presence (black) of escaped fish.

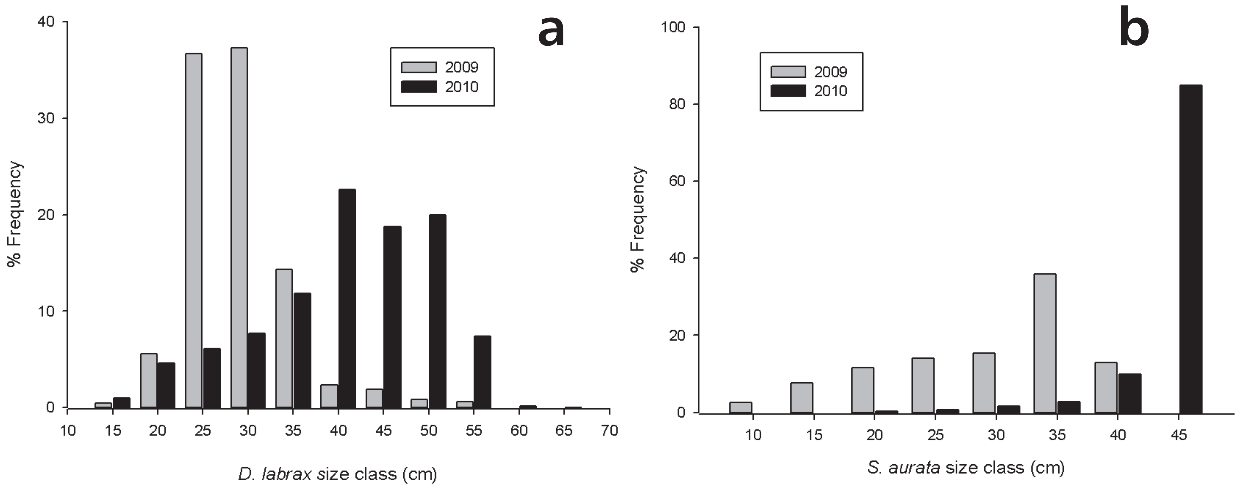

Figure 6.3. Size frequency of escaped sea bass (a) and sea bream (b), before (grey) and after (black) the massive escape event.

6.3.2 Escapees vs. wild assemblages

Pair-wise comparisons showed that biomass of escaped bass in the two sampled areas was equal or higher than the sum of the other medium-high trophic level species for all the sampled periods except in October 2010 (Fig. 6.4a). Conversely, biomass of escaped sea bream resulted always significantly lower than the biomass of other species with similar trophic level (Fig. 6.4b).

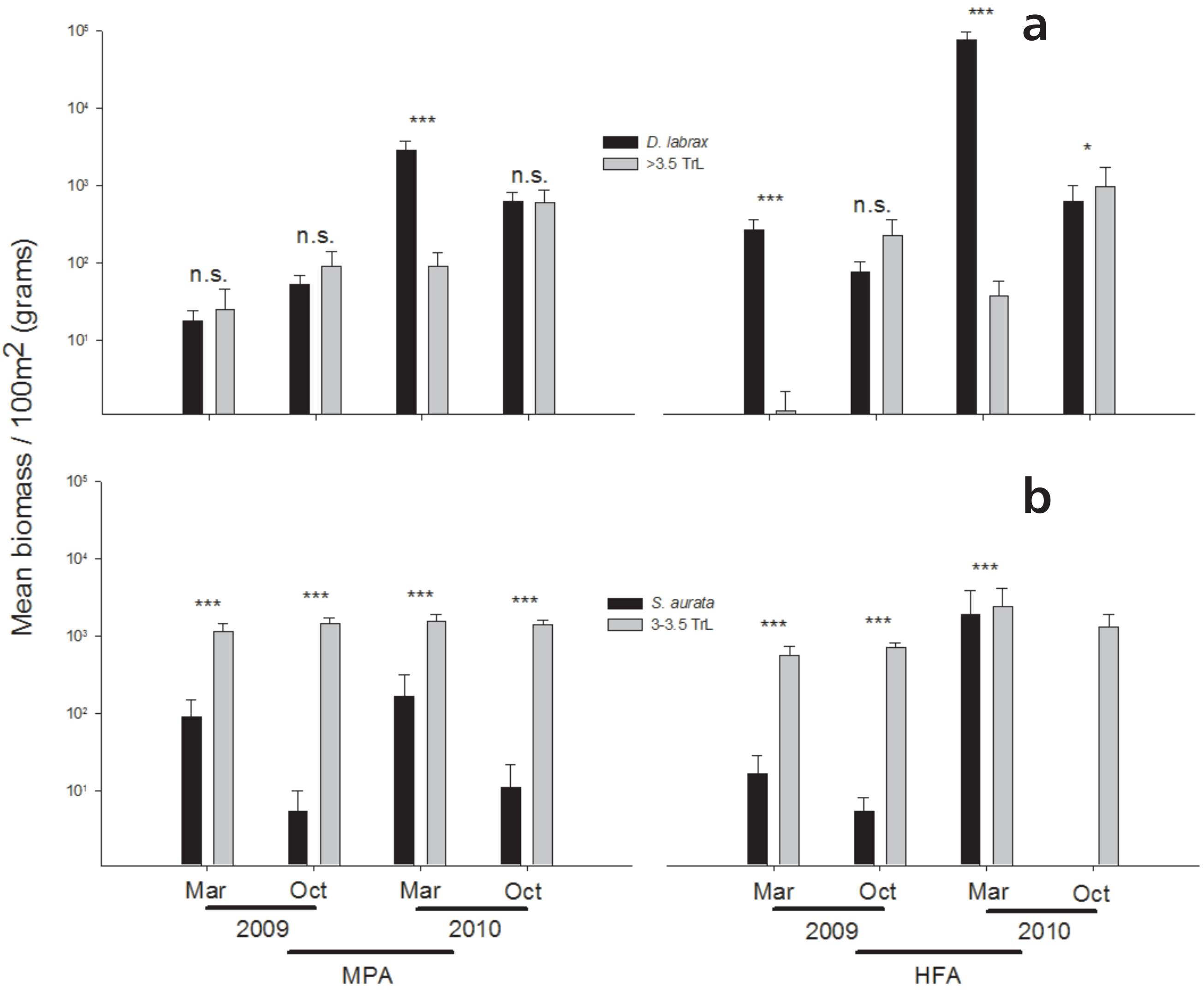

Figure 6.4. Mean biomass (± SE) of both escaped (a)sea bass and (b) sea bream (black bars) and other fish species with similar trophic level (grey bars) at MPA and HFA through sampling periods: n.s.: not significant, *: $p<0.05$, **: $p<0.01$, ***: $p<0.001$. Note the logarithmic scale in 'y' axis.

6.3.3 Spatiotemporal patterns

Permutational ANOVA did not detect differences in $mTrL_0$ (i.e. the mean trophic level removing the escaped fish of the data) for any of the main factors (Table 6.2; Fig. 6.5a). Regarding ΔTroph the interaction *Protection* x *Season* was significant, which prevented further interpretation of the significant main factor *Season* (Table 6.2). Pair-wise test showed that the interaction consisted in a differential response of ΔTroph in MPA and HFA. When periods were compared ΔTroph was higher in March than in October for HFA localities ($p=0.033$; Fig. 6.5b), at localities situated in the MPA there were no differences in ΔTroph between seasons ($p=0.0978$; Fig. 6.5b). Finally, the analysis detected spatiotemporal patterns of mTrL (i.e. mean trophic level taking into account escaped fish), these patterns consisted in higher mTrL in 2010, during March season and at HFA localities when they are compared to 2009, October season and MPA localities respectively (Table 6.2; Fig. 6.5c).

6.3.4 Use of trophic resources

Table 6.3 shows the diet composition and importance of each prey for the two groups of sea bass analysed. For the leak group (Table 6.3a), fish was the main prey group, followed by crustaceans, being the rest of the prey groups listed as accidental. It is remarkable that only one individual was found with pellets in the stomach. Lower prey diversity is observed in sea bass associated with massive escape (Table 6.3b). In this case, the main prey group was crustaceans; being the most preferred the decapod *Percnon gibessi*. Regarding the vacuity index, leak group had a 33.9% of empty stomachs, while the massive group showed a 12.5%.

MDS indicated that sea bass associated with massive escape in La Palma had different diet in comparison to the leak group (Fig. 6.7a.). The ordination responds to the importance of the three prey groups in the diet of each individual (Fig 6.7bcd). The group denoted as massive is situated in the area where crustaceans are the main item by weight in the stomachs. Permutational ANOVA confirms that sea bass of the leak and massive groups had differing diets ($p<0.001$), irrespective of their sizes (TL), but size resulted in an important variable when explaining the diet of escaped sea bass ($p<0.001$; Table 6.5).

Table 6.2. Univariate permutational ANOVAs, exploring spatiotemporal patterns of $mTrL_0$, ΔTroph and mTrL. Dashed line separates covariates from factors. In bold those p-values<0.05 for covariables, fixed factors and their relevant interactions.

		$mTrL_0$			ΔTroph			mTrL		
Source	**df**	**MS**	**Pseudo-F**	**P(perm)**	**MS**	**Pseudo-F**	**P(perm)**	**MS**	**Pseudo-F**	**P(perm)**
Distance	1	3.5805	5.0294	0.0792	1.3304	11.056	**0.0254**	0.55073	1.821	0.2614
Cliff	1	5.46E-02	0.20532	0.662	0.57703	6.8831	**0.0104**	0.27806	1.2067	0.28
Rocky Platform	1	0.55518	2.1957	0.1536	1.0669	12.353	**0.0004**	3.1525	13.589	**0.0002**
Sand	1	0.98259	4.6006	**0.032**	1.862	22.315	**0.0002**	5.5289	24.929	**0.0002**
Small Boulders	1	1.5349	5.7576	**0.0202**	0.55336	6.5897	**0.0108**	3.9254	17.01	**0.0002**
Medium Boulders	1	2.26E-02	0.10718	0.7412	9.71E-02	1.189	0.2682	2.8459E-2	0.13004	0.7116
Big Boulders	1	3.68E-02	0.17195	0.6786	1.41E-02	0.16861	0.6718	4.472E-3	2.012E-2	0.8938
Year	1	0.61579	7.1379	0.0512	3.137	6.924	0.06	6.5392	8.8445	**0.037**
Period	1	3.68E-03	3.29E-02	0.869	3.8887	34.688	**0.0036**	3.6593	27.253	**0.0074**
Protection	1	2.3992	4.0159	0.1108	0.51676	5.3362	0.0712	5.1611	15.583	**0.0132**
Locality(Pr)	4	0.49247	1.4696	0.2768	8.53E-02	0.39805	0.8028	0.26773	0.6316	0.657
YexPe	1	4.07E-03	4.01E-02	0.8524	0.92145	1.9679	0.231	0.8016	1.4114	0.2822
YexPr	1	0.18498	2.186	0.214	0.35071	0.7602	0.4366	1.054	1.4018	0.3066
PexPr	1	0.10742	0.98393	0.3784	1.1766	10.318	**0.029**	0.57365	4.253	0.1064
Site(Lo(Pr))	11	0.33972	2.0872	0.0228	0.2184	3.6946	0.0002	0.43044	2.394	0.0054
YexLo(Pr)	4	8.31E-02	0.32328	0.85	0.45764	3.9081	0.03	0.74504	1.9828	0.1684
PexLo(Pr)	4	0.10866	0.3679	0.8428	0.11214	1.6934	0.2148	0.13209	0.55836	0.6998
YexPexPr	1	0.11371	0.61619	0.4762	2.13E-03	4.95E-03	0.9468	8.5754E-2	0.15291	0.719
YexSi(Lo(Pr))	12	0.25759	1.5826	0.092	0.11684	1.9766	0.0274	0.37504	2.0858	0.018
PexSi(Lo(Pr))	12	0.29586	1.8177	0.0462	6.61E-02	1.1184	0.336	0.23687	1.3174	0.2008
YexPexLo(Pr)	4	0.18443	0.96185	0.4548	0.4673	2.851	0.0738	0.56443	1.7826	0.198
YexPexSi(Lo(Pr))	12	0.19147	1.1764	0.3	0.16216	2.7433	0.0006	0.31401	1.7464	0.0578
Res	354	0.16276			5.91E-02			0.1798		
Total	431									

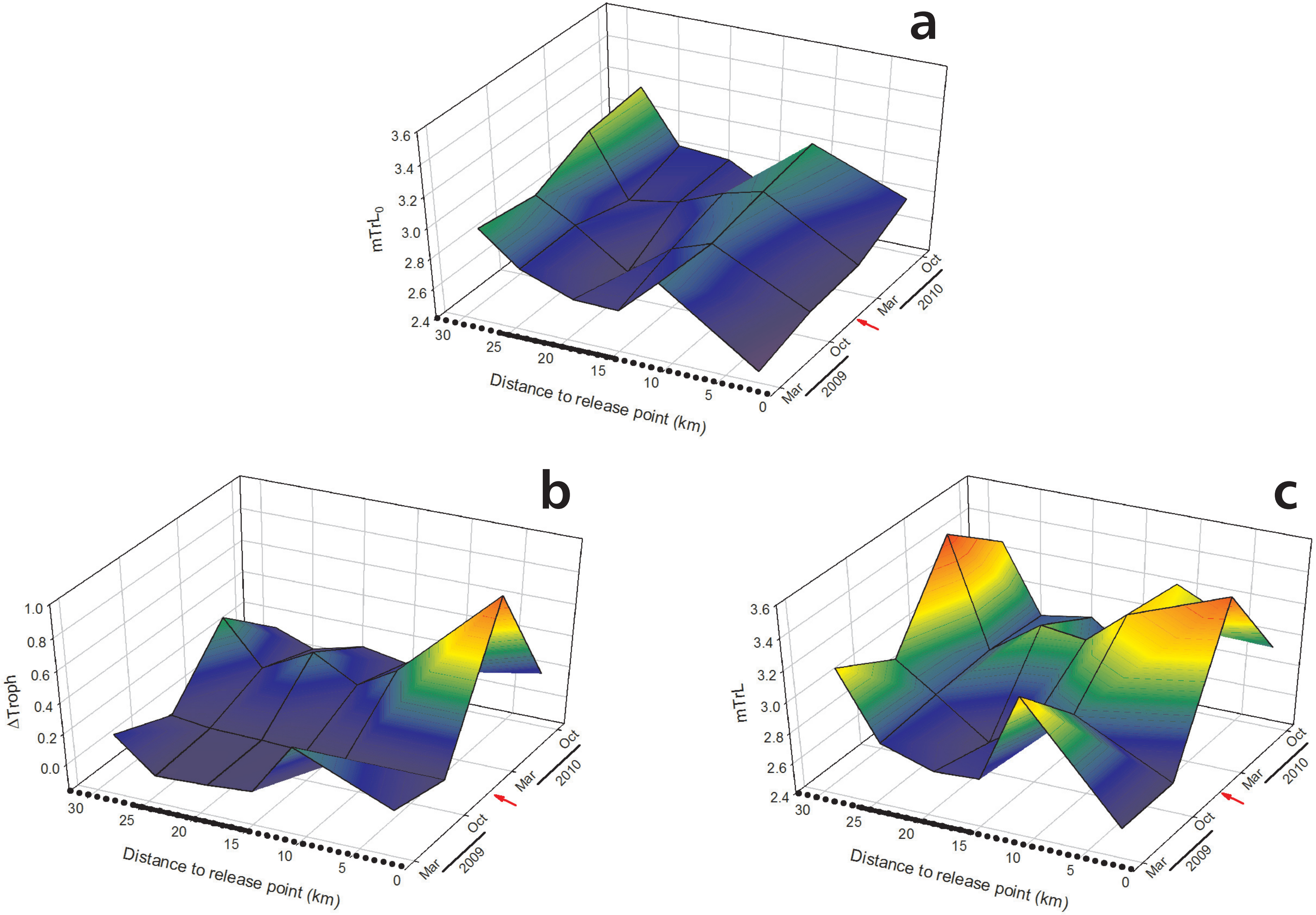

Figure 6.5. 3-dimensional plot of $mTrL_0$, ΔTroph and mTrL at locality level through sampling periods. Black line in ‘x’ axis covers the MPA, dotted line HFA. Red arrow points when the massive escape event occurred.

Table 6.3. Diet composition of the (a) 'leak' and (b) 'massive' escaped *Dicentrarchus labrax*.

n=112
Vacuity=33.9%

a

Prey	***N*%**	***W*%**	***O*%**	***Q***	**IRI**	**Prey preferences**
Fish	62.9	76.4	54.1	4803.2	7528	**Main preferred prey**
Atherina presbyter	2.4	0.4	4.1	1.0	11	
Sparisoma cretense	1.0	7.0	2.7	6.6	21	
Thalassoma pavo	1.4	10.3	2.7	14.7	32	
Scorpaena sp.	0.5	4.7	1.4	2.2	7	
Trachinus draco	0.5	5.7	1.4	2.7	8	
Sardinella aurita	33.3	23.9	5.4	795.7	309	
Unidentified fish	23.8	24.5	36.5	582.6	1762	
Crustaceans	14.3	5.1	32.4	73.4	630	**Secondary common prey**
Percnon gibbesi	1.0	2.9	2.7	2.7	10	
Plagusia depressa	0.5	<0.01	1.4	<0.01	1	
Pachygrapsus sp.	2.9	0.2	2.7	0.6	8	
Xantho sp.	0.5	0.1	1.4	<0.01	1	
Unidentified crustaceans	9.5	1.9	27.0	18.5	310	
Mollusks	2.4	0.8	4.1	1.9	13	**Accidental prey**
Cephalopoda	1.9	0.8	2.7	1.5	7	
Gastropoda	0.5	<0.01	1.4	<0.01	1	
Insects	10.5	0.7	28.4	7.4	317	**Accidental prey**
Blattaria	0.5	0.3	1.4	0.2	1	
Hymenoptera	1.9	<0.01	5.4	<0.01	10	
Coleoptera	0.5	<0.01	1.4	<0.01	1	
Unidentified insects	7.6	0.4	21.6	2.7	173	
Plants						
Cymodocea nodosa	1.9	1.3	5.4	2.4	17	**Accidental prey**
Mammals						
Rattus norvegicus	0.5	1.4	1.4	0.6	2	**Accidental prey**
Pellets	1.0	10.3	2.7	9.8	30	**Accidental prey**
Other Items	6.7	4.1	17.6	27.1	189	**Secondary common prey**

n=32
Vacuity=12.5%

b

Prey	***N*%**	***W*%**	***O*%**	***Q***	**IRI**	
Fish	2.7	0.1	3.6	0.4	10	**Accidental prey**
Unidentified fish	2.7	0.1	3.6	0.4	10	
Crustaceans	89.2	80.1	100.0	7142.7	16927	**Main preferred prey**
Percnon gibbesi	45.9	57.3	42.9	2634.0	4426	
Eriphia verrucosa	2.7	10.0	3.6	27.0	45	
Unidentified crustaceans	40.5	12.8	53.6	518.1	2856	
Other Items	5.4	1.2	7.1	6.5	47	**Accidental prey**

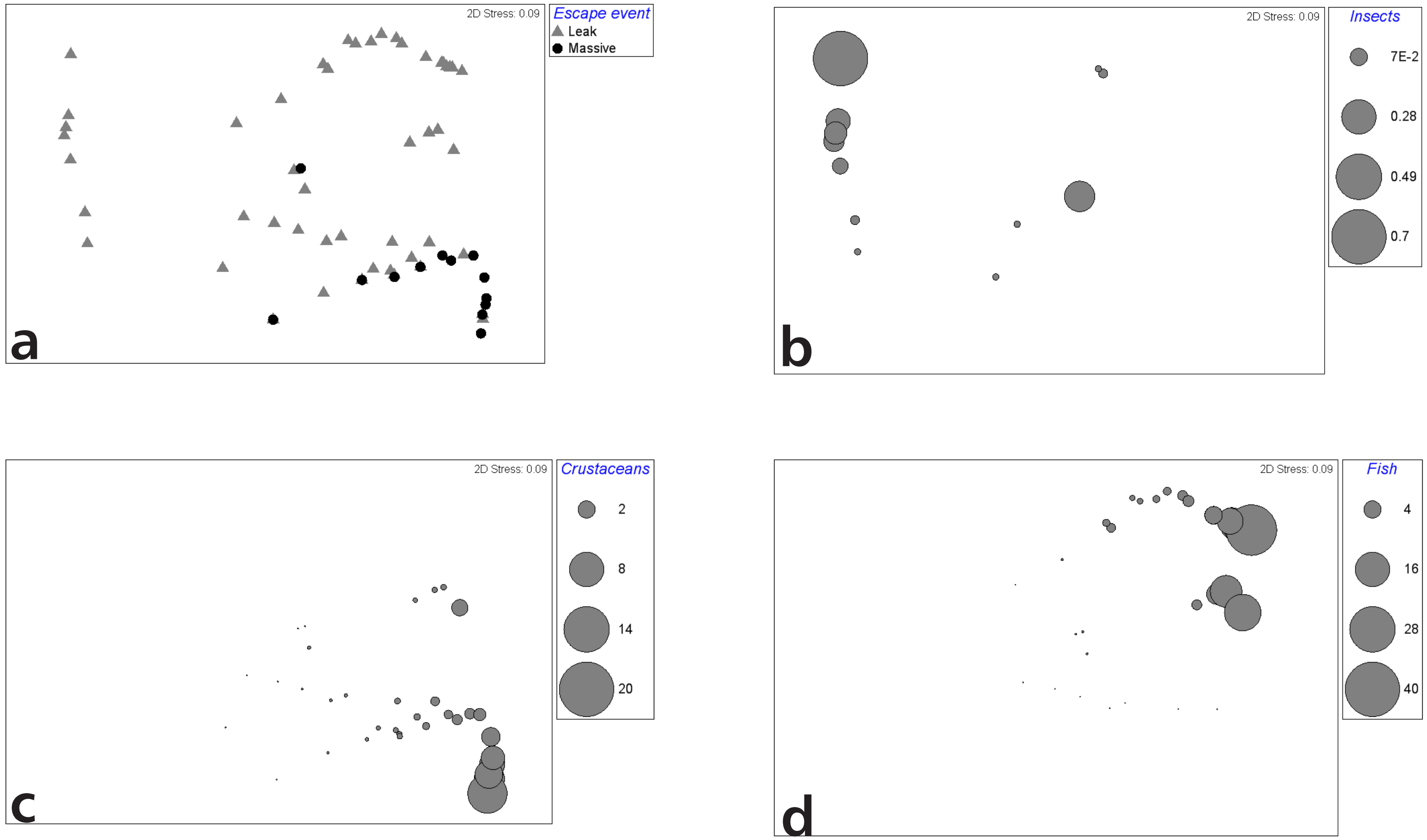

Figure 6.6. MDS plot showing the ordination of sea bass individuals by diet according to their (a) origin, and by weight of each group of preys: (b) insects, (c) crustaceans and (d) fish.

Table 6.4. Permutational ANOVA results comparing the diet of sea bass escaped in leak and massive events, including total length as a covariable. In bold those p-values<0.05.

Source	df	SS	MS	Pseudo-F	P(perm)	Unique perms
Total Length	1	16215	16215	3.7429	**0.0001**	9897
Leak vs. Massive	1	19094	19094	4.4076	**0.0001**	9898
Res	95	4.12E+05	4332.1			
Total	97	4.47E+05				

6.4 Discussion

A 'farming-up' effect due to the input of HTL fish by aquaculture is observed in this study. The presence of escaped fish raised mTrL of fish assemblages in shallow coastal waters of La Palma. This alteration was exacerbated by the massive escape, which also changed the size frequency distribution of escaped individuals in the wild. The MPA showed resilience to alterations in mTrL based mainly upon a higher abundance of herbivorous fishes that prevented the rising of mTrL. However, the temporal patterns of mTrL changes were similar at both MPA and HFA. This reflects that the potential negative effects caused by the input of HTL species could affect both areas equally. Additionally, escaped fish exploited natural resources according to their total length and time at liberty. These findings highlight the need for continuous monitoring of leak escapees, comprehensive emergency plans for massive escape events and adaptive management of nearby protected areas to avoid negative deleterious effects in shallow coastal ecosystems.

A clear increase in mTrL is observed due to the escaped fish. However, these alterations are related to the direct presence of escapees and not other effects such as trophic interactions or interspecific competition. Escapees have a TrL well above the mTrL of native fish assemblages found in shallow coastal waters in the area, thus, their presence leads to a rise in this indicator. mTrL and its alterations are influenced by environmental variables, which in turn drive the diversity and abundance of fish. For example, in sandy bottoms, where fish assemblages are scarce (Tuya *et al.*, 2005), the presence of escapees generates a great increase in mTrL. No negative or positive correlations were found between number of escapees and abundance of other fish species. However, an increased mTrL maintained through new escapees may, in the mid and long term, cause negative consequences through predator-prey interactions and cascade effects. Some studies have detected these kind of interaction due to the input or removal of predators in semi-closed marine systems (Ojaveer *et al.*, 2004; Casini *et al.*, 2008, 2009, 2012). We cannot define oceanic islands such as La Palma as semi-closed systems, where these processes are more prone to occur. However, the bathymetric characteristics of the Island are defined by a clear absence of coastal shelf, reaching 200 m depth not far from the coast line and surrounded by bottoms of 2,000 m depth (Acosta *et al.*, 2003). Thus, shallow bentho-demersal fish assemblages are restricted to areas near the coast, adult fish having a limited range of movements. Therefore, this is a case where the source of potential impact spreads around the Island but stays close to shore concentrating their effects in a reduced space (González-Lorenzo *et al.*, 2005; Toledo-Guedes *et al.*, 2009).

Size frequency distribution of escapees was altered by the massive input of big-sized individuals into the wild between 2009 and 2010. However, as technical reports have indicated (Ramírez *et al.*, 2011), small individuals were also released. Size of release could be a major factor influencing subsequent survival rate of escaped fish, as suggested for cod in Norway (Serra-Llinares *et al.*, 2013). Cannibalism behaviour of sea bass, especially when big individuals are mixed with small ones (Katavic *et al.*, 1989), in addition to increased predation or natural mortality of smaller sizes, could explain prevalence of larger individuals in the wild.

Regarding the resilience to changes in mTrL observed off localities situated in the MPA, it reflects how conservative this index is. The overall fish abundance has not a great effect on it, for instance $mTrL_0$ was similar in MPA and HFA. However, it is more sensible to the input of HTL species in highly impacted areas as HFA where fish abundance and diversity is impoverished (see appendix). Another reason for this relays on a higher abundance of herbivorous (i.e. low trophic level) species in the MPA. Owing to the protection against fishing, an increment of predators of the barren-ground founder sea urchin *Diadema africanum* (Rodríguez *et al.*, 2013) have been observed; subsequent depletion of the latter and further recovery of erect algae together with herbivorous fish species is a well-studied trophic cascade effect (Sangil *et al.*, 2012). Thus herbivorous biomass 'pulls down' the mTrL maintaining it at relative low levels despite the MPA is equally affected by the presence of escaped fish (Toledo-Guedes *et al.*, in press b; Chapter 5).

Sea bass has become the most abundant predator in shallow coastal waters (between 1 and 5 m depth) in La Palma (this study) and in those islands where sea bass is cultured (pers. obs.). Even in areas such as the MPA, where fish assemblages are supposed to be best preserved and abundances of top predators reach maximum (Newman *et al.*, 2006). Escaped sea bass outnumbers in biomass other medium-high trophic level species. Similar results have been indicated in other areas where top predators have been introduced; as *Cephalopholis argus* and *Lutjanus kasmira* in Hawaii (Friedlander *et al.*, 2002; Dierking, 2007) or the red lionfish (*Pterois spp.*) that is now established and in rapid expansion in the western North Atlantic (Whitfield *et al.*, 2002; Schofield, 2009). Nonetheless, the success of these invaders is based upon their ability to complete their life-cycle in wild habitats. Populations of escaped fish are strongly dependent on new escapees in the Canaries (Toledo-Guedes *et al.*, 2009, 2012). It is necessary to remark that our results are valid in the depth strata we have studied (i. e. very shallow coastal waters), where a large proportion of escaped fish are found (Toledo-Guedes *et al.*, 2009) and top predators are not common. In the case of escaped sea bream, their abundances in the surveyed areas are not as high, and fish species of their 'trophic surroundings' are well represented by several species, mainly sparids.

Functional diversity (*sensu lato*) is an indicator of ecosystem health and function (Clemente *et al.*, 2010) and has been suggested that it could prevent the insertion of non-indigenous species in recipient ecosystems (Stachowicz *et al.*, 1999). In this sense, the lack of top predators in the surveyed areas could favour escaped sea bass (avoiding competition and predation), while abundance of sparids could prevent the success of escaped sea bream in the wild. Nonetheless, a lower escape rate, together with a naive behaviour that could increase natural and fishing mortality are other plausible reasons for a lower abundance of sea bream escapees (Arechavala-Lopez *et al.*, 2012c; Toledo-Guedes *et al.*, submitted).

Our data on the diet of escaped sea bass supplement those previously published (Toledo-Guedes *et al.*, 2009). The results obtained for the individuals not associated to any known massive escape (leak group) are in line with the mentioned study. On the other hand, the diet of sea bass associated with the massive escape markedly differs to the leak group in several aspects (e.g. lower percentage of vacuity, lower diversity of preys and different diet composition). Even though the number of studied stomachs is limited, vacuity percentage was very low for the massive group. This indicates that six months after the massive escape event, surviving escapees were able to actively exploit available resources in natural habitats as the MPA. All the non-empty stomachs presented crustaceans remains, and half of them were of *Percnon gibbesi*, an abundant species in shallow coastal waters of the Canaries (González, 1995). Many studies have pointed to the onthogenic changes in diet suffered by sea bass in their natural range of distribution (Kelley, 1987; Rogdakis *et al.*, 2010 and

references therein). In extensive cases, we can say that small sea bass (<30cm TL) often prey over insects and small crustaceans, preferably in recruitment areas situated in the entrance of rivers. Medium-sized individuals (30-50 cm TL) prey over prawns and shrimps, and big individuals (>50 cm TL) show a mixed diet of large crustaceans as crabs and fish (Kelley, 1987; Rogdakis *et al.*, 2010). Actually, our results support the importance of fish's total length in its diet, and highlight the evidence that domestication of cultured sea bass does not entail difference in trophic behaviour in natural habitats, in comparison to their wild counterparts. Nonetheless, in the case of escapees, release size and time at liberty could be major factors explaining of observed diet. A feasible explanation to this is the requirement of a 'hunting learning' period during the first weeks in the wild, which has been suggested by other authors (Arechavala-Lopez *et al.*, 2012c).

6.4.1 Final recommendations

Despite constraints related to ethical and environmental issues, exotic species contribute about 17% to global aquaculture and will become increasingly important (Shelton and Rothbard, 2006). Thus, for a correct development of aquaculture industry, the need of risk assessment plans grounded on empirical data is clear. It is urgently required to implement them, having special care when aquaculture facilities are situated near sensible areas (e.g. MPAs).

Taking into account the high mobility of the escapees, remediation through regular eradication actions with highly selective fishing techniques (e.g. spearfishing) seems unaffordable in terms of costs. However, since natural and fishing mortality apparently control abundances of escaped fish (Toledo-Guedes *et al.*, in press b), eradication efforts should be centred in valuable areas as MPAs. Adaptive management of these areas would allow the prevention of future damages caused by escapees. Nonetheless, this would not be applicable to other regions (e.g. Mediterranean), where wild counterparts cohabit with escapees because most of the time, wild and escaped fish can only be differentiated after being caught (Arechavala-Lopez *et al.*, 2013a).

With this study we propose a further dimension of the concept 'farming-up' related not only to a rise in the trophic level in aquaculture (as presented by Stergiou *et al.*, 2008) but also a rise of mTrL of wild fish assemblages, due to the input of farmed fish. If we scale up the issue, the need for studies at wider spatial scales (e.g. Mediterranean) arises.

‘Farming-up’ may work in opposition to the well-studied ‘fishing-down’ described by Pauly *et al.* in 1998. Nonetheless, far from being a solution to the latter, the human-mediated rising of mTrL through aquaculture escapees could have negative consequences for marine ecosystems. A likely grow in aquaculture production worldwide, together with a concentration on a few proven species (several of which would be exotic or locally absent) may lead to a homogenization of fish assemblages. If aquaculture industry wants to lead the way to a sustainable production of proteins there is a need for a precautionary approach, since the detection and further restoration of negative impacts in coastal waters are extremely difficult.

CHAPTER 7

General Discussion

Throughout this thesis it has been shown that aquaculture activities have expanded *D. labrax* range of presence to islands where it was absent. A non-negligible number of escaped sea bass are able to survive in the wild, adapting to natural conditions (i.e. becoming feral) and interacting with wild assemblages and fisheries. Actually, feral sea bass was the most abundant predator in the surveyed areas (between 1 and 5 m depth around La Palma and Tenerife) and during the period of the study (from 2007 to 2010), including the studied MPA. This is the result of continuous release of farmed fish and is expected to remain unaltered as long as aquaculture activities continue.

7.1 Aquaculture-mediated range expansion of sea bass in a context of climate change

The natural distribution of sea bass in the Canaries is closely related to water temperature (Brito *et al.*, 2002). An east-west gradient of sea surface temperature is observed due to the up-welling system that brings cold water into the eastern part of the Archipelago (Barton *et al.*, 1998). This generates differences in temperature of up to 3ºC when we compare western and easternmost islands. At the same time, cold waters along the African coast allow sea bass to reach southern localities, they also permit them to maintain small wild populations off Lanzarote and Fuerteventura.

Climate change is predicted to raise sea surface temperature by an average of 1.5-3 ºC in the region by 2090 (IPCC, 2007), and is already causing the tropicalization of fish fauna (Brito *et al.*, 2005). Therefore, a northwards shift of the sea bass southern limit would be expected, together with an extension of its range in northern latitudes, that has already been detected (Bagdonas *et al.*, 2011).

Aquaculture has introduced large numbers of sea bass (a temperate species) around islands where it was absent (La Palma, Tenerife and Gran Canaria; see section 1.8). Thus, it has promoted an unexpected range expansion of sea bass into warmer waters of the Canaries. The depth between islands, that can reach 2,000 m, could be a factor preventing further spreading of farmed fish to islands where aquaculture is not established yet. Actually, restocking actions in the Balearic Islands showed that released fish stayed in coastal waters of the same island of release (Valencia *et al.*, 2008). Nonetheless, first records of farmed fish (both sea bass and sea bream) off La Gomera and El Hierro, where no aquaculture facilities exist, have been recently communicated (R. Herrera, A. Espinosa and J. R. Docoito, pers. comm.). A plausible explanation could be post-escape erratic swimming behaviour, which can occasionally lead escapees to cover long distances, especially after massive escape events, when they are aggregated in big shoals (González-Lorenzo *et al.*, 2005). On the other hand, the presence of individuals at those islands could be the result of the establishment of self-sustainable populations and further spreading of individuals during larval stages, which would represent part of an invasion process (Elton, 1958). Likelihood of reproduction in the wild is further discussed (see section 7.3.6), but in the period covering this study, sea bass populations seemed to rely upon the input of new escapees.

7.2 Extent of the problem

To assess the number of farmed fish that are entering wild ecosystems is crucial to visualize and understand the issue of escaped fish. Pioneering countries are Norway, Scotland, where it is compulsory to report all escape events since 2001, and Ireland since 1996 (Walker *et al.*, 2006; Jensen *et al.*, 2010; Green *et al.*, 2012a). Yet the number of escapees is thought to be underestimated, as not all escape events are reported (Jackson *et al.*, 2013). In any case, few countries have a comprehensive system to gather and analyse the number of escaped fish entering the wild (Jensen *et al.*, 2010), which reflects the global need of policies in such direction.

The sparse data on massive escape events occurring in the Canary Islands in the period 1998-2009 (Table 1.1) have allowed a rough calculation of the total amount (in tonnes) of escaped fish during those years. If total production is taken into account (Fig. 1.5) then the percentage of escaped fish per species is revealed: 5.26% of sea bass, 3.41% of sea bream and 1.25% of meagre produced in the Canary Islands escaped into the wild. Two sources of bias can be found in these figures. Firstly, the mean rate of escape for 1998-2009 does not reflect possible improvements in materials, designs and management of fish cages. Thus, these percentages would be expected to be lower nowadays. However, escape rates are probably underestimated because again not all the massive escapes are registered locally. Additionally, small recurrent escapes, that can mean 1% of the total biomass in culture each month (Jackson *et al.*, 2013), could clearly increase the escape rate.

Providing that fish can escape at any size and reared stock usually weigh between 50 g and 1 kg, number of escapees can be extrapolated setting the mean weight of escaped fish at 0.5 kg. In that case nearly 200,000 sea bass and the same amount of sea bream were released into the wild each year from 1998 to 2009. In the case of meagre, biomass release during the period it was farmed (2003-2010) represented 3,750 individuals per year. It is noteworthy that all the escape events related to technical failures during storms occurring between November and February (i.e. winter) and only two escape events in summer due to a boat collision and sabotage, respectively. This reinforces the hypothesis of a higher winter release presented in Chapter 5.

Restocking and stock enhancing would be the only actions comparable to escape events. Their aim is to restore depleted fish stocks or enhance those still 'healthy' by controlled release of tagged hatchery-raised fish (Blankeship and Leber, 1995). During the last years it has been questioned whether restocking and stock enhancing are a help or a harm for wild fish populations (reviewed in Araki and Schmid, 2010). In Spain, several pilot studies have been carried out for stock enhancement of sea bass, sea bream and meagre. In the Bay of Cádiz, 30,323 sea bream individuals ranging from 316 to 854 g were released between 1993 and 1997 (Sanchez-Lamadrid, 2002). In the Balearic Islands, 2,572 sea bream with a mean weight of 0.5 kg were released in 2001-2002 (Valencia *et al.*, 2008). In the same Islands, a total of 15,000 meagre individuals have been released from 2008 to 2012 (CSIC, 2012) and there are reports of restocking actions where 400 individuals of sea bass of 120 g weight were released in Palma de Mallorca MPA. Given these figures, it is clear that escape events largely surpass restocking actions in numbers released and must be carefully studied as their effects are unknown. Successful reintroduction programmes suggest that capacity for readaptation can be maintained and that sufficient initial fitness combined with high release numbers can kick-start the feralization process (Philippart, 1995; Young *et al.*, 2002)

7.3 Performance of escaped sea bass in the Canary Islands

How do escaped sea bass manage in the wild? This is one of the questions that this Ph.D. thesis tries to assess. For this, sea bass was studied at individual and population level (Fig. 7.1). Different individual traits (most of them functional traits *sensu* Violle *et al.*, 2007) are combined into performance traits that finally are a proxy of escapee fitness during the

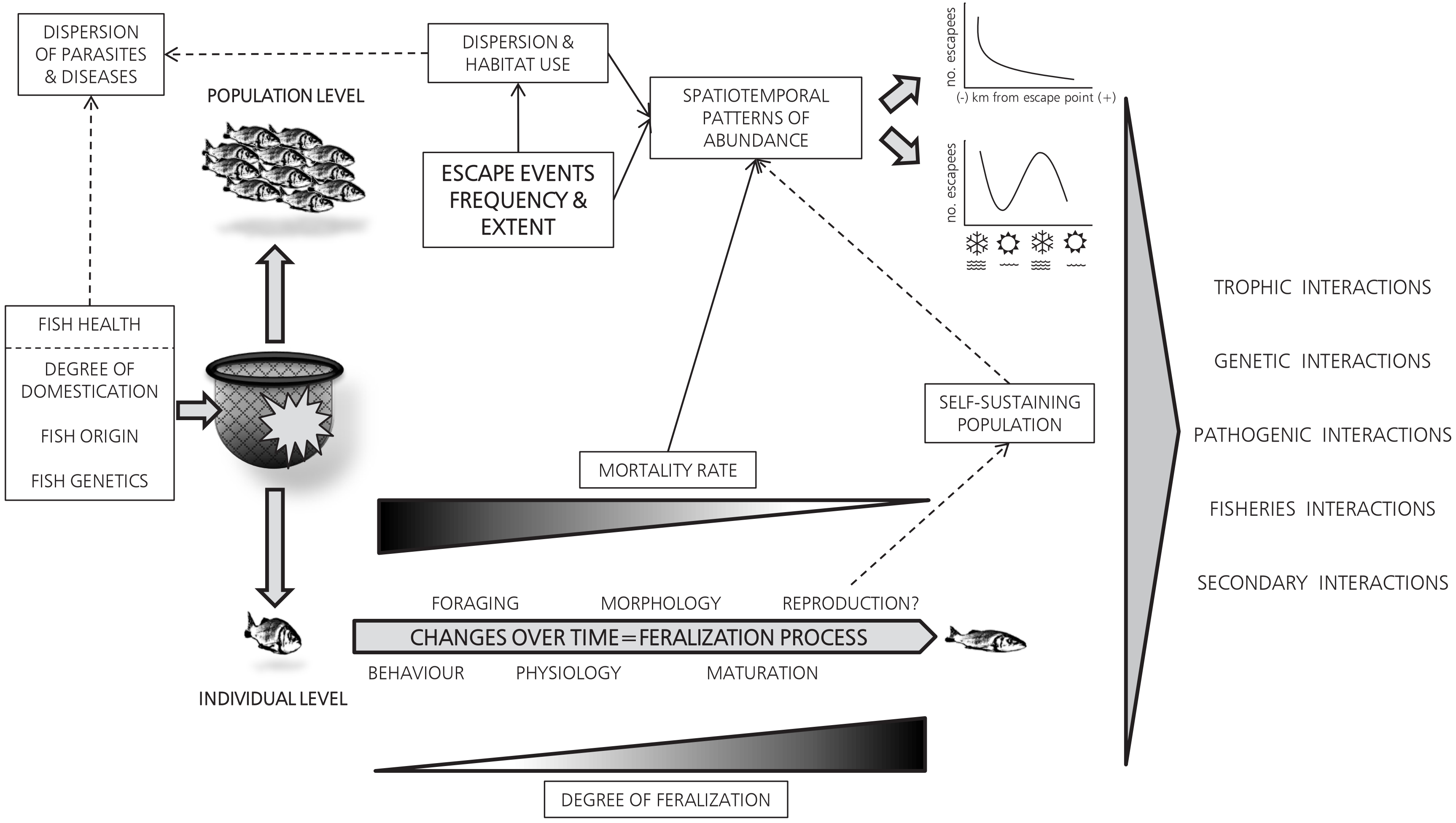

Figure 7.1. Conceptual model of escaped sea bass performance in the Canary Islands.

feralization process. In addition, population is studied through demographic traits that, in the case of escaped fish, are strongly linked to the extent and frequency of escape events and mortality rates (Fig. 7.1). Depending on the performance at individual (i.e. fitness) and population level, a series of potential (and detected) interactions arise. When no direct measurements of a specific trait or interaction were made (e.g. mortality, behaviour, genetic interactions), the most important outcomes of other studies in the Canaries and other regions and species are discussed.

7.3.1 Mortality

Most of the success of an escaped fish relies on its ability to survive the first days/weeks after the escape event. Different studies on restocking actions point to the high post-releasing mortality rates of farm origin fish (Olla *et al.*, 1998; Skaala *et al.*, 2012). In the case of escaped salmon, a study carried out after a massive escape in Chile revealed that the highest rate of mortality ($Z=1.2$) was the best predictor of actual abundance of escaped fish (Soto *et al.*, 2001). Studies on sea bass carried out in the Mediterranean (Arechavala-Lopez *et al.*, 2011; Grati *et al.*, 2011) equally suggest high mortality rates of tagged sea bass released into the wild. There is no reason to think mortality rates are different in the Canaries, and surely they are high.

Authors agree in suggesting that post-escape mortality is density and size-dependent (Pitcher, 1986; Kristiansen *et al.*, 2000). Additionally, the incidence of the different sources of mortality depends on individual phenotypic and genetic characteristics, acquired or selected in rearing conditions (Lorenzen *et al.*, 2012 and references therein). This is supported by studies under controlled conditions where farmed and wild sea bass juveniles were exposed to avian predation (Handelsman *et al.*, 2010). These authors found that the factor that best predicted survival of farmed sea bass was growth rate during the previous interval. Interestingly, in this case, a typical trait selected for farmed fish (as it is fast growing) could favour survival in wild conditions. Given the large inputs of fish through escape events (in the order of hundreds of thousands in the Canary Islands) the question may not be the mortality rates of escaped fish, known to be high, but how many of the escapees are able to survive and interact in the wild. Four main sources of mortality can be identified regarding escaped fish:

Professional and recreational fisheries

These are a major factor controlling densities of escaped fish in the Canaries, in particular for massive escape events (Chapter 5). Escaped sea bass seems to be especially vulnerable during first weeks after escape as reported by professional and recreational fishermen as well as data from tagging-recapture experiments with sea bass (Grati *et al.*, 2011; Arechavala-Lopez *et al.*, 2011).

Wild predators

Fish cages are known to act as Fish Attraction Devices (FAD´s). The structural complexity and, above all, the input of feed in the form of unconsumed pellets attract large fish biomass (Dempster *et al.*, 2004). The presence of farmed and aggregated fish in turn attracts piscivorous species that find more foraging opportunities (Sanchez-Jerez *et al.*, 2011). In the surroundings of aquaculture facilities off the Canaries, several species that actively predate on fish have been recorded: *Coryphaena hippurus, Seriola spp., Pomatomus saltatrix, Acanthocybium solandri*, *Sphyrna spp.*, *Carcharhinus spp.*, *Tursiops truncatus* (Sanchez-Jerez *et al.*, 2011; pers. obs.). Predators around fish cages act as a first contingency barrier, especially for small escape events of few individuals. In cases of massive escape events (i.e. from thousands to millions of individuals) its effectiveness would be overcome. Once on the coast (see next section), shoaling behaviour, seen especially after massive escape events (pers. obs.), could reduce escapee mortality (Pitcher, 1986). Additionally, number of predated fish is directly related to predator abundance, which is known to be low in shallow unprotected areas of the Archipelago (Falcón *et al.*, 1996).

Cannibalism

Sea bass show cannibalistic behaviour when individuals of different sizes share habitat, even in aquaculture facilities where they are fed *ad libitum* (Katavic *et al.*, 1989). This scenario is likely to occur immediately after massive escape events when several cages are affected and fish of different sizes are liberated at the same time. For example, small sea bass (TL <20 cm) accounted for 50% of the escaped fish (Ramírez *et al.*, 2011) in the massive escape event in La Palma (Chapter 5 and 6), while during surveys they represented a mere 5.6% of the counted individuals (unpublished data). This would support the hypothesis of post-escape cannibalism-mediated mortality of small sized individuals, and the size-dependency of mortality. In case of combined sea bass/sea bream escape events, sea bass could also predate on sea bream as reported by professional fishermen.

Starvation

It has been suggested that failures in adaptation to exploit natural resources could be a major factor in mortality (Ramírez *et al.*, 2011). However, several studies have pointed to the resistance of sea bass to long periods of starvation (up to five months; Echevarría *et al.*, 1997), and that escaped fish can start to exploit natural resources in a few days after escape (Arechavala-Lopez *et al.*, 2012c). Our vision is that starvation could explain a reduced fitness that eventually raises the likelihood of being predated or their catchability by fisheries, but the absence of mass mortality after large escape events rules out starvation as an important mortality source itself.

7.3.2 Dispersion

Post-escape dispersion of fugitive fish will determine the spatial extent of the escape event, this knowledge is particularly essential if recapture efforts are undertaken. Except in cases of massive escape events (Ramírez *et al.*, 2011), very few escaped individuals have been recorded around fish farms in the Canaries (Dempster *et al.*, 2005). This suggests that, soon after escape, fish reach shallow coastal waters near aquaculture facilities (González-Lorenzo *et al.*, 2005; Toledo-Guedes *et al.*, 2009). A feasible explanation to this is the absence of continental shelf around oceanic islands such as the Canaries (Hoernle and Carracedo, 2009). This geomorphological feature prevents escaped fish migration to offshore areas, since 100 m depth (the maximum sea bass is found at) is reached not far from the coastline (Acosta *et al.*, 2003). This also limits the location of floating fish-cages over bottoms of no more than 50 m depth, to facilitate maintenance operations. Thus, aquaculture facilities are situated very close to the coastline (0.2-1 km), which would facilitate the movement of escaped fish towards the coast. In contrast, the distribution of escaped fish in the Mediterranean could be less constrained since the continental shelf is wide in most parts of the coastline, and, consequently, aquaculture facilities can be placed several km away from the coast. Telemetry and external tagging studies have shown that some escaped individuals can stay in aquaculture facility surroundings several days but most of the escapees were recaptured in coastal areas

(Arechavala-Lopez *et al.*, 2011, 2012c). Other tagging experiments have also recorded post-release movements of farmed sea bass towards the coast in the Mediterranean (Grati *et al.*, 2011). Such behaviour could thus be expected, and may depend on local geomorphology.

Once in shallow coastal waters, distribution of escaped sea bass in the wild is strongly linked to the distance from source (i.e. aquaculture facilities; Chapters 2 and 5), that explains the abundance of sea bass on a scale of km. This showed a highly predictable pattern: exponential decay abundances are observed as we move away from aquaculture facilities (Figs. 2.4 and 5.3; Tables 2.3 and 5.1). This is compatible with high dispersion rates, as the combination of the latter with continuous 'leaking' and high mortality rates would result in the observed distribution pattern. The dispersion capacity of escaped fish seems to be enhanced when they move in big shoals (González-Lorenzo *et al.*, 2005). For instance, some weeks after the massive escape events in La Palma a shoal of 500 escaped sea bass approx. was observed 60 km from the escape point. As commented, this shoaling behaviour also reduces mortality rates, which would allow sufficient survival of escapees to reach distant zones. Without doubt, around those islands with aquaculture activities, farmed species are found along the entire coastline, from single individuals to large schools (González-Lorenzo *et al.*, 2005; Toledo-Guedes *et al.*, 2009; Ramírez *et al.*, 2011).

7.3.3 Habitat use

Habitat features are important in order to explain escapee abundance in shallow coastal habitats. Habitat use can be important in order to understand the impact on local communities and to concentrate eradication plans in areas where densities of escaped fish are higher. With this information their presence in valuable areas and habitats such as MPAs or seagrass meadows can be predicted. Feral sea bass in the Canaries are usually found in the first few metres of water (i.e. the surf zone), and they share this behaviour with their wild counterparts (Laffaille *et al.*, 2001). It seems that, at similar distances from the escape point, environmental variables (related to the substratum complexity) influence the distribution of escaped sea bass, which is found mainly in pebbles and mixed pebbles-sand habitats (Toledo-Guedes *et al.*, 2009; Chapters 2 and 5). Most clearly, at a scale of 100's of m the characteristics of the substratum set the likelihood of finding escaped sea bass in the wild. Pebbles and sandy are low-complex and highly-mobile substrate characterized by high turbidity. This condition could facilitate both protection against predators and provide better foraging opportunities, as suggested for their natural range of distribution (ICES, 2006).

It is also known that they visit seagrass, as some stomachs were found full of *Cymodocea nodosa* (Toledo-Guedes *et al.*, 2009; Chapter 2), but their presence there may be occasional given the absence of sea bass in surveys carried out in these vegetated areas (Tuya *et al.*, 2005; Espino *et al.*, 2011).

The present study has tried to assess the presence of sea bass in natural habitats off the Canary Islands. Therefore, human-created environments such as harbours and marinas have been avoided during the surveys. However, several reports and our own observations highlight the importance of this kind of artificial environment providing refuge to escaped fish (Toledo-Guedes *et al.*, 2009; Ramírez *et al.*, 2011; Arechavala-Lopez *et al.*, 2012c). Far from being altered behaviour of farmed fish, wild sea bass is resistant to some degree of pollution, often entering small harbours and marinas (Kelley, 1988) and is also attracted to artificial reefs (Fabi and Fiorentini, 1994). The harbours and marinas could act as protected locations, since recreational and professional fishing is usually limited, if not forbidden within them. Further dispersion from these points would partly explain the observed resilience of feral sea bass (Toledo-Guedes *et al.*, 2009) in wild habitats. Confirmation of this hypothesis can only be obtained through systematic surveys in human-created coastal habitats and tagging experiments.

7.3.4 Individual adaptation after escape

Success of escaped sea bass in the wild is intimately linked to the ability of escaped fish to adapt to environmental conditions; clearly different from that found in the fish cage (Brown and Laland, 2001, 2003; Chapter 3). Morphological, physiological and behavioural traits are driven by farming conditions (i.e. rearing traits) or chosen by selective breeding (i.e. commodity traits) in recently escaped sea bass. They therefore have to overcome the mismatch between their own farm-adapted traits and a highly unpredictable and complex habitat when they escape. Phenotypic plasticity allows those traits to change, and this occurs on different timescales depending on the trait (Lorenzen *et al.*, 2012):

Behaviour

The first challenge that escaped sea bass face is to lose their naive behaviour (Brown and Laland, 2001), namely to perform anti-predator and foraging skills. Farmed fish show more mobility and aggressiveness than their wild counterparts but are worse at foraging, resulting in high energy expenditure and low intake (Sosiak *et al.*, 1979; Ersbak and Haase, 1983), which result in a progressive fitness reduction. Recent experimental studies in sea bass also suggest that fish with high metabolic rates (i.e. more susceptible to hypoxia) and growth rates show more frequent boldness behaviours (Millot *et al.*, 2009ab). This would be translated into a higher likelihood of being predated (Killen *et al.*, 2012). Undoubtedly, anti-predator behaviour is evolutionarily more important than hunting, as showed by life/dinner principle: "the rabbit runs faster than the fox, because the rabbit is running for his life while the fox is only running for his dinner" (Dawkins and Krebs, 1979). Actually sea bass is quite tolerant to starvation periods, as we have mentioned before; consequently, escapees would have far more time to learn to hunt than to run away (i.e. they can fail hunting but not in running away from predators). Either way, authors agree in highlighting both as crucial steps for the success of farmed fish in the wild (Olla *et al.*, 1998; Brown and Laland, 2001, 2003). Changes in behaviour, together with environmental stimuli trigger further adaptations along a continuum that constitutes the feralization process during the lifetime of the animal (Daniels and Bekoff, 1989).

Morphology

There are two important post-escape alterations for fugitive fish, rearing environment and food regime. Both have been proven to be driving forces of fish morphometry, together with genetic influence (Costa *et al.*, 2010). Escaped sea bass suffers an elongation in the horizontal axis while a shortening in the vertical (see Chapter 3) if we compare them with farmed counterparts. This not happens only in the body but also in the head and even the size of the eye is affected by new conditions. Thus, the fish exhibit a more streamlined body shape that would be advantageous for good swimming performance and better acceleration rates (Benhaïm *et al.*, 2012; Vandamm *et al.*, 2012). Accordingly, morphology changes could improve survival by facilitating escape from predators and hunting highly mobile prey (i.e. fish).

Physiology

The escape event also poses physiological alterations. A more or less extended period of food deprivation is likely to follow (Toledo-Guedes *et al.*, in press a). As seen in rearing conditions, overweight sea bass mobilize lipids during the starvation period especially those in the liver and perivisceral fat (Pérez-Jiménez *et al.*, 2007). As a result, escaped fish show a lower hepatosomatic index and condition factor (K). Metabolizing farm-accumulated fat could aid in minimizing fitness reduction due to starvation (Echevarría *et al.*, 1997) and contribute to morphological changes like streamlining. Somatic growth is another physiological aspect subject to alteration after escape. A post-escape growth rate reduction is likely to occur in conditions of food deprivation (see review by Ali *et al.*, 2003). Compensatory growth after growth depression was detected in some of the escapees (Fig. 3.4). Growth rate was also more variable in escaped bass, an expected result since it has been detected in other species (Bernard and Myers, 1994). It reflects the passage from a constant supply of food in farm conditions to more unpredictable prey availability in natural habitats (Stokesbury *et al.*, 2001).

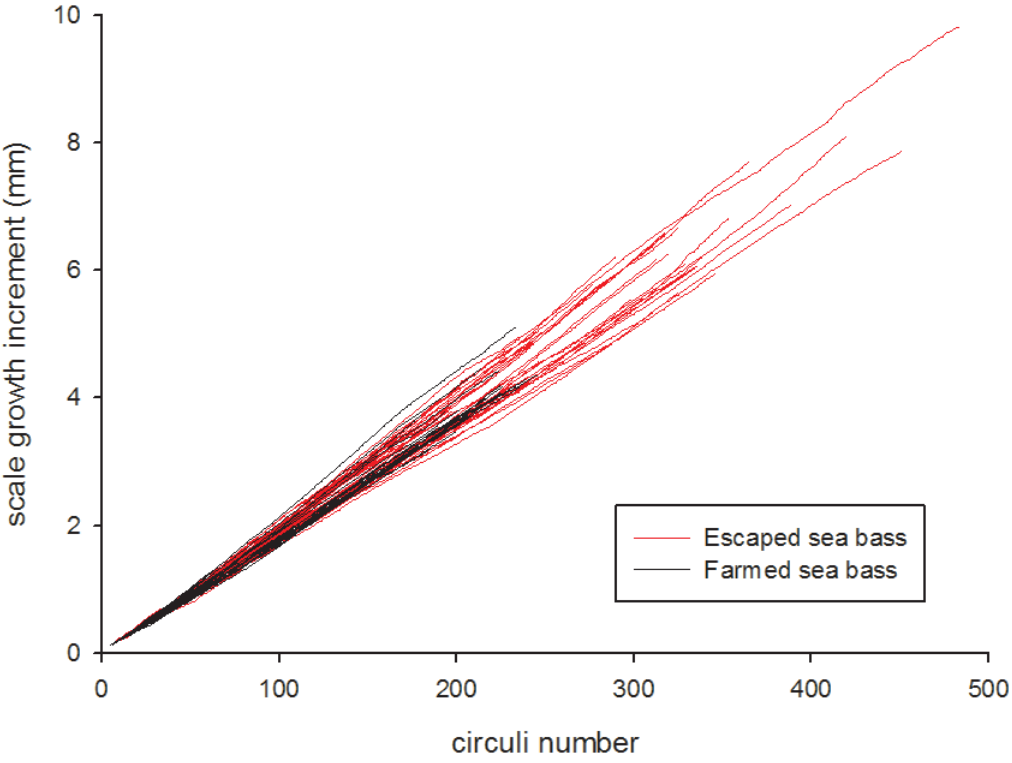

Figure 7.2. Individual growth profile in scales from escaped (red) and farmed (black) sea bass.

Either way, it can be concluded that those fugitives surviving in the wild grew as well as farmed fish did (Figure 7.2). This is an important finding as growth rate is a good proxy of the fitness and performance in fish (Bang, 2005). Arechavala-Lopez *et al.* (2012b) also found that wild sea bass grow as well as farmed counterparts do in the Mediterranean, this would indicate that aquaculture conditions promote growth in weight more than the somatic growth reflected in scales. But also could be due to the short period of sea bass breeding selection for growth traits (Haffray *et al.*, 2006). This would tone down the statements appearing in some technical reports suggesting that escaped fish seem 'malnourished' (Ramirez *et al.*, 2011; Ortega *et al.*, 2011). Weight-loss in an overweight fish is an expected result of the feralization process. Actually, the mean condition factor (K) of escaped sea bass in the Canaries (0.96±0.87), although more variable, was similar to that found for wild counterparts in the Mediterranean (1.03±0.12; Arechavala-Lopez *et al.*, 2012a) and lower than that of farmed fish in both areas (>1.5). General loss of weight the first four weeks after release has also been reported in sea bream stock-enhancement studies (Valencia *et al.*, 2008).

7.3.5 Trophic resources exploitation

Elucidating the diet of introduced predators can provide a better understanding of the ecological interactions they are disrupting and a fuller account of their potential impacts on biodiversity (Cucherousset *et al.*, 2012; Côté *et al.*, 2013). A total of 144 stomachs of escaped sea bass were analysed during this study. Of those, 29.2% were empty, which is consistent with other studies on wild bass diet (Rogdakis *et al.*, 2010). Sea bass are known to have a size-dependent diet, or which is the same, they suffer a trophic shift during their life-time (Kennedy and Fitzmaurice, 1972; Kelley, 1987; Rogdakis *et al.*, 2010). This shift consists in a higher importance of small crustaceans for smaller-sized bass while a prevalence of fish and large crustaceans is found for larger sizes (Rogdakis *et al.*, 2010). The same was found for feral sea bass in the Canaries (Chapter 6).

If we accept the need for a hunting learning-period then the size at which the fish escaped, time at liberty and actual size at capture are factors whose interactions will determine the observed diet. Our data support the existence of a learning period because oddities (i.e. plastic pieces, cigarette butts, remains of terrestrial plants, etc) were found in 7% of the stomachs with content. This would indicate that recently escaped bass are still looking for pellet-shaped food. Nonetheless, stomach content analysis also shows that the link between escaped fish and their aquaculture facilities of origin is weak. Only one individual was found with pellets in the stomach, probably because it escaped only a few hours before it was caught (Chapter 2 and 6). Another similarity with wild counterparts is that some escaped individuals have been found with stomachs full of seagrass (*Cymodocea nodosa*). Some authors suggest that it is due to a herbivorous behaviour trait (Fritsch, 2005), while we relate it to failed hunting attacks in vegetated areas (Chapter 2).

Diet also depends on the prey availability; some studies describe a low hunting performance of escaped sea bass because the diet they found was composed mainly of crustaceans found at harbours (Ramírez *et al.*, 2011). However, this diet sample is strongly linked to the areas where escaped fish were sampled (i.e. harbours and their surroundings). Thus, for a correct evaluation of the trophic performance of escaped fish, the sampling should be carried out in a range of natural habitats. Feral sea bass generally shows similar trophic behaviour to their wild counterparts. Actually, the overall trophic level calculated from our data gives a figure of 4.0 for feral sea bass in the Canaries, which is in the range for wild sea bass (3.8 ± 0.6; Froese and Pauly, 2012). In consequence, feral sea bass can be defined as one of the main top-predators (*sensu* Essington *et al.*, 2006) in shallow Canary Islands coastal waters.

7.3.6 Maturation and reproduction

Gonadal maturation and reproduction success trigger the establishment of self-sustainable populations of any introduced species. This means that no more inputs of individuals are needed to maintain (or increase) their populations. It is a crucial step in the invasion process (Elton, 1958) and in consequence it must be closely monitored. Sea bass has been demonstrated to be a very plastic species in relation to gonad onset and maturation, adapting to different environmental conditions (Pawson *et al.*, 2000; Vinagre *et al.*, 2009). In the Canaries, both male and female ferals that survive long enough in the wild, and reach sizes beyond 45 cm (males) and 55 cm (females) TL are able to develop mature functional gonads (Chapter 4). The frequency at which this occurs is unknown, as the study was preliminary with no further data recorded. During March 2010, visual surveys across shallow coastal waters off La Palma recorded nearly 12,000 sea bass; their estimated TL were larger than 45 cm and 1,116 individuals surpassed 55 cm. These data provide an insight into the high input of potentially mature fish in January 2010 due to the massive escape event. Nonetheless, Ramírez *et al.*, 2011 found respectively 15% and 5% of mature males and females in Stage 4 (of a 7-step maturity scale). They were caught in summer 2010 off the same Island. Thus, the low values are clearly related to the period of sampling as in southern latitudes gonad onset occurs in winter (i.e. January-March) when the water is colder and the days shorter (see Chapter 4 and references therein). Therefore, a greater sampling effort covering the whole year and range of sizes is necessary for a correct assessment of the season and size at maturity.

Escapes through spawning arise as a relative new concern since fish are often farmed to sizes at which they can reproduce in the cages (Jørstad *et al.*, 2008). The sex ratio of sea bass is biased towards males in aquaculture facilities (from 75 to 95%; Vandeputte *et al.*, 2012). Nonetheless, there are still males and females in the same cages. Thus, if the harvesting size goes beyond 50 cm TL the likelihood of finding mature sea bass in cages rises. In that case 'escape through spawning' could be a process that should be taken into account in the Canaries, as described in other areas (Somarakis *et al.*, 2013).

In any case, maturation is just a stage and does not strictly entail reproduction. There is no evidence of further fertilization, egg development, hatching and recruitment of larvae in islands where sea bass has been introduced. Actually the larval stages have only been found around Lanzarote and Fuerteventura where small wild populations exist (Brito *et al.*, 2002). However, especially regarding this little studied issue, "the absence of evidence is not evidence of absence" (Altman and Bland, 1995); therefore, more studies are needed to know if the escapees complete their life-cycle in the wild. What seems clear, during the period of time covered by this study, is that populations of feral sea bass in the central and western Canary Islands depend on the influx of new escapees.

7.4 Is sea bass domesticated?

A debate has been recently conducted on what is considered a domesticated fish and how many of the more than 250 farmed finfish species are really domesticated (Balon, 2004; Duarte *et al.*, 2007; Bilio, 2007; Lorenzen *et al.*, 2012; Teletchea and Fontaine, 2012).

Duarte *et al.* (2007) stated that all finfish once cultured are already domesticated. This leads to a biased vision where domestication of fish is growing rapidly in comparison to that of

land animals (Duarte *et al.*, 2007). In contrast, Balon (2004) argued that only two fish species (*Cyprinus carpio* and *Carassius auratus*) can be considered ‘true domesticated’ and the rest of them are only ‘captive exploited’. In the middle ground, other authors use different aspects related to the degree of human control over the lifecycle of fish species to classify a fish as domesticated. For instance, Bilio (2007) supports the domestication of 42 species based on the achievement of three generations subjected to selective breeding. Teletchea and Fontaine (2012) established a 6 level classification where 0 correspond to capture based aquaculture (e.g. tuna fattening) and 5 is the highest degree of domestication where a total of 30 species are placed (e.g. common carp, rainbow trout, Atlantic salmon or European sea bass). This latter classification is useful to assess the ‘state of the art’ in fish domestication and to plan future development of aquaculture, based on the most suitable species. However, in biological and ecological terms, the definition of domesticated fish given by Balon (2004), and its strict application, best reflects the ecological issues concerning escaped fish:

“In a truly domesticated organism, (a) the individual is valued and kept for a specific purpose, (b) its breeding is subject to human control, (c) its behaviour is different from that of the wild ancestor, (d) its morphology and physiology exhibit variations never seen in the wild and (e) some individuals at least would not survive without human protection” (Balon, 2004).

Thus, if a given fish is truly domesticated it is expected to exhibit all the criteria above mentioned. Domesticated fish show changes in form, function, colour and behaviour and often only partially resemble their wild ancestors (Balon, 2004). All those characteristics would lead to a poor performance of domesticated fish on escaping human control, so the feralization process would be unlikely or incomplete (Balon, 2004). In contrast, exploited captives are little changed from their wild ancestral form and can usually be returned to the wild. Many attempts at domestication remain only at the level of exploited captive because wild individuals are occasionally brought into the stock for breeding in captivity. This occurs to most fish species cultured for food or ornament (Balon, 2004), including sea bass (Chavanne *et al.*, 2008).

It seems clear that farmed sea bass retain enough fitness to perform well in wild habitats if they survive the high post-escape mortalities. The number of escapees reaching a high degree of feralization will increase with the total number of escaped individuals. In conclusion, at any given time, the escaped bass population in shallow coastal waters off the Canaries is composed of:

- Recent escapees with a low degree of feralization.

- Old escapees that have been in the wild for a long time (e.g. one individual was free-living for at least six years; Chapter 3), showing a high degree of feralization.

- Fish showing any given degree of feralization between the two extremes of the feralization process continuum.

7.5 Ecological interactions of feral sea bass in the Canary Islands

Authors agree on the difficulty in assessing the effects of the introduction of a new species in open and complex marine habitats (Underwood, 1997). Especially if this assessment has to be done in shallow coastal waters already subject to multiple stressors, with their high ecological complexity. So, to detect and isolate the effects of a species introduction from other pressures often becomes a challenge (Underwood, 1997). Actually, when clear cause-effect processes are detected by mere surveys in marine habitats, they usually involve huge changes that are in some cases non-reversible (Simberloff, 2003, 2007). Again, the absence of evidence of negative effects is not evidence that such effects are not occurring, or will occur (Carlton, 1996; Altman and Bland, 1995). In many cases the problem is that we fail to detect such effects with the tools (sampling method, sampling design, statistical tests) that are used, if not it is a simple response to the lack of scientifically-based knowledge (i.e. the problem is understudied). Additionally, the temporal factor is often neglected in the studies regarding species introduction. How long a period is needed to say that a certain species introduction does not entail any negative effect? The answer is that we do not know. As Elton (1958) and Carlton (1996) stated, changes in the recipient region can cause species introduced a long time ago to become invasive (with subsequent negative effects) at any time. Below there is a description of the potential and detected effects of feral sea bass in the Canaries, based on the findings presented in this thesis about its performance and population dynamics.

7.5.1 Trophic interactions

Feral sea bass can now be seen as a top-predator that actively exploits wild assemblages in shallow coastal waters off the Canary Islands (Chapter 2 and 6). The foraging activity of this fish, which surpasses the abundance (in number and biomass) of other high trophic level species (Fig. 6.5), may lead to alterations in the abundance of their prey species. This would occur through direct consumption, or competition with other species that share habitat and trophic niche with escapees. A potential trophic interaction is that between escaped sea bass and wild spotted bass (*D. punctatus*). They are known to be sympatric species that share habitat and trophic resources in their highly overlapped geographical distribution (Bonhomme *et al.*, 2002). Wild populations of spotted bass are found on the coast of Gran Canaria, Lanzarote and Fuerteventura. The sudden rise of escaped sea bass densities in shared habitats could eventually lead to alterations in the ecological equilibrium between the two species.

Furthermore, this could affect other less-related species through more complex top-down trophic cascade effects. A remarkable example of the latter is the effect of increased abundance of cod (*Gadus morhua*) observed in the Gulf of Riga due to migration from nearby areas, which led to a depletion of herring (a cod prey) in the area and subsequent rise of some zooplankton groups (preyed on by herrings; Casini *et al.*, 2012).

Another concern with respect to escapees is that these fish are entering food webs not only as predators but as prey too. Recently, it has been noted that native predators like the osprey (*Pandion haliaetus*) exploit escaped fish as trophic resource (Siverio *et al.*, 2011). Likewise other piscivorous species, such as bottlenose dolphins (*T. truncatus*) and bluefish (*P. saltatrix*), feed regularly around fish cages (Díaz, 2006; Sanchez-Jerez *et al.*, 2008). Such trophic dependency on farmed fish could cause piscivorous predators to fall into ecological or evolutionary traps (*sensu* Schlaepfer *et al.*, 2002), if they become habituated to feeding on species that follow boom-and-bust cycles, as is the case for fish escaping from sea cages. This would constitute a bottom-up process that remains unexplored.

It has already been shown that general trophic indexes such as mean trophic level can be altered by escaped fish locally, due to the high trophic level of cultured fish (referred to as a farming-up process; Chapter 6). The consequences of such changes are unknown but similar results have been found in the Mediterranean, related to the presence of Lessepsian migrants and the extirpation of native fish by them (Edelist *et al.*, 2013).

7.5.2 Genetic interactions

Genetic interactions are in theory limited to areas where wild counterparts of farmed species exist (section 1.7). The population structure of sea bass is one of the best studied among marine fish species. Numerous studies based on molecular markers (Martínez *et al.*, 1991; Allegrucci *et al.*, 1997; García de León *et al.*, 1997; Castilho and McAndrew, 1998; Lemaire *et al.*, 2000; Bahri-Sfar *et al.*, 2000; Bonhomme *et al.*, 2002; Castilho and Ciftci, 2005; Naciri *et al.*, 2007) have allowed the population to be divided into three main genetic groups: the North-Eastern Atlantic, the Western Mediterranean and the Eastern Mediterranean. The Atlantic and Western Mediterranean are quite homogeneous populations. The eastern group is more heterogeneous and structured into subpopulations that reflect the assignment to different basins of the region. This heterogeneity, together with higher farm production (e.g. Greece and Turkey), the use of non-local fry and broodstock, and smaller populations of wild bass in the area could promote genetic introgression of wild populations (Martínez *et al.*, 1991; Chavanne *et al.*, 2008). More studies are needed to ascertain the genetic effects of cultured sea bass in the Mediterranean. In the Atlantic Ocean, the use of Mediterranean broodstock has already been detected through the presence of Mediterranean haplotypes in wild sea bass populations in Norway and the Thames estuary (Coscia and Mariani, 2011).

In the case of the Canary Islands, genetic interactions would be limited to Lanzarote and Fuerteventura, the easternmost islands. Aquaculture facilities are present only off the south-east coast of Lanzarote. Wild populations in these areas are thought to be maintained through larval fluxes from the nearby African coast (Brito *et al.*, 2002). This would prevent genetic interactions between wild and farmed individuals. Nonetheless, owing to the obvious lack of information about natural populations of sea bass (González *et al.*, 2012), it is worth looking at the alternative scenario where small wild populations of sea bass are self-sustained. In that case interbreeding between wild and escaped fish could take place through the escape of individuals. Even through the input of unfertilized eggs in cases of female maturation at fish cages situated in hypothetical spawning grounds (Jørstad *et al.*, 2008; Somarakis *et al.*, 2013).

Some studies on salmonids have dealt with the genetic consequences of mixing a small wild population with a large farmed one (Fraser, 2008; Araki and Schimd, 2010). Briefly, the question whether or not genetic diversity is compromised through introgression depends on the effective size of each interbreeding population (i.e. number of breeders), reproduction fitness of farmed fish in the wild and number of escapees in comparison to wild population (Martínez *et al.*, 1991; Lorenzen *et al.*, 2012). The genetic diversity of the wild population may be increased if the latter had a lower effective size than the farmed one (Lorenzen *et al.*, 2012). In contrast, if the effective population size is larger in the wild population, which is the case in most farmed fish, genetic diversity would decrease (Madeira *et al.*, 2005). The input of large numbers of farmed fish could also dilute the local adaptations, thus compromising the continuity of small wild populations, reducing the ability of the population to respond to environmental change (González-Wangüemert *et al.*, 2012; Lorenzen *et al.*, 2012). Indeed, this is a risk already pointed out for wild sea bass (Youngson *et al.*, 2001). Most of the fry is brought to the Canaries from nurseries on the mainland that, in some cases, use Mediterranean broodstock, which are genetically differentiated from their Atlantic counterparts (Coscia and Mariani, 2011). Additionally, genetic fluxes from the nearby continent (Brochier *et al.*, 2011) should be taken into account in this scenario, which complicates the issue and expands the possible outputs. Based on these considerations, a clear need for genetic studies arises in order to ascertain the effects that aquaculture escapees could have on wild populations of sea bass in the easternmost Canaries.

A possible mitigation of genetic interactions has recently been described. ♀ *D. labrax* x ♂ *D. punctatus* hybrids are being produced at the IFAPA 'El Toruño' Research Centre (Junta de Andalucía, Puerto de Santa María, Cádiz, Spain) (Merlo *et al.*, 2010). The embryo survival was significantly higher in interspecific crosses compared to intraspecific controls, showing increased performance at early life stages (Ky *et al.*, 2012). If further research confirms their sterility, the culture of hybrids could avoid genetic interactions and also the establishment of self-sustainable feral populations (Huntingford *et al.*, 2012; Ky *et al.*, 2012).

7.5.3 Pathogenic interactions

Impacts on wild stocks from disease interactions may occur via three mechanisms: (1) introduction of alien pathogens, (2) transfer of pathogens that have evolved increased virulence in culture, (3) changes in host population density, age/size structure or immune status that affect the dynamics of established pathogens (Lorenzen *et al.*, 2012). Very little is known about the diseases and parasites that escaped fish bring with them to natural environments. In general, it can be said that the prevalence of numerous illnesses and parasites is higher in culture conditions than in wild populations (Krkošek, 2006). If the escaped fish are a subset of the cultured population then they also suffer a higher prevalence of different parasites and diseases that they carry with them into the wild (Arechavala-Lopez *et al.*, 2013b and references therein). However, except for studies on sea-lice in salmon (Heuch and Mo, 2001), this field remains widely unexplored. Moreover, life-cycles, transmission vectors and specificity of many diseases and parasites are unknown, which adds uncertainty to their effects on wild assemblages. This is the case of *Sphaerospora testicularis* (Alvarez-Pellitero, 1993) that is still the only parasite of escaped fish that has been studied in Spain to date (Chapter 3). It affects male sea bass gonads, causing parasitic castration (in cases of massive infections; Sitjà-Bobadilla and Álvarez-Pellitero, 1990), the latter would depress reproduction performance of feral sea bass. Nevertheless, the fact that prevalence never reaches 100%, and infections are in most cases partial, does not assure full parasitic castration of escaped fish (Chapter 3). The lack of studies of this parasite group avoids discarding direct fish-to-fish and cross infection that could affect other species (e.g. the congener *D. punctatus*). Additionally, the higher prevalence of *S. testicularis* in rearing facilities in comparison to wild populations (Sitjà-Bobadilla and Álvarez-Pellitero, 1990) could pose a threat to wild sea bass in the easternmost islands. In-depth studies of the parasites and diseases introduced and/or enhanced by aquaculture activities in the Canaries are urgently required for a correct management of this activity here and elsewhere.

7.5.4 Fisheries interactions

The clearest effects of escapees in the Canary Islands are detected on artisanal fisheries (Chapter 5). Escaped fish are caught by professional and recreational fishermen almost daily in those islands with aquaculture facilities. When large escape events take place, escaped fish could represent almost 40% of the total catch of bentho-demersal fish in a month for professional fishermen (Fig. 5.7). This means unexpected income for them, thus benefitting from the escape events, as reported in the Mediterranean (Arechavala-Lopez *et al.*, 2012c). For recreational anglers and spearfishers, escape events may lead to enhancement of their hobby. However, recent studies in Norway showed that willingness-to-pay for recreational fishing is reduced by 85% in rivers with escaped fish in comparison to a situation of ‘pure’ wild salmon stock (Olaussen and Liu, 2011). In the Canaries, fishermen also show concerns about the possible ecological effects of escaped fish (Chacón, 2010). In general it can be said that escape events are not formally well-received by professional or recreational fishermen, but they still take advantage of them (Ramón, 2011).

Fisheries could also be affected by a reduction in targeted species that are part of the trophic resources consumed by feral sea bass. Actually, the professional fishermen argued that escaped sea bass had depleted bait-fish (i.e. small coastal pelagic fish) after the massive escape event off La Palma in 2009-2010 (Chacón, 2010). Local fisheries and escaped sea bass share some target species namely: *Atherina presbyter*, *Sardinella aurita*, *Sparisoma cretense*, *Plagusia depressa* and *Xantho spp.* Of these, *A. presbyter* and *S. aurita* are used as bait-fish in artisanal tuna fishing (González *et al.*, 2012), but no reliable data are available for the catches of these species as they are not communicated to the 'first-sale' system implemented by the Canary Islands Government. The parrotfish *S. cretense* is a regionally appreciated (and heavily fished) species; 'first-sale' data reveal a reduction in the catches of around 25% from 2009 to 2010 in La Palma, which coincides with the massive escape event. Nonetheless, the possible influence of a reallocation of fishing effort over escaped fish after the massive escape event must be addressed for a correct interpretation of the landing data. Regarding crustaceans, the crabs *P. depressa* and *Xantho spp.* are presumably over-exploited in intertidal zones of the Canary Islands (González *et al.*, 2012), and the appearance of a new predator in high densities could pose an additional threat to populations of these species. Nevertheless, long term studies are needed to detect this kind of interactions.

7.5.5 Secondary interactions

Potential indirect interactions could also be taking place in the region. Alteration of fishing pressure in the surroundings of aquaculture facilities has already been focused on the Mediterranean (Akyol and Ertosluk, 2010). Although no data on this have been published for the Canaries, personal observations during the surveys for this thesis suggest that fishing effort may become intensified in areas close to recent escape events. This could indirectly promote over-fishing in areas close to aquaculture facilities.

An interaction, closely related to the above, can arise when systematic recapture efforts are carried out, as occurred after the massive escape off La Palma. On that occasion special permits were granted for the use of a forbidden fishing-gear called 'salemera' (i.e. a kind of purse-seine net adapted to very shallow waters) as professional fishermen declared it was the most suitable for recapture efforts (Fig. 7.3abc). No data of by-catch during those recapture efforts have been published, but special attention must be paid to this issue to prevent possible damage to native coastal fish assemblages.

Obviously, some of the escapees end up as a main course at many Canary Islands homes. Whether caught by professionals and bought in the market or fished by recreational anglers/spearfishers and brought back home, escaped fish lose their traceability once in the wild. Antibiotics and chemicals are administered at some point to all individuals, together with feed, to avoid the effects of different diseases and parasites on cultured stocks (Subasinghe, 2009). For instance, in a study dealing with the assessment of antibiotics in meat and farmed fish, ampicillin was detected in five samples at concentrations ranging from 22 to 45 μg/kg. Enrofloxacin was found in three samples, ranging from 32 to 87 μg/kg. Samples obtained from farmed fish were the most contaminated because they were taken after the treatment of the fish with antibacterials (Juan-García *et al.*, 2007). These fish are commonly subjected to a safety period before being killed for human consumption. However, in escape events involving recently treated fish the food safety is compromised. This issue should be closely studied to assure that consumption of escaped fish is safe for human health.

7.6 Other farmed species in the Canary Islands

This thesis has been mainly centred on studying *D. labrax* escapees, but there are other presently or previously farmed species in floating fish cages off the Canaries: gilthead seabream (*Sparus aurata*; Fig 7.4a) and meagre (*Argyrosomus regius*; Fig 7.4b). Like sea bass, both species are (or have been) released into the wild due to escape events. However, preliminary studies revealed that sea bream was not as abundant in the wild as sea bass (Chapter 4), and meagre had a low production (APROMAR, 2010) which prevented a significant presence of escaped individuals in the wild. In any case, due to the scarcity of studies on this species in the Canary Islands, it is worth discussing preliminary data on both species, since any management of escapees should take into account their peculiarities.

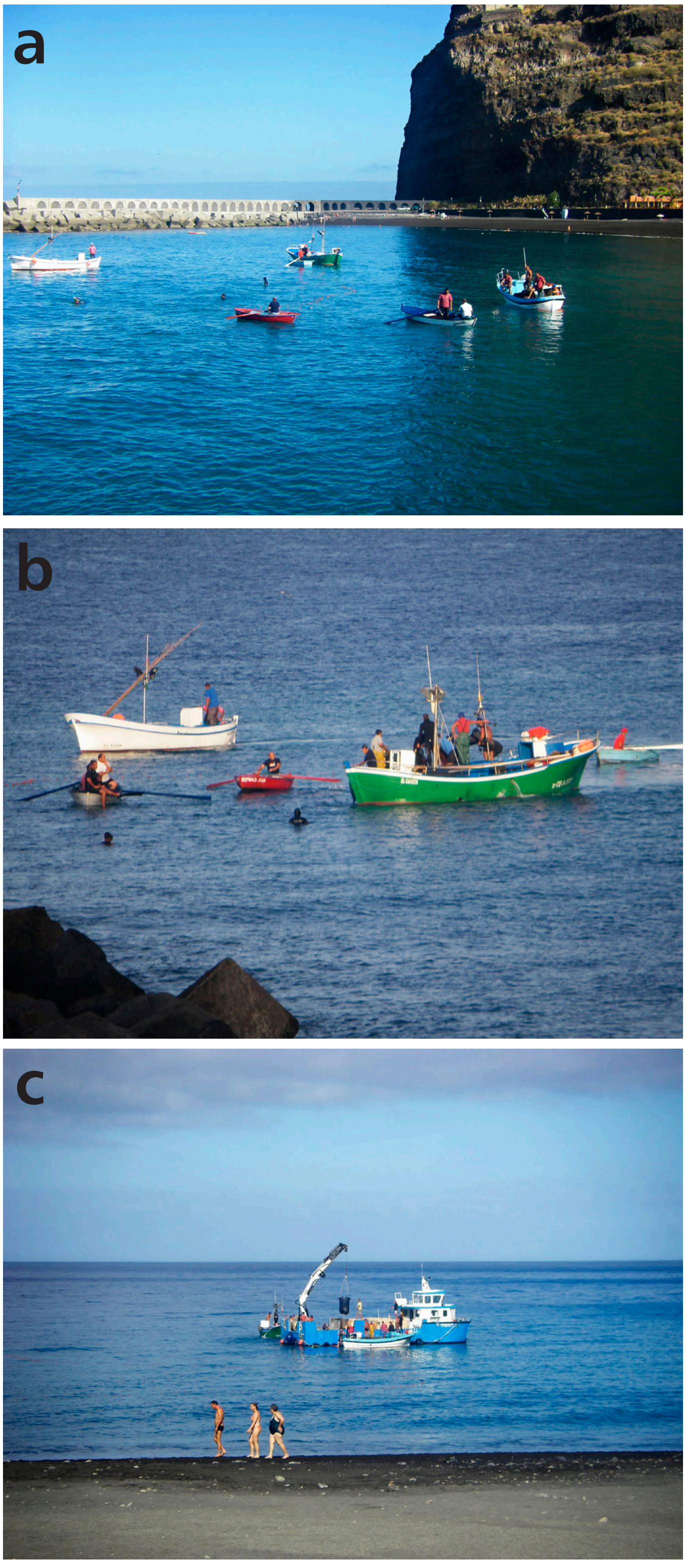

Figure 7.3. Recapture techniques used 6 months after the escape event (July 2010), at a beach near the escape point. (a) Artisanal boats setting a ‘salemera’, a purse-seine net used in shallow waters. (b) Snorkelling divers leading fish shoals to the net. (c) Fishing gear is closed and recaptured fish transferred to the aquaculture company’s vessel.

7.6.1 Gilthead seabream (*Sparus aurata*)

This species belongs to the family Sparidae and the production in the Canaries was initially larger than sea bass, yet during recent years both species have been produced in similar amounts (APROMAR, 2012; Fig. 1.5). Recent studies revealed biting behaviour, which could weaken net resistance and create small holes favouring both massive and leak escapes (Høy *et al.*, 2013). Our data on massive escapes do not support this hypothesis but given the biases detected they may be underestimated (see section 7.2).

Post-escape distribution of escaped sea bream has shown a similar pattern to sea bass fugitives, that is, higher abundances along coasts near aquaculture facilities (Mora-Vidal *et al.*, 2010). Sea bream have also shown high mobility, especially after massive escapes when fish move in big shoals (González-Lorenzo *et al.*, 2005). These preliminary data are in concordance with other studies in the Mediterranean (Arechavala-Lopez *et al.*, 2012c). Regarding the lower abundance of sea bream in shallow coastal waters, a higher mortality and/or migration rate can only be hypothesized. Some evidence supports the higher mortality rate: for instance sea bream appeared to have higher catchability than sea bass after the massive escape off La Palma (Chapter 4). During surveys, sea bream showed bolder behaviour than the bass (e.g. allowing divers to get closer), which could indicate a higher susceptibility to predation (pers. obs.). Predation on the bream by bass could be another reason for the lower abundances of the bream as both species are likely to escape at the same time during storms (see section 7.3.1). Migration to deeper areas has also been suggested as a reason for low abundances of sea bream in the areas surveyed (i.e. shallow coastal waters between 1 and 5 m depth). However, no evidence for this has been found, and the fact that wild bream reach deeper habitats (Froese and Pauly, 2012) is only a weak support for this hypothesis. Besides this, while sea bass is the main top predator in the areas surveyed, sea bream forms only a small part of the sparids inhabiting shallow coastal waters in the Canaries (Chapter 6). Thus escapees may be subject to a high degree of competitiveness, which could prevent further establishment of this species in shallow coastal habitats.

Escaped sea bream forage in natural habitats off the Canaries (Toledo-Guedes *et al.*, 2008). Its diet is composed mainly of decapods (e.g. *Xantho pilipes*, *Ethusa sp.*), molluscs (e.g. *Timoclea ovata*, Cerithidae) and echinoderms (*Diadema africanum*; Rodríguez *et al.*, 2013). In the Mediterranean it has been demonstrated that soon after escape they are able to

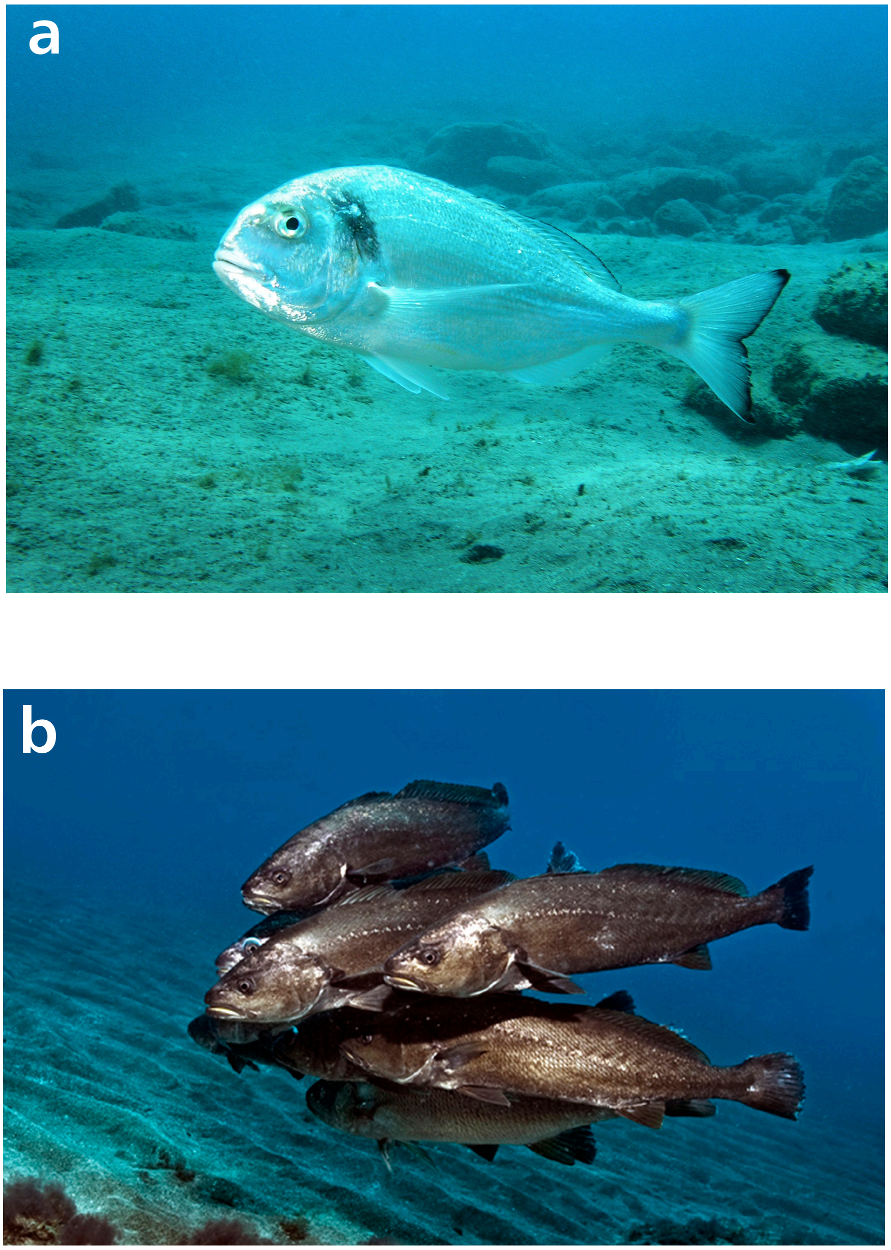

Figure 7.4. Other species that escape from floating cages in the Canary Islands. (a) *Sparus aurata* (sea bream) off Puertito de Adeje (SW Tenerife) and (b) *Argyrosomus regius* (meagre) off Tufia (E Gran Canaria).

exploit natural resources around aquaculture facilities, and after nine days in the wild their diet resembles that of their wild counterparts (Arechavala-Lopez *et al.*, 2012c). Most of the potential ecological interactions involving sea bass can be extrapolated for the bream, including genetic interactions, as small wild populations of sea bream are found in the easternmost islands (Brito *et al.*, 2002).

7.6.2 Meagre (*Argyrosomus regius*)

Belonging to the family Scianidae, this species has no wild populations in the Canaries (Brito *et al.*, 2002). Before aquaculture of this species took place (between 2003 and 2010; Ortega *et al.*, 2011; APROMAR, 2010), only four individuals had been captured in the region (Brito *et al.*, 2002) and they were large-sized vagrant individuals. However, this species is common along the African coast fished traditionally from boats based in Canary Islands ports (De Ory, 2004). It was introduced into fish farms off Gran Canaria and Tenerife in the framework of pilot studies to assess its commercial suitability (Ortega *et al.*, 2011). During that period at least one large escape (Table 1.1) was reported off Gran Canaria, while numerous catches of a few individuals were made by professional and recreational fishermen in Tenerife (González-Lorenzo pers. comm.).

The natural diet of meagre is mainly fish, and decapods to a lesser extent (Froese and Pauly, 2012). In a study commissioned by the Canary Islands Government (Ortega *et al.*, 2011), a total of 10 stomachs of escaped meagre were analysed. They found (in order of importance) clupeids, decapods and cephalopods, which reflects similar foraging behaviour to their wild counterparts. Is worth mentioning that meagre is a coastal top predator with a trophic level (4.3) well above that of sea bass (3.8), and reaches large sizes and weights (maximum recorded, 230 cm and 103 kg; Froese and Pauly, 2012). Therefore, processes such as 'farming-up' (Chapter 6) would be exacerbated by massive escapes of this species.

7.7 Fish as pollutants

Notable attention has been paid to develop and establish a regulatory framework for aquaculture activities in Spain (FOESA, 2013). These efforts are centred on assessing and minimizing the possible negative impacts that aquaculture wastes (e.g. unconsumed feed and fish faeces) could have on natural habitats. Despite great heterogeneity in legislation among regions, all new aquaculture facilities must be accompanied by an environmental impact assessment and a comprehensive monitoring plan (BOC, 2004). This is reasonable, as there is a need to avoid pollutants (e.g. organic matter, noxious chemicals) in such quantities that could endanger ecosystem health and functioning.

When we think about pollutants, there is a clear dichotomy: factors that negatively affect environmental quality in opposition to those that we would call ‘natural’ (Firestone and Barber, 2003). Popularly, there is a clear line between pollutants and substances naturally present, and a given factor should not lie on both sides of the line. Fish are considered natural (in a vast majority of cases), and either affect water quality positively or at least function as a tool to measure the effects of pollutants. In contrast, noxious chemicals are pollutants and can only negatively affect water quality (Firestone and Barber, 2003). It may seem odd to speak of live fish as pollutants, as odd as it would be to speak of noxious chemicals as natural. Nevertheless, the traditional definition of fish as natural may be changing with the appearance of new concerns about how accidental or poorly planned introductions of fish can adversely affect the environment (Naylor and Burke, 2005; Naylor *et al.*, 2009). As seen for salmon, these concerns are equally important if the released fish are exotic (Soto *et al.*, 2006), locally absent or native (Fleming *et al.*, 2000). Even their capacity for reproduction in the wild becomes a secondary aspect when aquaculture is the origin of fish, as their input is regular, simulating a self sustaining population (Arismendi *et al.*, 2009). Thus. it may be reasonable to treat fish escaped from aquaculture facilities as biological pollutants, since they accomplish their characteristics, by definition: anything that alters the purity or normal conditions of a thing or an environment.

Classical pollutants such as organic matter, chemicals, or drugs like antibiotics released from farms have patterns of dispersion or deposition that can be modelled (Henderson *et al.*, 2001), and even the concentrations above which they may have negative effects are known. In contrast, the behaviour and effects of a biological pollutant such as escaped fish are far from predictable. Given the potential of escaped fish to cause environmental damage, European Union Law establishes that a precautionary principle must be applied (EC, 2007). This precautionary approach states that if an action has a suspected risk of causing harm to the environment, in the absence of scientific consensus that the action is harmful, the burden of proof that it is not harmful falls on those carrying out that act.

In Spain, nevertheless, regional and national laws and regulations regarding aquaculture do not provide specific tools to prevent potential damage caused by escaped fish. In some cases national law regarding exotic species may be applicable to avoid the culture of exotic species (BOE, 2011). Some regions in Spain also require a contingency plan in case of escape events, but very often this plan literally consists in "recapture as many fish as possible" (pers. obs.). Taking into account the existing gaps, the following section will be devoted to proposing measures to evaluate and manage the risk associated with the escape of fish from aquaculture facilities and their potential ecological damage to marine ecosystems.

7.8 Risk evaluation framework

Many authors have tried to define risk in the context of risk evaluation. One of the definitions they propose fits the aquaculture context: "risk is the exposure to circumstances with potentially damaging effects arising from an event that is not handled appropriately" (Husdal, 2009). Risk evaluation involves all the actions taken to address both sides of an accidental event: the sources leading up to it and the consequences arising from it (Fig 7.5). In figurative terms, 'barriers' are put in place on both sides aimed at stopping a circumstance from evolving into an event, or aimed at stopping an event from developing negative consequences (Husdal, 2009). In an aquaculture facility composed of floating fish cages, the escape of part of the cultured fish would be the accidental event (i.e. escape event). A good maintenance program would be a source barrier, while a recapture procedure would be a consequence barrier.

The protocols used for exotic/locally absent species risk evaluation schemes are derivatives of the hazard management protocols developed during the latter part of the 20th century to ensure health and safety in the nuclear industry (Copp *et al.*, 2008). Four common elements to all risk evaluation schemes are:

1. Risk Identification
2. Risk Assessment
3. Risk Management: mitigation, information, contingency and restoration plans.
4. Risk Monitoring and Research

These elements should be implemented simultaneously rather than in sequence, for instance

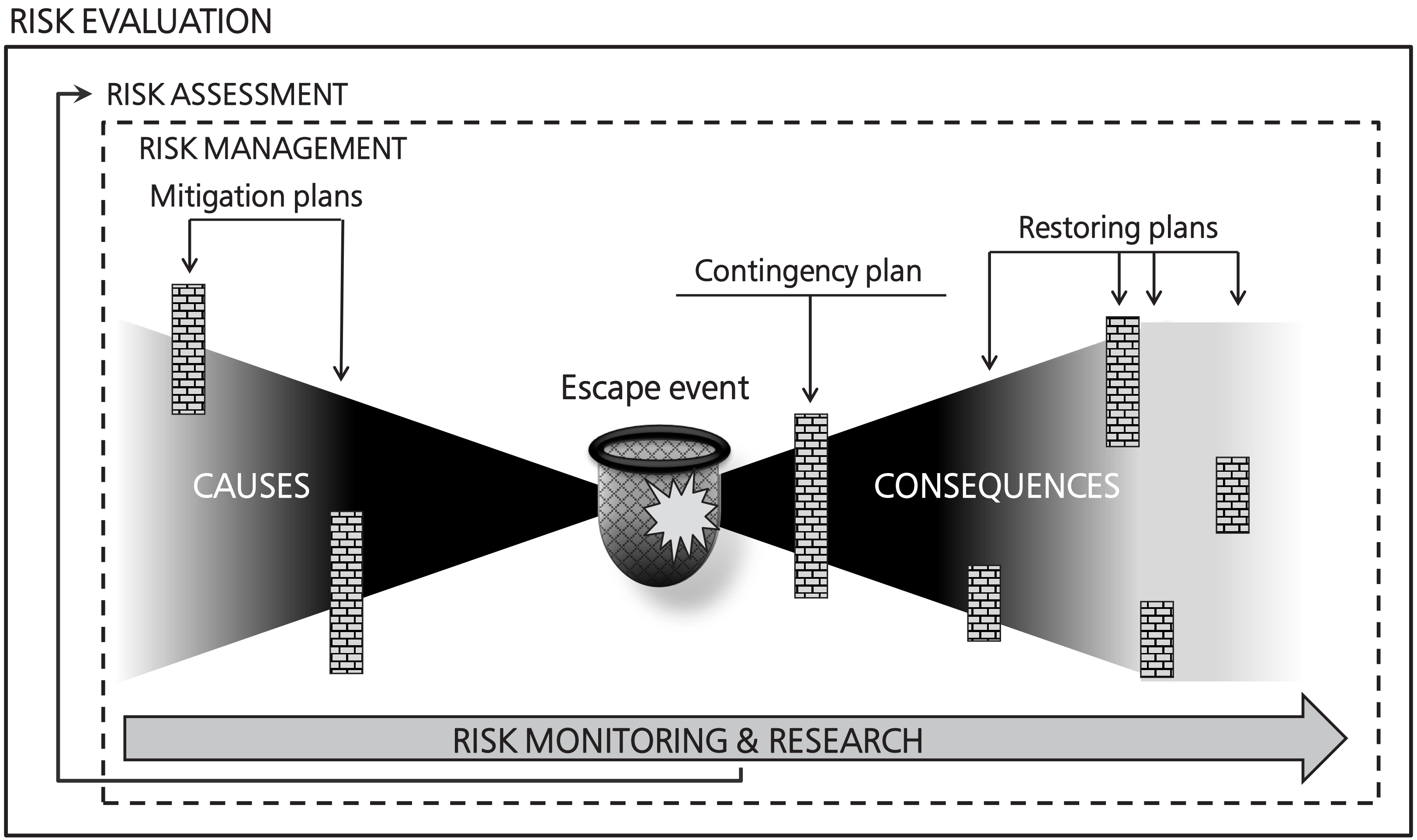

Figure 7.5. Conceptual model of the risk evaluation framework applied to adaptive management of escape events (modified from Husdal, 2009).

risks can be reduced merely by informing (and where necessary ‘educating’) industry and the general public about the hazards associated with the release of non-native/locally absent organisms into the open environment (Copp *et al.*, 2008).

7.8.1 Risk Identification

This consists of identifying a certain risk and the determination of potential causes leading to it, and consequences of exposure to that risk. Part of this thesis corresponds to this first step of risk management. Throughout this study, escape events have been identified as a risk and different causes and consequences have been pointed out and addressed.

7.8.2 Risk Assessment

This is a numerical approach to establish ‘how much’ risk is taken if an action is carried out. This kind of analysis can help to support decisions or evaluate if correct decisions have been taken (Holmer *et al.*, 2008). The European Union (EU) has implemented a risk assessment regarding permits for the introduction or translocation of species for aquaculture purposes (EC, 2007). This regulation is only applicable when this occurs between member states and not within them. This would generate some kind of insecurity regarding the introduction/translocation of species within a country, especially in those states having several biogeographic regions (e.g. Spain). In such cases EU encourages each country to develop specific legislation or adopt the regulation.

Briefly, this protocol consists of an adaptive science-based risk assessment for each introduction/translocation, should the species concerned be placed in an open aquaculture system (e.g. floating fish cages). In that assessment, a series of questions must be addressed, always based on scientific knowledge. For each response a degree of uncertainty is established. In the case no scientific knowledge is available (or no consensus has been reached) then the degree of uncertainty is set as ‘high’, and a precautionary approach must be followed. As regulatory EU law states: “Any refusal of a permit must be duly motivated on scientific grounds and, where scientific information is as yet insufficient, on the grounds of the precautionary principle” (EC, 2007).

The above would apply in cases such as the introduction of meagre in Tenerife, as fry was brought to the Island from hatcheries in France (Ortega *et al.*, 2011). However, as this pilot introduction took place in 2003 and the regulation has only been in force since January 2009, no measures were taken at that time. The potential impacts of escaped fish are multiple, given the complexity of natural ecosystems. As such, a single person is unlikely to have the necessary expertise to complete all aspects of the risk assessments, and it is assumed that a team of recognised specialists will be required to complete the assessment of any given species (Copp *et al.*, 2008).

Thus, there is a situation where tools for assessing the risks involved in introducing exotic/locally absent fish species are already available (Copp *et al.*, 2008; Britton *et al.*, 2010), but they are not applied. As a fragmented and highly variable territory, the Canary Islands should carry out this kind of protocols separately for each species and island where aquaculture is established. Future species introductions for aquaculture purposes need to be evaluated, along with those that have already taken place.

7.8.3 Risk Management

Mitigation plans

All the actions taken ‘before’ the escape event and leading to the prevention of such events are included in mitigation plans. Technical failures due to storms are cited as the first cause of escape events, especially of massive escapes (Jensen *et al.*, 2010; Chapters 5 and 6). Therefore improvements in materials and construction of fish cages are of key importance to reduce the frequency and magnitude of escape events. However, this issue is not within the scope of this thesis. Thus, only actions that can be carried out by any aquaculture facility are listed below:

- Place the facilities in sites with low likelihood of escape events (i.e. sites with low incidence of sea storms).
- Avoid mismatch between the design of the aquaculture facility and the local environmental conditions (i.e. weak designs in exposed conditions).
- Build the facility with the best materials and technology available.
- Culture individuals from local broodstock with sufficient genetic variability.
- Avoid culture of exotic or locally absent species.

- Culture sterile hybrids to avoid genetic interactions.
- Continuous staff training on identification and repair of damaged material.
- Comprehensive maintenance programme, reinforced before the period with highest recurrence of storms.

Nevertheless, mitigation actions begin with the adoption of regulations and policies (such as risk evaluation schemes) contributing to prevention of escape events and their potential effects. Aquaculture companies, as commercial businesses, will adopt those cost-effective measures proposed to minimize economic loss posed by escape events. But when the costs of preventive actions surpass the costs of escaped fish (which is usually the case because the stock is insured), then mitigation becomes non-profitable. This is where the Canary Government should encourage mitigation measures through a punitive system for those companies that release more fish, or even better, a reward system for aquaculture facilities with lower escape rates.

Contingency plans

These are detailed protocols aimed to avoid the potential negative consequences of escape events, as soon as possible afterwards. Recent studies have tried to model post-escape behaviour of sea bass, sea bream and cod (Uglem *et al.*, 2008; Arechavala-Lopez *et al.*, 2011, 2012c), and to test different fishing techniques to recapture escaped cod in Norway (Serra-Llinares *et al.*, 2013). Post-escape behaviour of escapees shows that it is possible to recapture a large proportion of the escaped individuals if recapture efforts start immediately after the escape event (Uglem *et al.*, 2008). However, specific techniques for recapture with low by-catch have not yet been developed (Serra-Llinares *et al.*, 2013). Data on massive escapes in the Canary Islands indicate that effective contingency plans should include the following:

- Pre-alert: all the massive escape events recorded involve storms with wave heights >2 m (Table 1.1). Thus, the plan should be pre-activated when waves affecting the facilities are predicted to exceed 2 m in height.

- Post-storm reports: as soon as sea conditions permit, a report on escape events, if any, should be communicated by facility managers to the authorities. The latter would decide if their magnitude is sufficient to justify recapture efforts.

- Agreements with professional fishermen: the recapture efforts carried out after La Palma massive escape event in 2010 suggest that professional fishermen are key stakeholders in developing and implementing contingency plans for the region (Chapter 5). All the actions leading to recapture of escaped fish should be coordinated within the framework of these agreements.

Additionally, aquaculture companies' insurance policies should cover (through liability clauses) possible costs derived from contingency, restoring and monitoring plans regarding escaped fish. Insured companies are paid according to losses attributable to storms (van Anrooy *et al.*, 2006) when no negligence is demonstrated, thus the recapture of the fish should also be covered by such insurance, which in order to be effective should be compulsory.

Restoring plans

Environmental restoration refers to all the actions aimed at returning the environment to the state prior to the occurrence of a certain impact (Pastorok *et al.*, 1997). In general, these measures are carried out after contingency plans, and usually span longer periods of time. In the case of escaped fish, the objective of restoring plans would ideally be to remove all escapees (i.e. the source of environmental risk) present in the environment. This objective can be achieved by either 'passive' or 'active' measures:

- Passive measures: farmed species are also coveted by fishermen, thus, all the measures that facilitate the capture of this fish would contribute to removing escaped fish from natural habitats. For example, deregulating fishing of escaped fish around those islands where they were introduced (i.e. Gran Canaria, Tenerife, La Palma, La Gomera and El Hierro). This implies that fishermen (both professional and recreational) could fish as many escapees as they want, irrespective of fish size. This is supported by other authors that recommend regulating the minimum catch size only in those islands where wild populations of farmed fish exist (i.e. Lanzarote and Fuerteventura; González *et al.*, 2012). However, special care must be taken by public authorities to ascertain and communicate if escaped fish are safe for consumption (see section 7.5.5).

- Active measures: in certain cases eradication procedures may be recommended in some sensitive areas and/or where fishing is entirely or partially forbidden. No-take zones of MPA's, areas with special status such as Sites of Community Importance (an EU protection figure) or Unesco Biosphere Reserves would be suitable for eradication campaigns. Concentrated local eradication could substantially reduce feral populations of escaped fish in harbours, marinas and beach areas. The best fishing technique for such interventions would be spearfishing as it is the most selective. Spearfishing tournaments which target escaped species or special prizes in regular tournaments for those catching escapees could be other proactive measures to remove fugitive fish from the environment. These actions would be restricted to islands where farmed fish have been introduced, as to distinguish them from their wild counterparts at a glance is virtually impossible (Chapter 3).

7.8.4 Risk Monitoring

Since we are at the frontier of knowledge about performance of escaped fish in the wild and their ecological consequences, there is a clear need for adaptive management that continuously evaluates the results obtained (i.e. monitoring) and looks for new findings to improve management (i.e. research). Then, the information obtained will feed back into the risk assessment to modify (or not) its outputs (Fig. 7.5). In this way, the risk evaluation framework is kept up to date and optimized. This minimizes the risk associated with escaped fish as much as possible applying the best knowledge available. The following critical points should be monitored in the Canary Islands:

Parasites and Diseases

The regional government is promoting aquaculture as one of the activities of the future, thus the number of facilities and total production may grow. Additionally, in some islands the possibility of concentrating the facilities in few locations is being considered (El Día, 2008). This would raise the possibilities of disease spread between nearby facilities. In consequence, a reliable monitoring of parasites and diseases affecting farmed and wild fish is needed. Comprehensive and regular reports on parasites and diseases affecting different facilities would be essential for a rapid response, and to avoid further spread to the wild fish assemblages concentrated around fish farms (Arechavala-Lopez *et al.*, 2013b). Additionally, this would allow monitoring the incidence of parasites and diseases on escaped fish that could be further transmitted (Toledo-Guedes *et al.*, 2012).

Treatment

Reports on treatments against parasites and diseases applied to stocked fish are needed to assess the risks posed by recently treated escapees for human health and food safety. European Union has already regulated de minimum residual level (MRL) of different antibiotics in fish for a safe consumption, and the methods to measure them are already reliable (Cañada-Cañada *et al.*, 2009). Thus, for food safety reasons, there is a strong need to monitor concentrations of antibiotics in escaped fish regularly.

Escape

Aquaculture companies should report reliable information on the number of individuals that are introduced in each fish cages as fry. Then, taking into account the total mortality and number of individuals harvested, it would be easy to estimate the number of individuals that has escaped during farming period. This procedure and the above mentioned reports are already sent to insurance companies in a monthly base (Secretan *et al.*, 2007). Thus, providing the needed confidentiality, it would be costless for aquaculture companies to make available this information to public managers.

Catch

First-sales data seems to be a good proxy of the number of escaped fish in the wild (Chapter 5). Again, this is a costless monitoring program as those data are already available and it would only be necessary to analyse farmed species separately in a weekly basis. This simple measure could detect unknown escape events and activate contingency plans in case of non-communicated accidents.

Recapture

If recapture efforts are carried out they must be monitored because by-catch of other species during contingency actions could have negative consequences. Therefore, monitoring could help to detect unsuitable techniques or inappropriate areas for recapture because of a negative incidence in natural assemblages.

7.8.5 Future research lines

The questions answered by this thesis are far fewer than those arising from it. The only way to address them is to generate rigorous science-based knowledge in this field. Management of escaped fish will be improved by the findings from future research lines, which should reveal the effectiveness of risk management and some new critical points at which to intervene.

Reproduction

How the problem of escaped fish is managed depends largely on the capacity of fugitives to establish self-sustaining populations. In such cases, feral fish populations would not depend on the input of new escapees and it would become more complex to manage the associated risks. Thus, the ability of farmed species to complete their lifecycle in conditions (e.g. temperature) different from their optima should be closely studied. The reproductive biology of the species is not fully understood, since farmed species have been proven to mature in conditions previously believed to be unfavourable (Toledo-Guedes *et al.*, 2012). In consequence, *in situ* studies to assess maturity of escaped fish and ichthyoplankton surveys to check the presence of larvae of farmed species in the wild are urgently needed.

Diet

Stomach content analysis is a cost effective technique to provide a preliminary assessment of the diet of escaped fish. However, recent studies show that other techniques such as stable isotope analysis (SIA; Cucherousset *et al.*, 2012) or DNA barcoding (Côté *et al.*, 2013) greatly improve the resolution in diet studies. DNA barcoding detects species that are not found or not identified in stomach content, and SIA can reveal mid- and long-term trophic relationships of escaped fish and their trophic role in the wild. Both techniques are also reliable tools to identify escapees and wild counterparts (Haffray *et al.*, 2006; Schröder and García de Leániz, 2011; but see review by Arechavala-Lopez *et al.*, 2013a)

Diseases and parasites

Several studies investigate their incidence in farmed species (Murray and Peeler, 2005). However, very little is known about parasite lifecycles and transmission of many prevalent diseases affecting farmed fish. The role of escaped fish as parasite and disease carriers is probably important, but remains unexplored (Arechavala-Lopez *et al.*, 2013b). Additionally, their incidence in wild assemblages should be surveyed in the region.

Genetic interactions

Molecular research into farmed stock and wild populations of sea bass and sea bream in the Canary Islands is needed. Of special interest would be to compare the genetic response of small wild populations off Lanzarote, where farming facilities have been gradually losing both bass and bream, with the Fuerteventura wild populations much further from those activities.

Recapture techniques

Few studies have tried to design specific gear for escaped fish recapture (Serra-Llinares *et al.*, 2013). Research focused on minimizing by-catch during recapture efforts will be essential in preparing contingency plans.

7.9 Which kind of aquaculture do we need?

Today, almost 75% of the earth's habitable land surface has been disturbed to a greater or lesser degree (Hannah *et al.*, 1994). Whilst mining, logging and urbanization have contributed to this alteration of land cover, agriculture (referring to plant and animal farming) has been, and remains, the most significant agent of environmental change (Mannion, 1999). By 2050, Earth's population is predicted to reach 9,200 million people (UN, 2006). Agriculture will probably reach its ceiling production before, due to two main limiting factors: freshwater and space (Cohen, 1995). These limitations are likely to be exacerbated by climate change (Lobell *et al.*, 2008). Fisheries are currently stagnated at 90 million tonnes per year (FAO, 2012). In this scenario, aquaculture is seen as a possible aid in feeding humanity (Duarte *et al.*, 2009). Despite concerns about the impact of aquaculture on the environment, they seem negligible if compared with the effects of agriculture on land (Diana, 2009). Nonetheless, this comparison can give a biased idea, as agriculture and livestock still have a food production that greatly surpass that of aquaculture, the latter only represents 2% of the total food produced in the world (Duarte *et al.*, 2009). Therefore, if the second food revolution (the aquaculture revolution) in human history is not environmentally sustainable, the degree of alteration in marine ecosystems could resemble that caused by agriculture on land (Goldburg and Naylor, 2005). Aquaculture's limitations and vulnerabilities are several, (e.g. use of antibiotics, input of organic matter and competition for coastal space, among others). Continuous advances are proposed and achieved to cope with them (Naylor *et al.*, 2009). However, aquaculture faces a major crossroads and the choice of path will determine its future as key provider of proteins for humans, and its impact on aquatic ecosystems. This turning point is related to the requirements of cultured animals (i.e. their trophic level) and the use of exotic or locally absent species for aquaculture purposes.

7.9.1 Carnivorous versus herbivorous species

One of the effects of fisheries on marine ecosystems is that they tend to remove the larger, higher-trophic-level species, and thus, progressively lower the mean trophic level (TrL) of the landings. This effect is known as 'fishing-down the food web' (Pauly *et al.*, 1998). Contrary to many perceptions, global aquaculture is dominated by shellfish and herbivorous and omnivorous pond fish either entirely or partly utilizing natural productivity (Bostock *et al.*, 2010). However, mariculture efforts are increasingly concentrating on producing high-TrL fish (i.e., 'farming-up food webs'; Pauly *et al.*, 2001; Stergiou *et al.*, 2008), mainly because of the higher profitability of these species (e.g. salmon, cod, sea bass, sea bream, meagre).

The increasing culture of carnivorous fin fish relies on the use of fish meal and fish oil to fed 'tigers of the sea' (Naylor and Burke, 2005; Duarte *et al.*, 2009). This dependency generates a paradox where wild stocks are used for feeding the farmed fish in such quantity that, nowadays, mariculture is depleting the wild stocks instead of enhancing those (Naylor *et al.*, 2009). Efforts on diminishing the use of fish meal and oil in aquafeed is being carried out (Tacon and Metian, 2008), which added to future non-extractive sources of these essential components (e. g. plant-based proteins and oil, single-cell proteins and oil, terrestrial animal by-products, seafood by-products and krill) could ameliorate the situation. But in the long term and due to the expected exponential increase in aquaculture production, a collapse in fish oil and meal supplies is predicted (Naylor *et al.*, 2009).

Aquaculture has a worldwide mean trophic level of 1.89 (Duarte *et al.*, 2009) while terrestrial food production shows 1.03. Therefore, if aquaculture aspires to be a real complement to help feed humanity this figure must be lowered. According to a race between the average aquaculture production annual growth of 7.5% and the procurement of fish oil and meal (and their substitutes), sooner or later the fin-fish mariculture industry must face the challenge of moving its production towards low trophic level species (i.e. herbivorous; Duarte *et al.*, 2009; Naylor *et al.*, 2009).

7.9.2 Non-native and locally absent versus native species

Farmed introduced species are of major importance in some countries (Casal, 2006). For instance, exotic fish represent 17% of the total aquaculture food production, and are economically important as sport fish in many countries (Shelton and Rothbard, 2006). Furthermore, non-native species are widely recognized as a major threat to species biodiversity (Worm *et al.*, 2006), causing habitat modification, changes in ecosystem functioning, extinction of native fauna and flora, disease transfer and genetic effects such as hybridization with native congeners (Ruiz *et al.*, 1997).

A debate on whether or not to use exotic or locally absent species for aquaculture purposes have been carried out, especially for freshwater fish, in recent times (Gozlan, 2008; Vitule *et al.*, 2009). Some authors argue that most of the introductions have negligible impacts and that the risk evaluation framework has already been developed to levels which permit the result of an introduction to be predicted (De Silva *et al.*, 2006; Gozlan, 2008). Others state that information regarding the impacts of introduced fish is so scarce that the uncertainties are too many at this time (Simberloff, 2003, 2007; Vitule *et al.*, 2009). Especially in under-developed and developing countries introductions are encouraged by governments without risk assessment and no impact studies yet exist (Vitule *et al.*, 2009 and references therein). This knowledge is poor for closed and semi-closed freshwater systems, in the case of the marine environment the effects of fish introductions are largely unknown (Randall, 1987; Baltz, 1991; Ruiz *et al.*, 1997). However, the growing literature on marine fish introduction suggests that their impacts are not negligible (Golani, 1998; Kalogirou *et al.*, 2007; Rilov and

Galil, 2009), and that open coastal systems are far more susceptible to fish invasions than initially thought (Edelist *et al.*, 2013).

In this context, the aquaculture industry and stakeholders must choose between two options: to base worldwide aquaculture on a few species that are already cultured, spreading them around the world, or to encourage the production of native species. Despite some authors highlighting the diversity of marine animals domesticated during the last few years (Duarte *et al.*, 2007), the reality is that most of them are only exploited captives (sensu Balon, 2004; section 7.4), and in the case of fin fish, 85% of the production is concentrated in only 15 species, which are farmed in numerous countries (Shelton and Rothbard, 2006). Therefore, a trend is observed towards the use of few, well-known and profitable species.

Taking into account the aforementioned constraints, it seems clear that we require a 180º turn in aquaculture trends if this is going to be the awaited real alternative to terrestrial proteins. Firstly, there is a need to decrease the trophic level of farmed species through the culture of herbivores. Secondly, the introduction of non-native or locally absent species should be avoided. In other words, governments should encourage and invest in research lines looking for the most suitable native herbivores to farm, and for coupled cultures to reach self-sustaining multitrophic aquaculture systems. This change needs to be accompanied by a strong improvement in species containment, and pollution and genetic management to prevent undesirable effects on marine environmental health and function. If this is not achieved and aquaculture continues to grow with its current characteristics, we will be doomed to carry out the second food revolution at the expense of marine ecosystems that will be largely and irreversibly altered.

Final Conclusions / Conclusiones Finales

1. Through escape events, a consequence of the aquaculture industry has been the introduction of sea bass into the coastal habitats of some of the western and central Canary Islands, where there were no wild populations. Even around El Hierro and La Gomera, where no aquaculture facilities have been installed, escapees have been recorded. An underestimated mean of 200,000 farmed bass escaped into the wild each year between 1998 and 2009, which greatly surpass any restocking action carried out in Spain.

2. Escaped sea bass are able to survive and forage in natural habitats off the Canary Islands. Their diet resembles that of wild counterparts in their natural range of distribution, and is composed mainly of fish and crustaceans, some of them targeted by local fisheries. Diet of escaped bass is influenced by size and time at liberty. Their high trophic level situates them as a top-predator in shallow coastal habitats.

3. The spatial distribution of escaped bass strongly depends on the distance from escape point. Higher abundance is found near fish farms but escapees can also be found at any location around the islands where aquaculture facilities are placed. Habitat features influence escapee abundance on a local scale, showing preference for low complexity bottoms in the wild.

1. Los escapes procedentes de la acuicultura han introducido lubinas en las islas centrales y occidentales del Archipiélago Canario, donde esta especie no tenía poblaciones salvajes. Incluso se han registrado individuos escapados en las islas de El Hierro y La Gomera, donde no hay instalaciones acuícolas. Una media infraestimada de 200.000 lubinas escaparon cada año entre 1998 y 2009, lo cual supera enormemente cualquier acción de repoblación llevada a cabo en España.

2. Las lubinas escapadas son capaces de sobrevivir y alimentarse en los hábitats naturales de las Islas Canarias. Su dieta se asemeja a la de sus congéneres salvajes en su rango natural de distribución, y está compuesta principalmente por peces y crustáceos, algunos de ellos de importancia pesquera. La dieta de las lubinas escapadas depende de la talla y el tiempo en libertad de los individuos. Su alto nivel trófico las sitúa como un depredador de primer rango en hábitats costeros.

3. La distribución espacial de los ejemplares escapados depende en gran medida de la distancia al punto de escape. Las abundancias son mayores cerca de las granjas de cultivo, pero también podemos encontrar individuos en cualquier punto alrededor de las islas donde hay instalaciones acuícolas. Las características del hábitat influyen en la abundancia de las lubinas escapadas a escala local, mostrando preferencia por fondos de baja complejidad en el medio natural.

4. The escapees' abundance in natural habitats is higher after winter than after summer, since most escape events take place during the cold season when storms are more frequent, while fishing mortality is higher during the summer season. The 2010 massive escape off La Palma constitutes an exacerbated expression of this temporal pattern.

5. Morphometric traits differ between farmed and escaped individuals. The latter are more streamlined due to a combination of food deprivation period, phenotypic plasticity and natural selection. Overweight farmed bass reduce their body condition indices once in the wild, to figures similar to their wild counterparts.

6. Escapees grow in the wild as well as farmed fish do in fish cages. Scale growth rates, although more variable, are similar in escaped and farmed fish, which reflects good performance of surviving escapees in natural habitats.

7. Large-sized male and female escaped bass mature in the wild. Maturation was observed during January and February, but this period could be wider. Mature gonads are functional, thus spawning taking place. However, recruitment in the wild, indicative of a successful reproduction, has not been observed yet.

4. La abundancia de lubinas en el medio es mayor después del invierno que tras el verano, ya que la mayor parte de los escapes ocurren durante la temporada fría, cuando las tormentas son periódicas, mientras que la mortalidad por pesca es mayor en verano. El escape masivo de 2010 en La Palma es un expresión exacerbada de este patrón estacional.

5. Los rasgos morfométricos difieren entre lubinas cultivadas y escapadas. Estas últimas son más estilizadas debido a una combinación de período de privación de alimento, plasticidad fenotípica y selección natural. Las lubinas cultivadas, con alto acúmulo de grasas, reducen sus índices de condición corporal cuando pasan al medio natural, y alcanzan valores similares a los de sus congéneres salvajes.

6. Los ejemplares escapados crecen en el medio natural tan bien como los cultivados lo hacen en condiciones de cultivo. Las tasas de crecimiento, aunque más variables, son similares en peces escapados y cultivados, lo que refleja un buen desarrollo de los primeros cuando sobreviven en hábitats naturales.

7. Los machos y hembras de lubinas de mayor talla maduran en el medio natural. La maduración se observa durante enero y febrero, pero este período puede ser más amplio. Las gónadas maduras son funcionales, por tanto el desove tiene lugar. Sin embargo, aún no se ha podido demostrar la existencia de reclutamiento en el medio, indicativo de una reproducción exitosa.

8. The Myxosporean parasite *Sphaerospora testicularis* is recorded for the first time in mature gonads of escaped bass males and this is also its first record in the Canaries. Nonetheless, the significant prevalence and degree of infection are not sufficient to cause parasitic castration of escapees.

9. The local fisheries of La Palma faithfully reflected the massive escape event that occurred in 2010, with large captures representing 22% of the total released biomass. Professional fishermen played an essential role during recapture actions and are a key element in the elaboration of contingency plans.

10. Aquaculture origin fish promote a 'farming-up' process, raising the mean trophic level of fish assemblages in shallow coastal waters. Trophic cascade effects are likely in this context. These could alter the abundance of the escapees' prey and competitors, affecting ecosystem structure.

11. La Palma MPA showed no influence on the abundance of escaped fish. Its density of escaped sea bass was similar to that found off 'highly fished areas'. Mean trophic level was also altered in the protected area, but to a lesser extent than in HFA, which suggests a certain degree of resilience thanks to the healthy state of fish assemblages within the MPA.

8. Se cita por primera vez el parásito myxospóreo *Sphaerospora testicularis* en gónadas maduras de machos de lubina escapada, siendo el primer registro de este parásito en Canarias. No obstante, la significativa prevalencia y grado de infección no son suficientes para causar castración parasítica.

9. Las pesquerías locales de La Palma reflejaron fielmente el escape masivo ocurrido en 2010, con grandes capturas que supusieron el 22% de la biomasa total escapada. Los pescadores profesionales jugaron un papel fundamental durante las acciones de recaptura y son una pieza clave en la elaboración de planes de contingencia.

10. Los peces escapados generan un proceso de 'farming-up', elevando el nivel trófico medio de la comunidad de peces en aguas someras. Efectos generados a través de cascadas tróficas son probables en este contexto, lo cual podría desencadenar alteraciones en las abundancias de presas o competidores que afecten a la estructura del ecosistema.

11. La Reserva Marina de La Palma no tuvo influencia sobre la abundancia de peces escapados. El número de ejemplares fue similar al encontrado en zonas con alta presión pesquera. El nivel trófico medio se vio alterado en la reserva, pero en menor media que en zonas no protegidas, lo cual sugiere cierto grado de resiliencia gracias al buen estado de las poblaciones de peces dentro de la reserva.

12. The number and biomass of escaped sea bass in the areas surveyed, including La Palma MPA, were always higher than other high trophic level species. Bass escapees have become an important constituent of the fish fauna in the shallow coastal waters of the Canaries. This situation will not change as long as farming of this species continues in its present form.

13. The surviving sea bass retain enough fitness to perform well and become feral in wild habitats off the Canary Islands.

14. Despite similar numbers of sea bream escaping into the wild, their presence there is occasional, possibly due to higher natural mortality and catchability rates in comparison to sea bass. The low production of meagre limited their detection in natural habitats, although there are records of escape events and subsequent captures.

15. It is necessary to implement a risk evaluation framework, including mitigation and contingency plans for escapees, to avoid compromising marine ecosystem health and function.

16. The potential ecological interactions of escapees are multiple and understudied. Therefore, the precautionary principle should guide decisions regarding the culture of high-trophic and exotic or locally absent species.

12. El número y la biomasa de lubinas escapadas en las áreas muestreadas, incluyendo la Reserva Marina de La Palma, fueron siempre mayores que los valores registrados para otras especies de alto nivel trófico. Las lubinas escapadas se han convertido en un elemento importante de la fauna íctica en las aguas someras de Canarias y esta situación no cambiará en tanto el cultivo se produzca en las mismas condiciones.

13. Las lubinas que sobreviven tras el escape mantienen suficientes aptitudes para desenvolverse bien y asilvestrarse en hábitats naturales de las Islas Canarias.

14. A pesar de que un número similar de doradas se escapan al medio natural su presencia es ocasional, posiblemente debido a unas mayores tasas de mortalidad natural y capturabilidad en comparación con la lubina. La baja producción de corvinas ha limitado su detección en hábitats naturales, sin embargo existen noticias de escapes y capturas.

15. Es necesario implementar un sistema de evaluación de riesgos, con planes de mitigación y contingencia de escapes, a fin de evitar comprometer la salud y el funcionamiento de los ecosistemas marinos.

16. Las interacciones ecológicas potenciales originadas por los escapes son múltiples y están poco estudiadas. Por tanto, el principio de precaución debería guiar las decisiones concernientes al cultivo de especies de alto nivel trófico, exóticas o localmente ausentes.

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De Natura Animalium (Claudius Aelianus, Praeneste, ca. 175 - ca. 235)

De lupis Maetoidis

Secundum Maeotidis paludis locum, Conopium nuncupatum lupi, quos non a domesticis canibus differre dicas, cum piscatoribus studiose versantur. Quod si maritimae praedae partem fuerint adsecuti, cum iis et pacem habent, et tanquam foedere devinciuntur; sin nihil consequuntur, eorum retia lacerant, et distrahunt, et pro eo, quod nihil dederunt, damnum retribuunt.

In Meótide lagoon area, the wolves are committed between cane and those fishermen who fish offshore, and, if you saw, say that they are indistinguishable from the dogs that saved the houses. It turns out that, if these wolves get a share of marine fisheries, there is peace and harmony between them and the fishermen, but if not, rip the nets and the spoil, and the punishment is imposed wolves fishermen for depriving them of their share.

En la zona de la laguna Meótide, los lobos andan confiados entre los pescadores a caña y aquéllos que practican la pesca mar adentro, y, si los vieras, dirías que ellos no se distinguen de los perros que guardan las casas. Resulta que, si estos lobos obtienen una parte de la pesca marina, reina la paz y la concordia entre ellos y los pescadores, pero, si no, les rasgan las redes y se las echan a perder, y es el castigo que los lobos imponen a los pescadores por haberles privado de su parte.

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