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# The herbivorous fish, *Aplodactylus punctatus*, as a potential facilitator of dispersal of kelp, *Lessonia trabeculata*, in Chile

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## ABSTRACT

Kelp forests are productive marine habitats known to facilitate many trophic and non-trophic interactions. While much of our understanding comes from positive effects of kelp on associated fauna, few studies focus on potential feedbacks that such fauna may provide to benefit kelp. This study aims to analyze the positive interactions between two closely associated fish and kelp species. *Lessonia trabeculata*, the bottom kelp, and the herbivorous fish, *Aplodactylus punctatus*, were sampled at four sites off northern-central Chile to evaluate the following: interactions during the ontogeny of the fish, the availability of reproductive tissue of the kelp blades, the effects of digestion by *A. punctatus* on *L. trabeculata* reproductive tissue, and the viability of zoospores after digestion. Our results show a network of direct and indirect positive interactions between these species. There was a positive correlation in their densities, possibly due to kelp functioning as a refuge and indirect food source. Juvenile *A. punctatus* feed on epifaunal species within the kelp, reducing grazer load and in turn generating a potential positive indirect effect on the kelp. Adult herbivorous fish consume kelp tissue as sustenance; when this kelp tissue is reproductive, digestion reduces epiphytic algal densities on the sori. Zoospores were found to remain viable after digestion, and microscopic sporophytes were produced at rates similar to those of undigested reproductive tissue. We conclude that positive links between *A. punctatus* and *L. trabeculata* occur along the geographic range distribution of both species and that this herbivorous fish could serve as a dispersal mechanism for *L. trabeculata*. To our knowledge, this is the first study that suggests that an herbivorous fish may have the potential to be a facilitator of kelp zoospore transport, and this may contribute positively to the recovery of natural kelp populations that are being intensively harvested in the region.

## 1. Introduction

Kelps, brown algae belonging to the order Laminariales, support abundant and diverse associate macrofaunal assemblages (Dayton, 1985; Steneck et al., 2008; Villegas et al., 2008). The benefits provided by kelp populations to associated species allow entire ecosystems to exist and therefore, they are considered foundation species (Bodkin, 1988; Stachowicz, 2001). These seaweeds provide shelter from predators (Carr, 1991), improve habitat quality by ameliorating environmental stress (Stachowicz, 2001; Teagle et al., 2017), and expand niches in which species can live (Dayton, 1985; Bruno et al., 2003; Graham, 2004; Steneck et al., 2008). Several fish species use kelp forests as nursery habitats, where survival is enhanced (Carr, 1991; Anderson, 1994; Carr, 1994). Moreover, kelp provide food both directly – from their tissue – and indirectly – from associated understory algae for herbivorous animals (Andrew and Jones, 1990) as well as the organisms that live on and within the kelp (Norderhaug et al., 2005; Koenigs et al., 2015; Miller et al., 2015), forming exceptionally complex food webs in these systems (Graham, 2004).

In temperate ecosystems, there are few examples of how fauna can positively influence their habitat (Hay et al., 2004). Witman (1987) established that mussel beds benefited from sea urchin grazing on kelp growing on the mussel shells, reducing the impact of storms due to dislodgment. Furthermore, Bertness and Leonard (1997) found that mussel beds allow the stabilization of the substrata while providing nutrients from their waste to saltmarshes. These examples indicate that

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positive interactions between associated fauna occur in both sessile and mobile species. Despite the few obligate fish species in kelp forests, positive effects of fish on kelp species have been demonstrated via indirect density-mediated effects by reducing grazer abundance (i.e., urchins and mesograzers) (Cowen, 1983; Davenport and Anderson, 2007; Newcombe and Taylor, 2010), and via trait-mediated effects in which the presence of predators influences the impact of grazers on host seaweed (Byrnes et al., 2006; Pérez-Matus and Shima, 2010). These interactions generate important links between kelps and associated species. Positive species interactions and their influence on community structure have been previously observed (Bruno et al., 2003; Hay et al., 2004) and habitats dominated by kelps are ideal to study these interactions because they are known to ameliorate environmental stress and establish connections among species (Bertness and Leonard, 1997; Byrnes et al., 2011).

Herbivory is an important interaction between flora and associated fauna, and the effects are influenced by different factors (Poore et al., 2012), including the type of herbivore (Jones and Andrew, 1990; Aguilera, 2011), morphological and/or chemical resistance to grazing (Jormalainen et al., 2005; Cerda et al., 2009), and environmental gradients (Vanderklift et al., 2009; Taylor and Schiel, 2010). In terrestrial systems, selective pressures from herbivory have resulted in the development of chemical or physical defenses to deter grazing, or conversely, adaptations that encourage grazing to enhance dispersal, such as seeds that are resistant to digestion (in some species, germination rates are elevated following digestion: Traveset and Verdú, 2002; Tiffney, 2004). Mammals and birds are the most common species that act as seed dispersers, but recent studies have added terrestrial invertebrates to the list (Duthie et al., 2015). In marine environments, the study of dispersal processes by biological vectors is complicated due to the great diversity of algal reproductive strategy (i.e., differentiated reproductive/vegetative tissue, asexual reproduction (Santelices, 1990)). Algal resistance to digestion depends on algal life history and traits (e.g., feeding mode) of the herbivorous species. Reproductive and vegetative tissues are able to regenerate or germinate after digestion by invertebrates among opportunistic algae that use asexual reproduction and have low complexity in their tissues (Santelices et al., 1983; Santelices and Ugarte, 1987; Cabral de Oliveira, 1991). Macroalgae with greater complexity (i.e., differentiated vegetative and reproductive tissues) have lower post-digestion survival rates due to the inability to regenerate from vegetative tissue and/or by the differentiation of reproductive tissue, which is less likely to be consumed (Santelices et al., 1983; Santelices and Ugarte, 1987; Skern et al., 2003).

As in terrestrial ecosystems, the dispersal abilities of algae by a biological vector have attracted the attention as it may represent benefits to macroalgae distribution dynamics. Buschmann and Bravo (1990) described preferential feeding of the amphipod, *Hyale media*, on reproductive structures of algae such as *Mazzaella*, facilitating spore release and dispersal when spores adhere to their legs (Buschmann and Santelices, 1987; Buschmann and Bravo, 1990). In tropical marine environments, Phaeophyceae (including foliose, filamentous, and crustose types) and Rhodophyta (corallines and filamentous turfs) have the capacity to reattach and grow after digestion by parrotfishes and surgeonfishes, potentially increasing dispersion (Vermeij et al., 2013; Tâmega et al., 2015). In temperate environments, Paya and Santelices (1989) found that an opportunistic alga resisted digestion by an intertidal clingfish. This pattern is also present on marine gymnosperms such as seagrasses, which also resist fish herbivory (Sumoski and Orth, 2012). Since some algae cannot survive digestion by invertebrate species, herbivorous fishes can be biological vector for algal dispersal due to the differences in the digestion processes, assimilation capabilities and greater mobility (Choat et al., 2002; Clements et al., 2017).

Kelps (order Laminariales) are globally distributed brown seaweeds, characterized by a complex life cycle with motile flagellated zoospores that are capable of short distance dispersal (but see *Macrocystis pyrifera*: Macaya et al., 2005). The short duration of zoospore viability (typically hours) is generally considered to limit average dispersal distances to the scale of several meters to up to a kilometer (Reed et al., 1992; Gaylord et al., 2004; Steneck et al., 2008). Past studies have indicated that dispersal success is determined by a combination of physical and biological factors (Steneck et al., 2008). All Laminariales species have a diplohaplontic heteromorphic life cycle, where zoospores are released into the water column and must find suitable substrate in order to attach, germinate, form into male and female gametophytes, and undergo fertilization, for successful recruitment to occur. High zoospore settlement densities ($>$ 1 zoospore per $mm^2$; Reed et al., 1992) are critical for kelp recruitment success, and densities have been shown to decline with increased distance from adult individuals (Buschmann and Santelices, 1987; Gaylord et al., 2004). Therefore, processes that increase the aggregation and dispersion of zoospores (e.g., aggregating, rafting, herbivore-assisted dispersal; Santelices and Paya, 1989; Santelices and Ugarte, 1987; Thiel and Gutow, 2005) may enhance the chances for kelp to colonize new rocky areas.

The goals of the present study were to explore the positive interactions between the most abundant herbivorous temperate reef fish and the subtidal kelp *Lessonia trabeculata*. We also conducted a series of mensurative and manipulative experiments to assess the influence of *Aplodactylus punctatus* in kelp beds by: (1) verifying the overlapping distributions and associations; (2) analyzing ontogenetic changes in the diet of *A. punctatus*; and (3) testing the effects of digestion by *A. punctatus* on *L. trabeculata* reproductive tissue and viability of zoospores, potentially demonstrating *A. punctatus* as a disperser of *L. trabeculata*.

## 2. Material and methods

### 2.1. Kelp (L. trabeculata) and fish (A. punctatus) distribution and density

The subtidal rocky habitat on the cold-temperate southeast Pacific coast is dominated by *Lessonia trabeculata* (Villouta and Santelices, 1986), which is distributed from Peru (14°S) to Ancud, Chiloe Island, Chile (42°S) from 0.5 to 30 m depth with massive holdfast and multiples stipes reaching up to 2.5 m (Villouta and Santelices, 1986). *Lessonia trabeculata* is a perennial species that produces its reproductive tissue on ordinary blades and is present year-round with seasonal reproductive peaks, possibly associated with low light intensity, temperature, and high nutrient availability (Tala et al., 2004; Murua et al., 2013).

The herbivore "jerguilla" ("marblefish" in English) *Aplodactylus punctatus* (Valenciennes, 1832) is distributed from Paita (5°S Peru) to Gulf of Arauco in Chile (36°S) (see Froese and Pauly, 2016). However, in this current study we found populations south of this southernmost distribution boundary. We sampled and recorded the presence of this species in kelp (*L. trabeculata*) beds (8–15 m depth). This fish is the most abundant herbivore in kelp beds (Cáceres et al., 1993; Pérez-Matus et al., 2007, 2017). Their diet is influenced by food availability (Cáceres et al., 1993; Pérez-Matus et al., 2012) and adult diets are composed of 75% kelp (*L. trabeculata*) and 10% other algae (i.e., *Gelidium*, *Ulva*, and corallines) (Benavides et al., 1994; Pérez-Matus et al., 2012). Juveniles ($<$ 30 cm in total length) of this species consume mainly epifauna such as amphipods, bryozoans, hydrozoans, polychaetes, and porcelain crabs as well as epiphytes and other turf algae (Cáceres et al., 1993; Benavides et al., 1994).

During austral fall (March 27 through April 11) and spring (October 30 through November 13) 2012, we monitored 4 kelp-dominated semi-exposed to wave action sites of the north and central Chilean coast spanning ~350 km to quantify *L. trabeculata* and *A. punctatus* densities. The sites included El Francés (30.09°S, 71.37°W), Punta Talca (30.87°S, 71.69°W), Quintay (33.19°S, 71.70°W), and Algarrobo (33.36°S, 71.69°W). Visual surveys using SCUBA were conducted at each site, employing four 50 m transects running perpendicular to the coast at each site between 5 and 20 m depth. Fish abundances and the total